







RESEARCH ARTICLE

Spatial variation in density of American black bears in northern Yellowstone National Park

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Abstract

The quality and availability of resources are known to influence spatial patterns of animal density. In Yellowstone National Park, relationships between the availability of resources and the distribution of grizzly bears (*Ursus arctos*) have been explored but have yet to be examined in American black bears (*Ursus americanus*). We conducted non-invasive genetic sampling during 2017–2018 (mid-May to mid-July) and applied spatially explicit capture-recapture models to estimate density of black bears and examine associations with landscape features. In both years, density estimates were higher in forested vegetation communities, which provide food resources and thermal and security cover preferred by black bears, compared with non-forested areas. In 2017, density also varied by sex, with female densities being higher than males. Based on our estimates, the northern range of Yellowstone National Park supports one of the highest densities of black bears (20 black bears/100 km²) in the northern Rocky Mountains (6–12 black bears/100 km² in other regions). Given these high densities, black bears could influence other wildlife populations more than previously thought, such as through displacement of sympatric predators from kills. Our study provides the first spatially explicit estimates of density for black bears within an ecosystem that contains the majority of North America's large mammal species. Our density estimates provide a baseline that can be used for future

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research and management decisions of black bears, including efforts to reduce human–bear conflicts.

KEYWORDS

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

The quality and availability of resources influence the density and distribution of wildlife populations (Brown et al. 1995, Ives and Klopfer 1997, Greene and Stamps 2001). When high-quality resources and habitat (abundant abiotic and biotic resources needed for survival and reproduction) are readily available, wildlife populations can occur at higher densities, but when resources are limited or unevenly distributed, densities are typically lower and tend to be concentrated around resource or habitat patches (Pettorelli et al. 2001, Crait et al. 2015). For example, when vegetation with mast (e.g., fruits and nuts) is abundant in temperate regions, many wildlife species will congregate within forested vegetation communities but will move to a mix of forested and non-forested areas when mast production is low (Diamond et al. 2000, McCarty et al. 2002, Ryan et al. 2004). Similarly, when prey species become abundant within an area, predators may shift their movements to capitalize on spatially dense prey, resulting in changes in the distribution of predators (Owen-Smith et al. 2005, Wang et al. 2009, Hansen et al. 2013). In addition, many wildlife species avoid humans and roads, but when resources become limited, or predation or competition pressure is high, some species may shift their distributions to be closer to humans (Hebblewhite and Merrill 2009, Gaynor et al. 2018, Kautz et al. 2021). Understanding how wildlife populations respond to the varying availability of resources is important for monitoring population trends and determining management options.

In North America, densities of American black bears (*Ursus americanus*) vary based on the availability and quality of resources (Costello and Sage 1994, Pelton 2003, Robbins et al. 2004, Teunissen van Manen et al. 2014). In areas where resources and habitat quality are limited, black bears tend to occur at lower densities (<5 bears/100 km²; Drewry et al. 2013), but higher densities (>37 bears/100 km²; Tredick and Vaughan 2009) are possible where resource quality is high. Black bears often congregate within forested and wetland areas where mast is abundant in summer and fall, and may redistribute across larger areas in search of alternative foods when food abundance is limited (Ryan et al. 2004, Johnson et al. 2015, Gould et al. 2018). Similarly, black bears tend to select areas with abundant, high-quality vegetative resources in spring (Bastille-Rousseau et al. 2011, Duquette et al. 2017, Bowersock et al. 2021) and may shift to areas with lower-quality vegetation when neonate ungulates are available (Ray et al. 2018). Although black bears generally avoid areas of high human use (Tredick and Vaughan 2009, Drewry et al. 2013, Loosen et al. 2019), where they are sympatric with grizzly bears (*Ursus arctos*) or when resources are limited, black bears are sometimes more tolerant of people, roads, and human developments, potentially increasing human–bear interactions (Belant et al. 2006, Berger 2007, Stetz et al. 2014, Gould et al. 2018, Ladle et al. 2018).

In Yellowstone National Park in the United States, bears have shown responses in recent decades to factors including drought, fire, forest pests, invasive species, and changes in prey availability (Fortin et al. 2013, Costello et al. 2014, Teisberg et al. 2014). Relationships between the availability of resources and the density distribution of grizzly bears have been studied previously (Fortin et al. 2013, Bjornlie et al. 2014, Costello et al. 2014), but have yet to be explored for black bears. Estimating densities of black bears could provide important baseline information needed to assess population trends, understand trophic interactions, and address other ecological questions, particularly against a backdrop of changing resources and climate conditions (Mattson et al. 2005; Stetz et al. 2014, 2019; Svoboda et al. 2019; Hostetler et al. 2021). Characterizing spatial patterns of black bear density also could assist with efforts to reduce human–bear conflicts (Fusaro et al. 2017, Gunther et al. 2018, Zeller et al. 2019).

