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Research

Using spatially-explicit capture–recapture models to explain variation in seasonal density patterns of sympatric ursids

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Understanding how environmental factors interact to determine the abundance and distribution of animals is a primary goal of ecology, and fundamental to the conservation of wildlife populations. Studies of these relationships, however, often assume static environmental conditions, and rarely consider effects of competition with ecologically similar species. In many parts of their shared ranges, grizzly bears *Ursus arctos* and American black bears *U. americanus* have nearly complete dietary overlap and share similar life history traits. We therefore tested the hypothesis that density patterns of both bear species would reflect seasonal variation in available resources, with areas of higher primary productivity supporting higher densities of both species. We also hypothesized that interspecific competition would influence seasonal density patterns. Specifically, we predicted that grizzly bear density would be locally reduced due to the ability of black bears to more efficiently exploit patchy food resources such as seasonally abundant fruits. To test our hypotheses, we used detections of 309 grizzly and 597 black bears from two independent genetic sampling methods in spatially-explicit capture–recapture (SECR) models. Our results suggest grizzly bear density was lower in areas of high black bear density during spring and summer, although intraspecific densities were also important, particularly during the breeding season. Black bears had lower densities in areas of high grizzly bear density in spring; however, density of black bears in early and late summer was best explained by primary productivity. Our results are consistent with the hypothesis that smaller-bodied, more abundant black bears may influence the density patterns of behaviorally-dominant grizzly bears through exploitative competition. We also suggest that seasonal variation in resource availability be considered in efforts to relate environmental conditions to animal density.

Keywords: demography, density, noninvasive genetic sampling

Introduction

Animal density is the metric of population performance perhaps most relied upon for assessing and managing wildlife populations (Williams et al. 2002, Fuller et al. 2016). Density reflects the sum of births, deaths, immigration, and emigration for a defined

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area and time, with each being influenced by the suitability of the local environment to the species' requirements (Brown et al. 1995, Coulson et al. 1997). Understanding how density and the environment are related remains a fundamental pursuit in ecology, and may inform efforts to promote long term population viability (Andrewartha and Birch 1986, Brown et al. 1995).

Population density is expected to reflect the quality of habitat for a given population, with higher densities suggesting higher quality habitat, and vice versa (Brown et al. 1995, Bock and Jones 2004). More abundant resources, such as food, security cover, and mates, should generally result in larger numbers of individuals per unit area (Delibes et al. 2001b), assuming minimal effects of competition or predation favoring one species over another. These relationships may be nonlinear (Morris 2003), and could appear contradictory in situations of ecological traps where higher densities coincide with lower survival or reproductive rates (Van Horne 1983, Battin 2004). Although there are multiple ways to assess habitat, linking environmental conditions to demographic measures like density, reproduction, and survival should be a research priority (Garshelis 2000, Mosser et al. 2009).

Spatiotemporal variation in the suitability and availability of resources is a primary driver of the fitness of animals (Brown 1984, Wiegand et al. 2002), which can produce substantial heterogeneity in density patterns within and among populations (Festa-Bianchet 1988, Pulliam et al. 1992). Intrapopulation variation in density is, however, particularly difficult to explain given typically coarse resolution of data (Brown et al. 1995, Nielsen et al. 2010). Most studies have therefore used static indices of environmental factors at fixed spatial scales based on average movement rates or home range size (Brown et al. 1995, Wiegand et al. 1999), although exceptions are becoming more common (Ciarniello et al. 2007, Wiegand et al. 2008).

Beyond the intrinsic suitability of an area, the value of resources to individuals can be diminished through competition among members of one or more species, thereby impacting population performance (Rosenzweig 1981, Sih et al. 1985, Begon et al. 1986). Competition can take different forms, including interference, where animals directly interact and compete for resources (Vanak and Gompper 2010, Steinmetz et al. 2013), or exploitative, where multiple individuals attempt to use the same resources (Wiens 1993, Linnell and Strand 2000). Furthermore, both forms can occur within a species, between ≥ 2 species, or both (Connell 1983, Gurevitch et al. 2000). Thus, effects of competition can be real in the sense of reduced quantities of resources, or perceived in the sense that animals avoid areas of higher densities of competitors (Abrahams 1986, Delibes et al. 2001a).

Despite its importance, the effects of competition on the dynamics of natural populations are rarely quantified (Palomares and Caro 1999, van Beest et al. 2016). Field and laboratory experiments have suggested that the effect size of interspecific competition is often greater than that of intraspecific competition (Connell 1983), although such experiments

typically have not assessed the effects of competition relative to other, potentially more important, factors such as effects of variation in resource availability (Wiens 1989, Butt and Turner 2012). Experimental manipulation of wild populations, however, is rare (Harrington et al. 2009), particularly for terrestrial carnivores and species of conservation concern (Caro and Stoner 2003, Miller et al. 2015). Competition studies are therefore often relegated to relatively simple indices such as species co-occurrence models (Fisher et al. 2013, Farris et al. 2016).