The primary objective of our study was to use genetic sampling and spatially explicit capture-recapture models to estimate black bear density and examine spatial variation associated with landscape features. We predicted higher

densities of black bears in areas associated with food resources, namely areas with productive vegetative foods (Fortin et al. 2013, Costello et al. 2016, Bowersock et al. 2021). Black bears are a forest-adapted species, so we also predicted the highest densities of black bears would occur in forested vegetation communities that provide cover for thermoregulation and security, in addition to food (Barnes and Bray 1967, Herrero 1972, Sawaya et al. 2016). Finally, following principles of the human shield hypothesis, where subordinate animals use humans as cover from dominant animals (Berger 2007, Swaminathan et al. 2023), we predicted higher densities of black bears near roads; black bears may use these areas to avoid grizzly bears, which tend to select areas farther from roads (Kasworm and Manley 1990, Ladle et al. 2018).

STUDY AREA

Our study area was on the northern range (1,530 km²) of Yellowstone National Park and focused specifically on a 650-km² region in the central portion of the northern range, located in southern Montana and northern Wyoming, USA (Figure 1). Winters are cold and long, and summers are cool and short (Frank and McNaughton 1992). From June to September, daily average minimum and maximum temperatures range from -2 to 37°C and monthly average precipitation ranges from 3.3 cm to 5.0 cm (National Oceanic and Atmospheric Administration 2023). Elevations range from 1,590 m to 3,360 m. Whitebark pine (*Pinus albicaulis*) and subalpine fir (*Abies lasiocarpa*) are most common at elevations of 2,600–2,900 m, whereas Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and trembling aspen (*Populus tremuloides*) comprise lower-elevation forests around 1,900–2,200 m. A mix

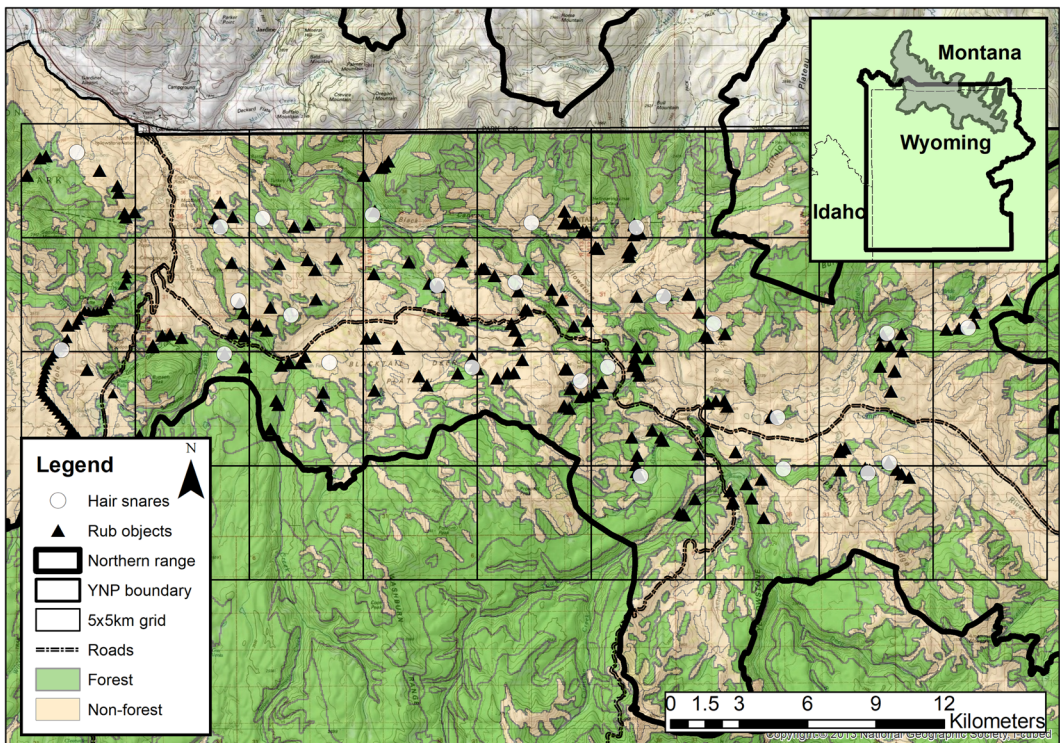


FIGURE 1 Study area within the northern range (gray, on inset map) of Yellowstone National Park (YNP) with the 5 × 5-km sampling grid, Wyoming and Montana, USA, 2017–2018. We collected hair samples from black bears using hair snares (white circles) in both years and rub objects (primarily rub trees and some utility poles; black triangles) in 2018. Forested areas (depicted in green) comprised 62% of our study area compared with non-forested areas (in orange, 38% of the area). Few paved roads run through the park, including within the defined study area.

of sagebrush (*Artemisia* spp.), grasses, sedges (*Carex* spp.), and forbs are in open meadows (Frank and McNaughton 1992, Singer et al. 1994). The northern range includes important wintering grounds for elk (*Cervus canadensis*) and deer (*Odocoileus* spp.) and is home to 8 ungulate species with elk, pronghorn (*Antilocapra americana*), and bison (*Bison bison*) being the most common in spring and summer (Frank and McNaughton 1992, White and Garrett 2005). A guild of large carnivores, including gray wolves (*Canis lupus*), coyotes (*Canis latrans*), and cougars (*Puma concolor*) also inhabit the northern range (Barber-Meyer et al. 2008). Additionally, the northern range represents core habitat for grizzly bears in the Greater Yellowstone Ecosystem, where the population is expanding in portions of the Mountain West (Haroldson et al. 2021). Our sampling was limited to areas within the national park, where hunting is prohibited; hunting seasons exist for black bears on public and private lands north of the park boundary. Road access is limited, yet the few roads that exist are heavily used during the summer tourism season (Gunther et al. 2018).

METHODS

Non-invasive genetic sampling and analysis

We collected hair samples to obtain DNA for microsatellite analysis using hair snare corrals (hair snares; Woods et al. 1999) and bear rub objects (Kendall et al. 2008) during 2017 and 2018. We established a network of hair snares by overlaying a sampling grid across the study area (Figure 1; Mowat and Strobeck 2000, Kendall et al. 2009, Sawaya et al. 2012). We chose a 5 × 5-km grid (25-km² cells) based on the average home-range size of female black bears (34 km²) in the Mountain West region, which is smaller than the average home range of males (232 km²), thus enhancing the probability of detecting individuals of both sexes and ensuring that all bears had access to ≥1 hair snare site (Grogan and Lindzey 1999, Holm et al. 1999, Nilsen et al. 2005). We established a single hair snare in each grid cell, which remained in the same location for the entire study. For human safety, snares were located out of sight, >500 m from developed areas, and >200 m from trails, campsites, or roads (Kendall et al. 2008, 2009). Hair snares consisted of a single strand of 4-point barbed wire stretched at a height of approximately 50 cm around ≥3 trees to create an enclosure. This design targeted collection of hair from yearling, subadult, and adult bears but reduced the likelihood of sampling cubs-of-the-year. We poured a scent lure on a brush pile constructed in the center of each enclosure to encourage bears to investigate the site and leave a hair sample by crossing over or under the wire. We used one of 4 scent lures during each sampling occasion: 2 commercial lures (smoky bacon or raspberry doughnuts; Moultrie Feeders, AL, USA) and 2 natural scent lures (rotten cattle blood or a mixture of rotten cattle blood and fish oil) in an attempt to increase detections in lieu of moving sample locations on a weekly basis (Kendall et al. 2008, 2009; Sawaya et al. 2012). We visited each hair snare site weekly from mid-May through mid-July in 2017 and 2018, resulting in 8 sampling occasions per year.

In 2018, we used rub objects, such as trees and utility poles, as our second hair collection method to enhance the spatial coverage of our sampling effort (Figure 1; Kendall et al. 2008, 2009). We searched for and established these sample sites in 2017 and collected hair samples in 2018. Rub objects were identified by bite and scratch marks, the presence of bear hair, and the 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 a high-quality, discrete hair sample would be deposited; we did not modify other rub objects (Kendall et al. 2008). From mid-May to mid-July 2018, concurrent with hair snare sampling, we checked rub objects every 7 days when feasible, but always within 14 days of the previous sampling occasion, resulting in 8 sampling occasions.

An important assumption of spatially explicit capture-recapture models is that the population is closed. All births occurred prior to the sampling period and our sampling was designed to avoid detection of cubs. Mortalities were limited because of the protected status within Yellowstone National Park, although some transboundary bears may have been vulnerable to harvest outside the park during the first half of the sampling period (Montana spring

hunting season). Some individuals may have entered or left the study area during the sampling period, yet the relatively short sampling period of 8 weeks likely limited this bias. The timing of our sampling period also coincided with when most bears are active at lower elevations of our study area because of the availability of food resources (Fortin et al. 2013, Costello et al. 2016) and snow remaining in areas at higher elevations, further reducing the probability of animals moving in and out of the study area.