To advance understanding of how animals perceive the quality of spatiotemporally-varying resources in the presence of competition, we examined seasonal variation in density patterns of two species believed to engage in both exploitative and interference competition. Across most of their range in continental North America, grizzly bears (grizzlies) *Ursus arctos* are sympatric with American black bears *U. americanus*. Both species are generalist omnivores, although each has evolved morphological and behavioral adaptations to better exploit specific resources (Herrero 1978). The front claws of grizzly bears, for example, are adapted to excavate subterranean foods, whereas black bear claws facilitate climbing trees for security and to access tree-borne foods (Herrero 1978). In many parts of their shared ranges, however, their diets show nearly complete overlap (Jacoby et al. 1999, Mattson et al. 2005), and their digestive efficiencies are essentially identical (Pritchard and Robbins 1990).

A common assumption is that grizzly bears will dominate in direct competitions with black bears because adult grizzlies typically are larger and more aggressive than black bears. While there are empirical examples of this (Gunther et al. 2002), recent studies exploring interference competition have found exceptions to this assumption, with the outcome having more to do with motivation and perception of risk than body size (Miller et al. 2015, Allen et al. 2016). Actual encounter rates, their outcome, and effects on emergent properties (Salt 1979) like density have not been thoroughly evaluated for either species (Mattson et al. 2005, Schwartz et al. 2010).

Despite these expectations, competition between these species is likely to favor black bears at a population level in areas lacking highly concentrated resources such as spawning salmon (Herrero 1978, Mattson et al. 2005). Where sympatric, black bears can exist at densities 10 times that of grizzly bears, and are more efficient at exploiting dispersed foods, such as small berry patches (Jonkel 1971). The smaller, more intensively used home ranges of black bears should also allow them to respond to changes in resource availability more rapidly than grizzly bears (Aune 1994, Mattson et al. 2005). In northwestern Montana, USA, for example, preferred bear foods are often patchy and dispersed, with both species relying heavily on berries and forbs (McLellan 2011). Along the Rocky Mountain Front, Aune (1994) found substantial overlap in grizzly and black bear home ranges, with only subtle differences in habitat use and food habits that were likely facilitated by temporal partitioning of shared resources.

Similarly, high diet and range overlap were found in the Apgar Mountains of Glacier National Park (GNP) with both bear species relying heavily on herbaceous vegetation at low elevation in early summer, and berries in mid-summer, with similar use of insects, carrion, and other foods throughout the summer (Shaffer 1971). Again, temporal partitioning was believed to explain the high degree of overlap between grizzly and black bear food habits, as has long been proposed (Hornocker 1962).

Due to the seasonal nature of high quality foods in temperate, mountainous areas, both grizzly and black bears use hibernation as a strategy to survive long periods of food scarcity (Herrero 1978, Hilderbrand et al. 2000). To prepare for hibernation, both species initiate hyperphagia in late summer as berries, in particular, become abundant, with daily caloric intake increasing 3–4 fold (Nelson et al. 1983). The significance of seasonal food availability, and the adaptations that animals have evolved to deal with them, is a critical but often overlooked component of assessing habitat quality (Belant et al. 2006, Wiegand et al. 2008).

Recognizing the dietary and physiological similarities of these species, we used predicted density surfaces to test the hypothesis that interspecific competition influences the population performance of bears in a large area known to support robust populations of both species (Kendall et al. 2008, Stetz et al. 2014). We further hypothesized that seasonal variation in resource availability was important to how bears perceive habitat quality (Wiegand et al. 2008), with subsequent changes to density patterns. From our hypotheses, we predicted that resources used by both species would be sufficiently reduced to produce asymmetric effects on the seasonal density patterns of grizzly and black bears (Mattson et al. 2005). Additionally, we predicted that the effects of interspecific competition on density patterns would vary seasonally due to changes in both resource availability and changing behavioral and nutritional needs (Nelson et al. 1983).

We also considered effects of sexual segregation, where females use lower quality areas to avoid interactions with males (Clutton-Brock et al. 1987), on seasonal density patterns of both bear species. In nearby populations of black bears, Czetwertynski et al. (2007) tested competing hypotheses related to intraspecific competition on demography. Similar to other studies (Wielgus and Bunnell 1995), they found no support for the food hypothesis, where females avoid areas occupied by males that may compete for food or even cannibalize subordinate bears as a food source, and limited support for the sex hypothesis, where adult females avoid areas with adult males (Czetwertynski et al. 2007). From these examples and our knowledge of grizzly and black bear ecology in this region, we predicted that, if present, sexual segregation would be most pronounced during the mating season for both bear species, with males displacing females from areas of more suitable habitat.

To test our hypotheses, we used data from two large non-invasive genetic sampling (NGS) studies in conjunction with spatially-explicit capture–recapture (SECR) models (Borchers and Efford 2008). The basic SECR model combines a state

model predicting the distribution of activity centers with an observation model that regards detection probability as a function of distance from the activity center (Borchers and Efford 2008). Using SECR, we explored a suite of spatiotemporally-varying covariates to relate the variation in density to environmental conditions (Royle et al. 2013), including predicted density patterns of conspecifics and heterospecifics. Although our approach explicitly tested for relationships between density and putative causative factors, we recognize that our results are correlative, absent data on reproductive rates in these populations.

Study area

Our 7350 km² study area included all lands within 10 km of GNP, truncated at the U.S.–Canada border (Fig. 1). Fifty-six percent of the study area was within GNP, which was largely roadless and managed as wilderness, yet receives > 2 million visitors annually. Outside of GNP, lands were managed for multiple uses, including hunting, recreation, and low-density residential development. All areas adjacent to GNP had spring and fall black bear hunts except Waterton Lakes National Park, located just north of GNP in Alberta.

Elevation ranged from 900 to 3190 m a.s.l. High elevations received more precipitation and contained more exposed rock and permanent snow and ice than did valleys. Average annual precipitation, much of which was deposited as snow in winter, was 63 cm. The study area spanned the Continental Divide, which affected local climate and vegetation composition. Areas west of the Divide generally received more precipitation and had more densely forested areas with less grassland than the drier areas east of the Divide. Human

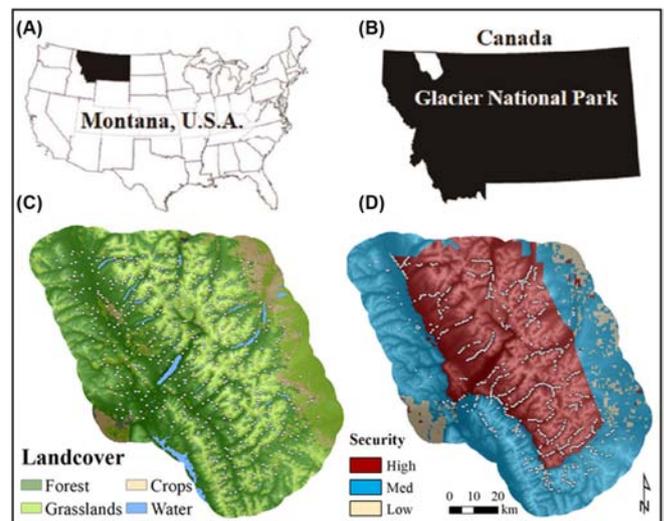


Figure 1. (A, B) Location of study area in northwestern Montana. Locations of (C) 550 hair traps in relation to landcover class derived from 2004 MODIS imagery, and of (D) 1366 surveyed bear rubs in relation to level of security for bears. Hair collection occurred in 2004 from 15 June–8 August for hair traps and 15 June–7 September for bear rubs.

development was greater on the west side of the Divide, although there were no cities or towns within the study area.

Methods

Field methods

We used two noninvasive methods concurrently to sample these grizzly and black bear populations: baited hair traps and unbaited bear rubs (Fig. 1). Hair traps consisted of one strand of barbed wire stretched around 3–6 trees, at the center of which we poured a liquid lure on a pile of forest debris (Woods et al. 1999). We established one hair trap per 7×7 -km cell for 14 d, after which all hair samples were collected, and the trap was moved >1 km (Kendall et al. 2009).

We also repeatedly surveyed 1366 natural, unbaited bear rubs found along maintained trails (Kendall et al. 2008). We affixed several 30-cm strands of barbed wire to each bear rub to improve sample quality and minimize mixing hairs from > 1 bear. We defined a sample as all hairs found on one set of barbs. To minimize DNA degradation, we stored samples in conditions that minimized exposure to moisture or UV radiation (Stetz et al. 2015).

Genetic analyses

All genetic analyses followed the protocols of Woods et al. (1999), Paetkau (2003), and Kendall et al. (2009) to ensure adequate marker power and to minimize genotyping errors. We determined the species and individual identity of bears by analyzing 7 microsatellite loci for grizzly bears and 6 loci for black bears, plus the amelogenin marker (Pilgrim et al. 2005) to identify sex of individuals of both species. Due to the large number of black bear samples, we subsampled hairs following Stetz et al. (2014). Details of our sample sizes, subsampling routine, marker power, and error rates for grizzly and black bear analyses can be found in Kendall et al. (2009) and Stetz et al. (2014), respectively.

Modeling density

We performed two stages of modeling by developing suites of a priori SECR models (Borchers and Efford 2008) for each combination of species, sex, and season using DNA-based encounter histories. The first stage used biotic and abiotic landscape characteristics that we hypothesized were related to density patterns of grizzly and black bears. The second included predicted density surfaces created from the results of the first stage to explore how density is affected by conspecific and sympatric species' densities.

SECR models estimate the density of animal activity centers in an area large enough that animals residing beyond it have a negligible chance of being detected (Borchers and Efford 2008). We therefore defined our study area as extending 15 km beyond all sampling points based on functions in the 'secr' package in R (Efford 2011, R Development

Core Team). From this 15 204 km² area, we removed areas of rock, persistent snow and ice, and lakes > 1 ha, which we considered to be 'non-habitat' (Stetz et al. 2014).