We placed each hair sample in a paper coin envelope, which we dried and stored in plastic containers with desiccant in a climate-controlled room until samples were sent to Wildlife Genetics International (WGI, Nelson, British Columbia, Canada) for microsatellite genotyping. Given budget allocations for genetic analysis, we optimized individual identification by subsampling hair samples each year based on recommendations from WGI personnel and past studies (Sawaya et al. 2012). We analyzed a maximum of 8 samples per hair snare during each sampling occasion. If multiple samples were present along adjacent 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 2 samples per rub object per sampling occasion. This subsampling was random and did not depend on where the sample was collected on the rub object. Personnel at WGI targeted the highest-quality samples to maximize the probability of yielding a genotype.

Technicians extracted DNA from hair samples using QIAGEN DNeasy kits (Qiagen, Valencia, CA, USA) following standard protocols for analyzing non-invasive genetic samples (Paetkau 2003). Individual bears were identified based on an established regional set of 9 microsatellite markers (G10B, G1D, G10H, G10J, G10P, G10M, G1A, G10X, G10L), and the marker for sex (ZFX/ZFY; Paetkau et al. 1998, Proctor et al. 2005, Durnin et al. 2007). The G10J microsatellite marker was used to differentiate between black and grizzly bears (Kendall et al. 2008). To reduce genotyping errors, samples that were weak or difficult to read were rerun multiple times (Paetkau 2003, Kendall et al. 2009). If such samples failed to amplify further, they were removed from analysis. All samples were referenced to existing genotype records from black bears in the Greater Yellowstone Ecosystem, Northern Continental Divide Ecosystem, and Cabinet-Yaak Ecosystem to identify additional genotyping errors by comparing multi-locus genotypes and mismatched loci.

Estimating density and abundance

We used spatially explicit capture-recapture models to estimate black bear density using the secr package (version 3.2.1-2019; Efford 2019) in program R (R Development Core Team 2013). These models estimate 3 spatially dependent parameters: detection probability at an individual animal's activity center (g_0 ; center of their home range; Royle et al. 2014), a spatially scaled detection parameter based on the distance from an animal's activity center (σ), and density (D ; Efford et al. 2009, Roffler et al. 2016). We created encounter histories for each individual bear based on the location, sampling occasion, and collection method. In 2017, detection histories only focused on samples from hair snares. In 2018, we included samples from hair snares and rub objects to increase detection probabilities, similar to other studies (Sawaya et al. 2012, Stetz et al. 2014, Kendall et al. 2015). We created sampling histories for each sample site to account for the different number of sampling occasions for hair snares and rub objects. To assess spatial variation in black bear density, we built habitat masks consisting of a buffered grid of points around each sample site (hair snare locations in 2017, both hair snares and rub objects in 2018) to extract information about landscape descriptors. We used the suggest.buffer function within the secr package to determine the most-appropriate scale and applied a 9-km buffer around each sample site (Efford 2019). We then used the make.mask function to create a habitat mask that spaced grid points 1 km apart based on the recommendation of $\sigma < 0.5$ by Royle et al. (2014), resulting in a habitat mask encompassing 1,416 km² in 2017 and 1,592 km² in 2018. 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).

We used a 2-step approach to evaluate covariates in our models (Gould et al. 2018, Loosen et al. 2019). We first focused on factors that might influence the detection parameters g_0 and σ each year, while keeping D spatially

uniform. Home ranges of black bears typically differ between males and females, so we used sex as a group covariate for estimating g_0 and σ (Kendall et al. 2015, Whittington and Sawaya 2015, Efford 2019, Welfelt et al. 2019). The ability to detect individual bears may differ between hair snares and rub objects, so we considered collection method as a covariate for g_0 and σ for samples collected in 2018 (Boulanger et al. 2008, Kendall et al. 2008). Additionally, previous visitation to hair snares or rub objects might influence detection probability for some individuals, so we considered a site-specific behavioral response covariate (bk) for g_0 (Harris et al. 2011, Loosen et al. 2019). We further assumed there was heterogeneity in detection among individuals, so we considered 2-class finite mixtures ($h2$) for σ to test for potential differences among individuals in the population (Pledger 2000, Drewry et al. 2013, Hooker et al. 2015). Finally, we included sampling occasion (t) as an additional covariate for g_0 . We considered additive combinations of covariates (g_0 : sex, collection method [for 2018], behavior, time of sampling occasion; σ : sex, collection method [for 2018], spatial heterogeneity) to create models for each year. We then used Akaike's Information Criterion corrected for small sample sizes (AIC_c) to compare models. We examined competing models ($\Delta AIC_c \leq 4$) and focused on 95% confidence intervals of beta estimates that did not overlap zero (Burnham and Anderson 2004).