We were also interested in how seasonal changes to landscape characteristics, including density patterns of sympatric species, may explain variation in bear density. Following Mace et al. (1996) we defined the period through 15 July as spring, which contains the peak of the breeding season for both species of bears (Waller and Mace 1997). Based on changes in preferred foods (Mace and Jonkel 1986, Aune 1994), we defined the subsequent month as early summer, and the final month as late summer, during which time bears' diets consist largely of fleshy fruits (Mace and Jonkel 1986, Raine and Kansas 1990). We therefore parsed our detection data into three one-month periods for each species and sex for use in SECR analyses.

For each of these time periods, we used ArcGIS (ver. 10.2; ESRI) to develop spatial covariates that we hypothesized influence bear density patterns. We considered two biotic habitat variables, landcover class and the enhanced vegetation index (EVI; Huete et al. 2002), which, alone or in combination with other variables, pertain to availability of bear foods (Zedrosser et al. 2011). We derived both variables from 2004 MODIS 500 m datasets (Nemani and Running 1997, Pettorelli et al. 2014). The EVI is sensitive to temporal and spatial variation in photosynthetic output across a range of conditions, including mountainous regions that show strong seasonal patterns (Villamuelas et al. 2016). We hypothesized three ways in which EVI could reflect the quality of resources available to bears. First, EVI values could reflect the energetic value of emergent foods such as grasses and sedges, particularly during spring (Posse and Cingolani 2004). Second, there may be a lag between peak photosynthetic activity and the production of berries and other late-summer foods (Holden et al. 2012). Third, the cumulative amount of photosynthetic activity may reflect the energy content of foods including ants (Bentley 1976) and grasses and shrubs (Gamon et al. 1995). We therefore calculated the average EVI value for each pixel from the two 16-d scenes that most closely aligned with each one-month modeling season. To accommodate lag effects, we also used EVI values from each season to explain density patterns in subsequent seasons. Finally, to compare cumulative EVI to within-season values, we summed the average values across time periods.

We explored how landcover influenced bear density and how use of cover types changed seasonally by classifying each 500 m pixel in our study area into one of six classes: forest, shrublands, grasslands, permanent wetlands, urban, and croplands. We chose these classes because they have been shown (Waller and Mace 1997, Apps et al. 2016) or hypothesized (Jonkel 1971, Ciarniello et al. 2007) to be important factors to explain bear density.

We also included abiotic factors that have been hypothesized as predictors of bear density, including terrain roughness, elevation, and habitat security, for modeling variation in density (Fig. 1; Apps et al. 2006, Graves et al. 2011). For

elevation, we resampled a 30 m digital elevation model to 250 m pixels using bilinear interpolation, from which we also derived the relative topographic position, which may reflect soil and hydrological profiles that influence biological diversity and productivity (Jenness 2002). Finally, areas with lower mortality rates or anthropogenic disturbance provide greater security and, thus, may support higher animal densities than less protected areas of similar resource quality (Woodroffe and Ginsberg 1998). We assigned parks and protected areas the highest security level; other multiple-use federal, state, provincial, and tribal lands were assigned medium security; with private lands assigned the lowest security (similar to Mace et al. 1996 and Graves et al. 2011; Fig. 1).

To test how density of sympatric species and conspecifics influence bear density patterns, we first developed suites of competing models (i.e. biological hypotheses) using biotic and abiotic covariates to create predicted density surfaces for each species, sex, and season combination. This first modeling stage did not include densities of sympatric species or conspecifics as covariates. We ranked model support at this stage using AICc, and used model averaging based on AICc weights to account for model selection uncertainty (Burnham and Anderson 2001). In the second stage, we competed additional models that included these density surfaces, as well as total density of each species and of both species combined, as explanatory covariates (henceforth, predicted density covariates). We then ranked model support within each complete suite of models using AICc. Given the high degree of ecological similarity between grizzly and black bears, we considered an inverse relationship between species' density patterns as consistent with our predictions regarding effects of competition.

Within each full model suite, we considered models with AICc values ≤ 2 units of the top model to be supported by the data (Symonds and Moussalli 2011). We inspected estimates and standard errors for signs of models failing to run successfully (O'Brien and Kinnaird 2011), and used the goodness-of-fit test from Proffitt et al. (2015) for each scenario.

Data deposition

Data available from the U.S. Geological Survey data release: <<https://doi.org/10.5066/F7TQ60TB>> (Kendall et al. 2018).

Results

Hair collection and genetic analyses

During 15 June–18 August 2004, we collected 5645 bear hair samples from 550 hair traps, of which 1193 and 1890 were classified as grizzly and black bear, respectively. From these, we identified 248 individual grizzly bears (147 F, 101 M) and 468 black bears (249 F, 219 M). We also collected 3493 hair samples from 4860 surveys of 1366 bear rubs during 15 June–7 September 2004. Of these, 833 and 956 were classified as grizzly and black bear, respectively. From these, we identified 154 individual grizzly bears (66 F, 88 M), and 223 black bears (89 F, 134 M). In total, we identified 309 individual grizzly bears (170 F, 139 M), and 597 black bears (303 F, 294 M). We assigned all grizzly and black bear detections into one of six 14-d occasions, which we then parsed into our three seasons (Table 1). Details of detection and recapture frequencies, including goodness-of-fit results, are reported in Supplementary material Appendix 2 and 3.

Table 1. Summary of grizzly *Ursus arctos* and American black *U. americanus* bear detection data, by sex and sampling method, used in spatially-explicit capture–recapture analyses of grizzly and black bear density. Sample collection occurred in northwestern Montana, 15 June–7 September, 2004. See Supplementary material Appendix 2 and 3 for details of detection data and goodness-of-fit results.

		Season ^a					
		Spring		Early summer		Late summer	
Grizzly bear	Hair trap effort ^b	1918	1946	1904	1932	–	–
	Bear rub effort ^c	5433	12026	13459	16657	26055	19563
	No. unique males	50	57	49	68	35	13
	No. male detections	98	130	73	95	50	22
	No. recaptures ^d	140		72		29	
	No. unique females	39	39	69	74	28	18
	No. female detections	42	44	75	89	34	23
No. recaptures	13		44		14		
Black bear	No. unique males	96	111	73	77	30	27
	No. male detections	118	143	88	84	34	27
	No. recaptures ^d	80		36		5	
	No. unique females	97	96	75	60	26	31
	No. female detections	99	102	87	65	33	44
No. recaptures	27		27		23		

^a Each season consists of two 14-d sampling occasions. Hair traps were active for spring and early summer only.

^b Total number of days that hair traps were available to detect bears per two-week sampling occasion.

^c Number of days since the previous survey of a given bear rub summed across all bear rubs surveyed in a given occasion.

^d Total number of recaptures within a given session regardless of detector type.

Bear density

Here, we present the most supported models for each species-sex-season combination from our complete modeling exercise, which included models with and without predicted density surface covariates. Supplementary material Appendix 6 includes model selection results for all models with > 0 AICc weight.

Our most supported models of female grizzly bear density for the spring season contained a single covariate, the predicted total density of black bears during the same season (Table 2, Fig. 2), which was negative and significant (i.e. the 95% confidence interval did not include zero; Table 3). Top models for female grizzly bear density in early summer included predicted density of male grizzlies with an additive effect of spring EVI, which were both negative and significant. The top model for female grizzly density in late summer included only the total predicted density of black bears, which was negative but not significant.

Top models for male grizzly bears in spring contained only the predicted density of female grizzlies during the same period (Table 2, Fig. 2), which was positive and significant (Table 3). Top density models for early summer suggested a negative relationship with total predicted bear density and a positive relationship with terrain roughness, although only total predicted density was significant. Similarly, top late summer models suggested a negative relationship with total predicted density of bears, although the 95% CI included zero.

Female and male black bears had the same top model during spring, with total predicted density of grizzly bears being the sole supported covariate (Table 2, Fig. 2); the relationship was negative and significant for both sexes (Table 3). In contrast with grizzlies, top density models for both sexes of black bears in early and late summer did not include any covariates of predicted bear density. Top models for early summer density of female black bears included a positive relationship with spring EVI and a negative relationship with terrain roughness, both of which were significant. Late

summer models were similar to early summer, although the positive relationship between EVI and density was no longer significant; a significant negative relationship with terrain roughness remained (Table 4).

Top density models for male black bears also had positive and significant relationships with spring EVI in both early and late summer (Table 2, Fig. 2). Density in early summer was also significantly higher in areas we defined as low habitat security, and lowest in areas of moderate security, although this relationship was not significant. Spring EVI was the only supported covariate for late summer density of male black bears (Table 4). We present complete SECR model selection results in Supplementary material Appendix 6.

Discussion

We found partial support for the hypothesis that seasonal variation in resource quality influenced how bears perceive habitat quality, as areas of higher primary productivity contained higher densities of black bears in most seasons. For both sexes of black bears, spring EVI was predictive of both early and late summer density, consistent with our hypothesis that photosynthetic activity in the spring would result in more abundant bear foods such as huckleberries *Vaccinium* spp. later in the year. Conversely, we found little evidence of a relationship between primary productivity and grizzly bear density; the only time EVI was found to be predictive for grizzlies was a negative relationship between females in early summer and spring EVI, contrary to our predictions. This finding may be explained by considering the strongly positive relationship between EVI and black bear density in both early and late summer. We hypothesize that EVI may have acted as a proxy for black bear density, as the relationships were similar. Further, our next best model for female grizzlies during this season contained total bear density as the only factor, although support was limited (Supplementary material Appendix 6).

Table 2. The most supported SECR model, based on AICc, for seasonal density of grizzly bears *Ursus arctos* and American black bears *U. americanus* in northwestern Montana, USA, 2004. Number of estimated parameters (K) and model weight (w_i) are shown. See Supplementary material Appendix 6 for complete model results.