In the second step, we used the top model for detection in each year and focused on covariates associated with bear density. Throughout their range, black bears typically select for forested areas with abundant herbaceous vegetation (Herrero 1972, Bastille-Rousseau et al. 2011, Fortin et al. 2013, Costello et al. 2016, Bowersock et al. 2021). To assess this for our study area, we classified vegetation communities as being forested or non-forested (Figure 1) based on habitat vegetation layers (50-m resolution; Spatial Analysis Center 2010) and potential natural vegetation (PNV) data (Brohman and Bryant 2005) that we used in our habitat mask using the raster package in program R (Hijmans et al. 2015). To assess how black bear densities varied with herbaceous vegetation, we used net primary productivity (NPP) to describe variation in the amount of energy available on the landscape from vegetation (Xu et al. 2012). We used mean annual NPP (kg carbon/m²/year) data at a 250-m resolution from 2017 and 2018 (Numerical Terradynamic Simulation Group MOD 17 MODIS; <http://www.nts.umd.edu>, accessed 10 Sep 2019). The presence of roads also can influence the spatial and temporal distribution of black bears (Kasworm and Manley 1990, Berger 2007, Gunther et al. 2018, Gantchoff et al. 2019, Zeller et al. 2019). Therefore, we used a geospatial layer of paved roads (Spatial Analysis Center 2010) and the `st_distance` function in the `sf` package in program R (R Development Core Team 2013, Pebesma 2018) to compute proximity to the nearest paved road. Finally, to explore potential differences in density between females and males, we included sex as a covariate for density.

We centered and scaled all continuous covariates (Gelman 2008) and set forested areas as the reference category for vegetation communities. Before creating the density models, we examined correlations between pairs of covariates. Values of NPP were correlated with vegetation community categories, so we did not include both covariates in the same model. We considered a series of additive models that allowed density to vary according to covariates for each year (Table S1, available in Supporting Information). We again used AIC_c to compare models and used the top model in each year for inference about density. We also estimated overall abundance of black bears within the study area with the `region.N` function in the `secr` package (Efford 2019).

RESULTS

We collected 2,600 hair samples from 26 hair snares (921 samples in 2017 and 640 in 2018) and 270 rub objects (1,039 samples in 2018; 217 rub trees and 53 other rub objects), and identified 119 unique black bears (62 females, 57 males) from the genotyped samples. We identified 68 individual bears (43 females, 25 males) in 2017 and 99 individuals (48 females, 51 males) in 2018; 47 individuals (28 females, 19 males) were detected both years (Table 1). In 2018, 24 females and 42 males were detected at rub objects, 27 of these individuals (6 females, 21 males) were only detected at rub objects. Individual bears were detected an average of 1.8 times in 2017 (range

TABLE 1 Summary of samples collected from hair snares and rub objects to estimate density of female (F) and male (M) American black bears, northern range, Yellowstone National Park, Wyoming and Montana, USA, 2017–2018.

Year	Sample type	Sampling occasion	New individuals detected		Total individuals detected		Mean samples per site	Number of samples
			F	M	F	M		
2017	Hair snare	1	5	3	5	3	2.4	62
		2	8	5	10	6	6.4	159
		3	4	2	7	5	2.7	70
		4	14	8	22	15	10.4	269
		5	6	3	11	7	4.9	127
		6	0	1	6	4	2.8	74
		7	0	0	5	3	1.6	49
		8	6	3	13	5	3.7	96
	Total	43	25			4.6	906	
2018	Hair snare	1	8	3	8	3	2.8	73
		2	7	1	11	1	3.1	78
		3	3	1	5	1	2.7	69
		4	2	3	5	3	2.7	69
		5	4	8	6	9	2.7	71
		6	7	3	13	7	3.9	111
		7	1	0	4	1	2.0	54
		8	4	2	12	3	4.0	108
	Total	36	21			2.9	633	
2018	Rub object	1	10	15	10	15	1.5	261
		2	4	9	6	15	1.4	250
		3	4	9	8	23	1.3	263
		4	6	3	10	20	1.3	239
		5	5	3	14	17	1.4	211
		6	9	7	18	15	0.9	195
		7	8	1	23	9	1.0	203
		8	0	0	1	6	0.4	60
	Total	46	47			1.2	1,682	

of detections per individual = 1–5) and 2.1 times in 2018 (range = 1–7). At the sample site level in 2018, we detected bears an average of 1.6 times at hair snares (range of detections per individual = 1–5) and 1.9 times (range = 1–7) at rub objects.

The top models included a positive behavioral response for bears to return to a sample site during both years of sampling (Tables S1 and S2, available in Supporting Information). In 2017, detection probabilities also varied with

sampling occasion (Table S2), with an initial detection probability (g_0) of 0.06 (95% CI = 0.03–0.14) that varied over time and a cumulative detection probability of 0.63. In 2018, the top model included sex-specific detection probabilities (Table S2), with males having a slightly higher detection probability ($g_0 = 0.07$, 95% CI = 0.05–0.10) compared with females ($g_0 = 0.04$, 95% CI = 0.03–0.07). Based on model selection, σ differed by finite mixture in 2017 and finite mixture and sex in 2018 (Table S1). In 2017, σ was greatest for finite mixture group 1 ($\sigma = 6,706$ m, 95% CI = 4,130–10,889 m), which comprised only 1% of bears. In comparison, bears in finite mixture group 2 had smaller estimates for σ ($\sigma = 1,849$ m, 95% CI = 1,513–1,736 m) and comprised 99% of bears. In 2018, mixture group 1 similarly had larger estimates of σ (females: $\sigma = 6,161$ m, 95% CI = 4,888–7,766 m; males: $\sigma = 4,823$ m, 95% CI = 4,097–5,678 m) compared with mixture group 2 (females: $\sigma = 1,430$ m, 95% CI = 1,177–1,736 m; males: $\sigma = 1,119$ m, 95% CI = 927–1,351 m), with most bears (97%) belonging to mixture group 2.

For 2017, the best supported model for density estimation included vegetation community and sex (Tables 2 and S3, available in Supporting Information). Density estimates for female black bears were greater than for males and higher in forested areas (females: 21.9 bears/100 km²; males: 13.0 bears/100 km²) compared with non-forested areas (females: 5.2 bears/100 km²; males: 3.1 bears/100 km²; Tables 3 and 4). Across vegetation communities in 2017, we estimated an average of 16 bears/100 km² (Table 4), or a total of 226 black bears (95% CI = 138–370) within the 1,416-km² habitat mask.

The best supported model for 2018 included only vegetation community (Tables 2 and S3). Densities of black bears were higher in forested areas (31.3 bears/100 km²) than in non-forested areas (2.6 bears/100 km²; Tables 3

TABLE 2 Model selection results for competing models ($\Delta\text{AIC}_c \leq 4$) focused on variables associated with density (D) of black bears based on spatially explicit capture-recapture models, northern range, Yellowstone National Park, Wyoming and Montana, USA, 2017–2018. We centered and scaled all continuous covariates (distance to roads and net primary productivity [NPP]). Vegetation community (forested or non-forested) and sex were categorical covariates. For the 2017 models, the detection parameter (g_0) varied by behavior and occasion and in 2018 it varied by behavior and sex. In both years, the scale parameter (σ) varied by 2 finite mixture groups and in 2018 it also varied by sex.

Year	Model	K^a	logLik ^b	AIC_c^c	ΔAIC_c^d	Weight ^e
2017	$D \sim 1 + \text{vegetation community} + \text{sex}$	15	-437.59	914.60	0.00	0.25
	$D \sim 1$	13	-441.04	914.94	0.34	0.21
	$D \sim 1 + \text{vegetation community}$	14	-439.77	915.62	1.03	0.15
	$D \sim 1 + \text{distance to road} + \text{sex}$	15	-438.48	916.38	1.78	0.10
	$D \sim 1 + \text{NPP} + \text{sex}$	15	-438.85	917.12	2.52	0.07
	$D \sim 1 + \text{distance to road}$	14	-440.66	917.41	2.81	0.06
	$D \sim 1 + \text{vegetation community} + \text{distance to road} + \text{sex}$	16	-437.43	917.73	3.13	0.05
	$D \sim 1 + \text{NPP}$	14	-441.03	918.14	3.55	0.04
2018	$D \sim 1 + \text{vegetation community}$	9	-1,187.95	2,395.91	0.00	0.52
	$D \sim 1 + \text{vegetation community} + \text{sex}$	10	-1,187.41	2,397.33	1.42	0.25
	$D \sim 1 + \text{vegetation community} + \text{distance to road}$	10	-1,187.94	2,398.37	2.46	0.15
	$D \sim 1 + \text{vegetation community} + \text{distance to road} + \text{sex}$	11	-1,187.40	2,399.84	3.93	0.07

^aNumber of parameters.