Species	Sex	Season	Density	K	w_i
Grizzly	F	Spring	Black bear density in spring	10	0.14
	F	Early summer	Male grizzly bear density in early summer + spring EVI ^a	10	0.54
	F	Late summer	Black bear density in late summer	9	0.11
Grizzly	M	Spring	Female grizzly bear density in spring	9	0.26
	M	Early summer	Total bear density in early summer + terrain roughness	12	0.48
	M	Late summer	Total bear density in early summer	6	0.07
Black	F	Spring	Grizzly bear density in spring	12	0.37
	F	Early summer	Spring EVI + terrain roughness	8	0.44
	F	Late summer	Spring EVI + terrain roughness	6	0.08
Black	M	Spring	Grizzly bear density in spring	9	0.61
	M	Early summer	Spring EVI + habitat security	19	0.32
	M	Late summer	Spring EVI	4	0.08

^a EVI: enhanced vegetation index (Huete et al. 2002).

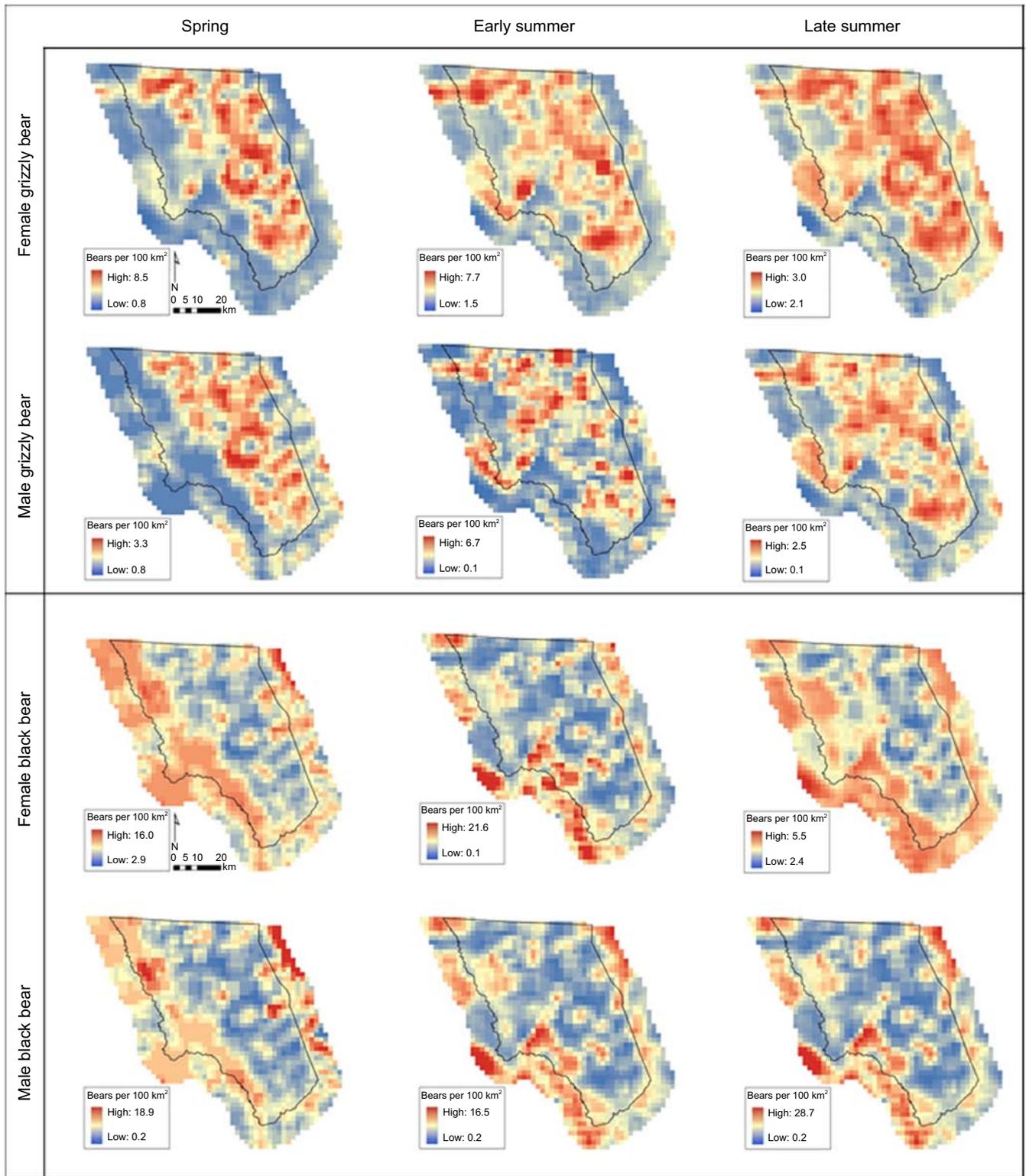


Figure 2. Predicted densities of grizzly *Ursus arctos* and American black bears *U. americanus* by sex and season using the most supported SECR model based on AICc values (Table 2). Note that density scales are unique to each map to highlight relative differences, as comparing absolute densities was not our objective. We conducted sampling during June–September 2004, on all lands in Montana within 10 km of Glacier National Park, which is shown in black outline.