^bLog likelihood used to derive the maximum likelihood of estimated parameters.

^cAkaike's Information Criterion corrected for small sample size.

^dDifference in AIC_c compared with top model.

^e AIC_c model weight, indicating relative support for model.

TABLE 3 Beta coefficients (β), standard errors (SE), and 95% confidence intervals (CI) for covariates from the top models in each year used to estimate density of American black bears, northern range, Yellowstone National Park, Wyoming and Montana, USA, 2017 and 2018. Beta estimates are expressed on the logit scale. Beta estimates for vegetation communities are for forested areas relative to the reference class of non-forested areas, whereas estimates for sex in 2017 are for males relative to the reference class of females.

Year	Covariate	β	SE	95% CI	
2017	Intercept	-6.12	0.34	-6.80	-5.45
	Vegetation community	-1.43	1.11	-3.60	0.74
	Sex	-0.52	0.25	-1.01	-0.02
2018	Intercept	-5.77	0.18	-6.13	-5.41
	Vegetation community	-2.48	1.18	-4.79	-0.17

TABLE 4 Estimated density (bears/100 km²) and 95% confidence intervals (CI) of American black bears by year, sex, and vegetation community based on the top model in each year, northern range, Yellowstone National Park, Wyoming and Montana, USA, 2017 and 2018.

Year	Sex	Vegetation community	Density	95% CI	
2017	Female	Forested	21.9	11.2	43.0
		Non-forested	5.2	1.0	28.2
	Male	Forested	13.0	6.4	26.8
		Non-forested	3.1	0.6	17.1
		Overall	16.0	10.0	26.0
2018		Forested	31.3	21.8	44.9
		Non-forested	2.6	0.3	21.6
		Overall	20.0	15.0	28.0

and 4). Across vegetation communities in 2018, the estimated average density of black bears was 20 bears/100 km² (Table 4), or a total of 324 black bears (95% CI = 239–439) within the 1,592-km² habitat mask.

DISCUSSION

Our results indicate that the northern range of Yellowstone National Park supports high densities of black bears (average = 20 bears/100 km²) relative to other areas in the northern Rocky Mountains, and higher than those reported for other studies of black bears in the Greater Yellowstone Ecosystem (8–12 bears/100 km², Mace and Chilton-Radandt 2011; 6 bears/100 km², Kindermann and Bjornlie 2019). Our black bear density estimates were within the range of values previously reported for western North America (average = 24.2 bears/100 km², Mattson et al. 2005; 16.5 bears/100 km², Gould et al. 2018; 20.1 bears/100 km², Welfelt et al. 2019) but lower than several eastern populations of black bears (37–103 bears/100 km², Tredick and Vaughan 2009; 10.5–201 bears/100 km², Sawaya et al. 2013).

Our density estimates were markedly higher in forested (31.3 bears/100 km²) compared with non-forested vegetation communities (2.6 bears/100 km²). Although grasses and sedges in open, non-forested areas provide

some of the first food resources for black bears during spring, these plants become more fibrous and difficult to digest over time (Pritchard and Robbins 1990, Rode et al. 2001, Robbins et al. 2004). In contrast, forested vegetation communities provide nutrient-rich foods in different seasons, such as riparian plants, fruiting vegetation, insects, cambium, and pine nuts (Barnes and Bray 1967, Fortin et al. 2013, Costello et al. 2016, Duquette et al. 2017, Herrero 2018). Additionally, forested areas provide cover for thermoregulation, particularly during summer (Sawaya et al. 2016), and escape cover from competitors such as grizzly bears (Pigeon et al. 2016).

We did not find evidence of a relationship between plant productivity and black bear density; the categorical covariate for vegetation community better explained spatial variation in bear density than NPP. Forested areas, particularly coniferous forest, typically are associated with higher values of NPP compared with grasslands (Xu et al. 2012). We speculate that our classification of forested communities provided a better metric of multiple resources important to black bears that were not captured by differences in NPP. Additionally, the northern range is located at lower elevations of Yellowstone National Park and experiences longer green-up periods, supplying black bears with more abundant vegetative resources compared with other regions of the park (Singer et al. 1994, Costello et al. 2016, Frank et al. 2016, Notaro et al. 2019), which might also help explain the higher density estimates we found in this region.

We also did not detect a relationship between bear density and proximity to roads. This finding is contrary to our prediction about higher densities of black bears near roads, as a way to avoid grizzly bears (Kasworm and Manley 1990, Berger 2007, Ladle et al. 2018). Instead, frequent use of roadsides by black bears observed on the northern range may simply be related to resource selection without reflecting a density effect, but further research is needed to explore this result.

Our detection probabilities varied slightly between years but were generally similar to those reported in other studies of black bears (Drewry et al. 2013, Humm et al. 2017, Gould et al. 2018, Welfelt et al. 2019). We did not find a difference in detection probabilities between sexes in 2017, but did in 2018, which might be the result of adding rub objects. Although we did not find a difference in detection probabilities between collection methods, male bears tend to have higher detection rates at rub objects compared with females (Table 1; Sawaya et al. 2012, Stetz et al. 2014, Loosen et al. 2019). In addition, female bears change their movement patterns when caring for cubs, avoiding areas frequented by males or other dominant animals, which could influence detection (Sawaya et al. 2012, Stetz et al. 2014, Loosen et al. 2019).

By increasing the number of sample sites and combining 2 different collection methods (rub objects and hair snares) in 2018, the precision of our abundance and density estimates increased. We collected fewer samples from hair snares in 2018 compared with 2017, which may be a function of not moving hair snares among sampling sessions and years, unlike other studies (Sawaya et al. 2013). Adding rub objects as sample sites to the sampling design compensated for this decrease in samples, further demonstrating the importance of using multiple collection methods, which helped reduce sampling bias and enhanced accuracy of our estimates, resulting in more robust inferences, consistent with other studies (Boulanger et al. 2008, Stetz et al. 2014, Kendall et al. 2015).

The relatively high density of black bears on the northern range is of particular interest given that this population is sympatric with grizzly bears. Although a formal density estimate is lacking for grizzly bears on the northern range, we detected fewer individual grizzly bears (14 females, 21 males) than black bears during this study. On an individual level, grizzly bears generally outcompete black bears where resources are high quality or when the 2 bear species occur at similar densities (Belant et al. 2006, Schwartz et al. 2010, Frattaroli 2011, Fortin et al. 2013, Harrer and Levi 2018). Yet black bears can occur at higher densities than grizzly bears when resources are lower quality (e.g., lower availability of terrestrial meat resources; McLellan 2011), and grizzly bears may avoid areas with high densities of black bears to decrease the probability of agonistic interactions (Aune 1994, Mattson et al. 2005, Stetz et al. 2019). In other regions of the Greater Yellowstone Ecosystem, grizzly bears kill (Mattson et al. 1992, Gunther et al. 2002), displace, or outcompete black bears, but our results support suppositions from previous studies that habitat conditions on the northern range allow black bears to occur at higher densities (Holm et al. 1999, Schwartz et al. 2010, Fortin et al. 2013, Teisberg et al. 2014).

Black and grizzly bears also can influence kill rates of other predators (Elbroch et al. 2015, Tallian et al. 2017). In northern California, cougars experienced a net energy loss when black bears usurped kills, causing cougars to alter their foraging behaviors (Allen et al. 2014, 2021). Similarly, bears in Yellowstone National Park visited >42% of kills made by cougars and displaced them from >10% of these kills during spring (Murphy et al. 1998). Forested areas also are heavily used by cougars (Kohl et al. 2019) and high densities of black bears in these areas could result in cougars changing their predatory behavior (Engebretsen et al. 2021). Abundant questions remain regarding the trophic interactions among black bears and other wildlife species in Yellowstone National Park. The estimates and spatial variation of black bear density we documented provide a baseline for future research to better understand the dynamics of those interspecific interactions.

MANAGEMENT IMPLICATIONS

With robust and spatially explicit estimates of black bear population density, managers can better assess how bears are distributed across the landscape and develop focused management objectives and strategies. Our results provide baseline information for further studies on the northern range of Yellowstone National Park, home to most of North America's large mammal species, offering a unique opportunity to better understand the impacts of climate change and other environmental perturbations on the inter- and intraspecific interactions of this suite of species. Understanding the spatial distribution of black bears can also help with efforts to address human–bear conflicts, such as deploying more food storage boxes in forested backcountry areas where black bear densities are highest.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

This study was completed under Montana State University Institutional Animal Care and Use Committee protocol number 2017-24 and United States Department of the Interior National Park Service Scientific Research and Collecting Permit study number YELL-07090 and permit numbers YELL-2017-SCI-7090 and YELL-2018-SCI-7090.

DATA AVAILABILITY STATEMENT

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

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

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