Table 3. Model averaged estimates, standard errors, and 95% confidence intervals from the most supported full likelihood spatially-explicit capture–recapture density models for grizzly bears *Ursus arctos* in northwestern Montana, 2004, by sex and season. Each season represents two 14-d sampling occasions. See Supplemental materials Appendix 4 and 5 for details of the observation submodel.

Sex	Season	Density submodel parameters	β	SE	LCL	UCL
F	Spring	Baseline density ^a	1.072	0.449	0.488	2.359
		Total black bear density in spring	-0.092	0.024	-0.139	-0.045
	Early summer	Baseline density	1.273	0.397	0.700	2.313
		Male grizzly bear density in early summer	-1.545	0.380	-2.289	-0.800
		Spring EVI	-0.508	0.104	-0.711	-0.305
Late summer	Baseline density	2.396	1.010	1.085	5.295	
	Total black bear density in late summer	-0.013	0.037	-0.086	0.059	
M	Spring	Baseline density	0.960	0.317	0.511	1.805
		Female grizzly bear density in spring	0.189	0.082	0.028	0.350
	Early summer	Baseline density	0.036	0.052	0.005	0.287
		Total bear density in early summer	-0.202	0.070	-0.341	-0.064
		terrain roughness	1.277	0.815	-0.321	2.875
	Late summer	Baseline density	0.148	0.183	0.022	0.981
		Total bear density in early summer	-0.127	0.067	-0.255	0.007

^aDensity is reported in bears 100 km⁻² at the base level of covariates.

Surprisingly, we found no support for relationships between density patterns of either species and landcover type or elevation, both of which have been found elsewhere (Mowat et al. 2005, Apps et al. 2006, Graves et al. 2011). We do not, however, propose that bears respond indifferently to landcover, nor that these relationships are temporally invariable. As with previous studies, we recognize that our landcover categories may not adequately capture how bears perceive their environment and may miss potentially valuable resources such as army cutworm moths *Euxoa auxiliaris* (White et al. 1998) or understory vegetation (Apps et al. 2006). Conversely, elevation is a generic factor not directly linked to specific biological processes, even though it may be correlated with bear density. Our results suggest that the other factors we considered, particularly the putative effects of competition and primary productivity, were better suited

to explain variation in density than factors used in previous analyses. Nonetheless, we recognize that we cannot ascribe causation and that other, unmeasured factors may influence the patterns we observed.

Collectively, our results provide support for the hypothesis that more topographically complex areas support more abundant and diverse bear foods, at least with respect to the density of bears. Specifically, terrain roughness was important in predicting female black bear density in early and late summer, although the direction of the relationship changed between seasons. We hypothesize that this may reflect the use of flatter valley bottoms when grasses and emergent foods are abundant, with a transition to more topographically complex areas in late summer as berries ripen, similar to the findings of Apps et al. (2006) in a nearby black bear population.

Table 4. Model averaged estimates, standard errors, and 95% confidence intervals from the most supported full likelihood spatially-explicit capture–recapture density models for American black bears *Ursus americanus* in northwestern Montana, 2004, by sex and season. Each season represents two 14-d sampling occasions. See Supplemental materials Appendix 4 and 5 for details of the observation submodel.

Sex	Season	Density submodel parameters	β	SE	LCL	UCL
F	Spring	Baseline density ^a	11.795	2.158	8.265	16.832
		Total grizzly bear density in spring	-0.180	0.078	-0.333	-0.028
	Early summer	Baseline density	14.304	3.148	9.339	21.908
		Spring EVI	0.969	0.251	0.477	1.460
		Terrain roughness	-0.700	0.279	-1.246	-0.154
	Late summer	Baseline density	3.324	1.509	1.423	7.766
Spring EVI		0.077	0.079	-0.079	0.233	
Terrain roughness		1.115	0.514	0.108	2.122	
M	Spring	Baseline density	7.409	0.789	6.017	9.124
		Total grizzly bear density in spring	-0.502	0.155	-0.807	-0.198
	Early summer	Baseline density	11.918	3.518	6.763	21.002
		Spring EVI	0.937	0.301	0.348	1.527
		Low security	1.417	0.484	0.468	2.366
	Late summer	Medium security	-0.139	0.423	-0.969	0.690
		Baseline density	20.603	9.795	8.505	49.906
		Spring EVI	1.089	0.425	0.257	1.921

^aDensity is reported in bears 100 km⁻² at the base level of covariates.

We also found little support for habitat security influencing bear densities. In the only case where a significant relationship existed, the effect was opposite of our predictions, with areas of lowest security having the highest density of male black bears in early summer. This suggests that bears' perception of security influenced their space use more than other factors we considered. Although regulated black bear hunts occurred before and after our sampling, we hypothesize that our results could reflect the fact that most mortalities occurred on these multiple-use lands, particularly for male black bears, with lower levels of mortality occurring on private lands and protected areas. This reinforces the complex relationship between many carnivore populations, whether hunted or not, and concepts of habitat security (Mitchell and Hebblewhite 2012).

Our results are generally consistent with the hypothesis that competition among ecologically similar species influences how animals perceive the suitability of their environment, which can manifest as reduced local densities of even a larger, more aggressive competitor. Evidence of this was strongest with female grizzly bears, which exhibited reduced densities in areas of higher black bear densities in two of three seasons. Further, we observed potential effects of competition on density patterns for both sexes of both species in at least one season each. In every case where density was related to the sympatric species' density, the relationship was negative, significant, and usually was the only supported factor.

The relationship we observed between male and female grizzly bear densities in spring and early summer is consistent with predictions of sexual segregation during their breeding season. Male grizzly density in spring had a significant positive relationship with female grizzly density, the only positive relationship between densities that we observed. Based on this and the significantly negative relationship that female grizzly density had with male density in the following season, we hypothesize that females were still responding to pursu-ant males and avoiding areas that may pose greater risk to dependent offspring from infanticidal males (Steyaert et al. 2012). That female grizzly bears had negative relationships with conspecific or black bear densities in every season suggests that they are more sensitive to competition than other classes of bears.

We found that black bear density, whether alone or as part of total bear density, was important in predicting the density of both sexes of grizzlies in most seasons. Although we also found that black bear density had a negative relationship with grizzly density during spring, black bears showed a markedly different pattern in both early and late summer. During these seasons, the density of both sexes was positively related to higher EVI, with no support for effects of grizzly bear density. Had we observed a negative relationship between densities of both species across all seasons, it could be possible that each species was showing preference for different resources or that one species was excluding the other. Instead, we found that a single value (i.e. density of sympatric ursids) better explained density patterns than the potentially complex interactions

of multiple environmental factors. The differences we found between black and grizzly bears during summer supports the notion that our analyses identified plausible relationships between density patterns of both species and the conditions that we hypothesized to be important.

Understanding how ecologically similar species partition resources is vitally important to linking concepts of habitat quality with population performance (Amarasekare 2003). This is particularly important if covariance between density and other vital rates exists across populations (Ives 1988), as is likely with such ecologically-similar species as grizzly and black bears (Mattson et al. 2005). Although a fundamental component in niche theory (Chase and Leibold 2003), inter-specific competition is rarely considered in habitat studies, with the focus remaining on behavior-based resource selection (Garshelis 2000, Morris 2003). Further, most empirical studies that have considered effects of competition have used species distribution models that provide little insight into demographic consequences of competition (Belant et al. 2006, Sozio and Mortelliti 2016).

Ideally, concurrent measures of population density and other vital rates should be made when assessing habitat quality (Van Horne 1983). As has been long recognized although frequently overlooked, ecological traps can effectively disrupt the relationship between animals' perception of habitat quality and population performance, resulting in source-sink dynamics (Dias 1996, Griffin and Mills 2009). Based on our experiences working in the greater GNP system, we are aware of no evidence of traps or sinks, particularly for grizzlies, which are a protected species with nearly every human-caused mortality, which occurs at a very low rate, accounted for. This is perhaps less assured for black bears, although human-caused mortality is low, closely monitored, and there was no hunting during our sampling. We are therefore confident that our density surfaces reflect decisions made by individual bears in populations at or near long-term equilibria (Pulliam 1988) and are consistent with such ecologically and physiologically similar species.

Although previous research has demonstrated extensive overlap in the diets and habitat use of these species, these are necessary yet insufficient conditions to ensure that competition exists (Wiens 1989). Our models provide empirical evidence that density-dependent effects among black and grizzly bears may play an important role in how these species perceive habitat quality, with measurable, seasonal effects on the densities of both species. This supports calls to include effects of competition alongside spatiotemporally-varying environmental conditions, both to test ecological theory and to inform conservation (Wiens et al. 1993, van Beest et al. 2016).

A common challenge in explaining variation in animal density is the sparse data on measures of population performance and the poor power that analytical tools have to identify relationships with dynamic environmental conditions. We propose that using large-scale detection data in a SECR framework may provide opportunities to test

hypotheses that, although long-held in ecology, have seen little attention in practice, including effects on density and space use that competition between sympatric species may exert. Further, and as with traditional capture–recapture methods, the concurrent use of multiple types of detection data is a particularly powerful approach that has been shown to improve the quality of SECR analyses (Sollmann et al. 2013, Stetz et al. 2014). Such additional data sources serve not only to reduce detection biases, but also improve the spatial and temporal resolution of analyses, and should be considered whenever possible.

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Supplementary material (Appendix ECOG-03556 at <www.ecography.org/appendix/ecog-03556>). Appendix 1–6.