The Genetic Structure of American Black Bear Populations in The Southern Rocky Mountains

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Abstract:

Large and wide-ranging carnivores typically display genetic connectivity across their distributional range. American black bears (*Ursus americanus*) are vagile carnivores and habitat generalists. However, they are strongly associated with forested habitats; consequently, habitat patchiness and fragmentation have the potential to drive connectivity and the resultant structure between black bear subpopulations. Our analysis of genetic structure of black bears in the southern Rocky Mountains of Wyoming and Colorado (n = 296) revealed two discrete populations: bears in northern Wyoming were distinct (F_{ST} = 0.217) from bears in southern Wyoming and Colorado, despite higher densities of anthropogenic development within Colorado. The differentiation we observed indicates that bears in Wyoming originated from two different clades with structure driven by the pattern of contiguous forest, rather than the simple distance between populations. We posit that forested habitat and competitive interactions with brown bears reinforced patterns of genetic structure resulting from historic colonization. Our work suggests that forested habitat is an important force structuring populations in the southern Rocky Mountains, even for populations of highly vagile carnivores.

Key words: competition, connectivity, landscape, microsatellite, Ursidae

Introduction

Highly mobile mammals, especially those that display plasticity in their resource use, are often well-connected by dispersal and exhibit little genetic structure (i.e., genetic variation between subpopulations; Evanno et al. 2005) across their range (Wayne and Koepfli 1996). Such connectivity is especially evident among carnivores, which generally possess strong dispersal power (Lee and Vaughan 2003). For example, forest carnivores such as lynx (*Lynx canadensis*) and martens (*Martes americana*) exhibit little genetic structure across much of their distributional range in North America (Schwartz et al. 2002; Kyle and Strobeck 2003), and puma (*Puma concolor*) populations are panmictic across the central Rocky Mountains (Anderson et al. 2004). Even populations of carnivores inhabiting systems featuring strong barriers to dispersal, such as island archipelagos, can exhibit much connectivity and gene flow between populations (Paetkau et al. 1998). There are, however, notable exceptions with wolverines (*Gulo gulo*) in Scandinavia (Walker et al. 2001) and wolves (*Canis lupus*) in northeastern Europe displaying significant genetic structure (Hindrickson et al. 2013).

American black bears (*Ursus americanus*) are habitat generalists with strong dispersal power (Lee and Vaughn 2003); nevertheless, genetic differentiation has been documented during the assessment of cross-continental translocation efforts (Triant et al. 2004) and along the southern periphery of black bear range in Florida and Arizona (Dixon et al. 2006; Atwood et al. 2011). Previous studies examining the drivers of genetic diversity among black bear populations have attributed structure to isolation by distance (Triant et al. 2004; Pelletier et al. 2012), or barriers from topography (Cushman et al. 2006; Bull et al. 2011) and habitat loss (Csiki et al. 2003; Triant et al. 2004; Dixon et al. 2006; Onorato et al. 2007; Atwood et al. 2011). The amount of forest cover, in particular, can structure bear populations by limiting gene flow when forest cover is naturally patchy or fragmented due to anthropogenic change (Bull et al. 2011).

Forest cover not only provides suitable habitat for black bears but it also buffers interspecific interactions with brown bears (*Ursus arctos*; Aune et al. 1994; Apps et al. 2006). Competition between black and brown bears in western North America can influence the spatial distribution of these species (Apps et al. 2006) with coexistence facilitated by niche partitioning (Herrero 1972; Aune et al. 1994). When brown bears are present, black bears possess smaller territories and are displaced from open habitats into forested areas (Holm et al. 1999). Among carnivores, such competition and niche partitioning can also be an important barrier to gene flow and even lead to genetic structuring, especially for the subordinate competitor (e.g., Ruiz-Gonzalez et al. 2015).

While much attention has focused on how habitat loss and fragmentation and anthropogenic barriers reduce genetic connectivity (Sawaya et al. 2014) and increase genetic structure (Coster and Kovach 2012), anthropogenic development is not a uniform dispersal barrier (Bull et al. 2011). In particular, bears in urbanized landscapes demonstrate flexibility in behavior and resource use (Kirby et al. 2016) and in some cases, even benefit from human development (Beckmann and Berger 2003).

To date, little is known about the subpopulation structure of black bears in the southern Rocky Mountains. Previous work on black bear phylogeography revealed three haplotypes structured into nine regional groups across North America, with bears in Colorado and the southern Rocky Mountains belonging to a group separate from those in Montana and the northern Rocky Mountains (Puckett et al. 2015). Since bear populations throughout Wyoming were not sampled, the origin of these populations and finer-scale population structure in this region are unknown. Herein, we analyzed the genetic population structure of black bears across the southern Rocky Mountains to identify the clade to which this previously unsampled region belongs and assessed the potential importance of landscape features in determining population structure. We hypothesized that black bears in northern and central Wyoming would belong to different clades when compared to southern Wyoming and Colorado and that this southern clade would display less genetic structure and more connectivity compared to the northern clade, due to the greater amount of contiguous forest.

Study area

We collected hair from hunter-harvested black bears (n = 150) during the fall 2011 hunting season throughout their range in Colorado, which encompasses the western two-thirds of the state, including the Front Range in the northeast and San Juan Mountains in the southwest. We sampled bears in Wyoming (n = 146) from baited hair traps and from hunter-harvested bears from 1994 through 1997 at three study sites: the Tetons in the Black Rock area outside the Moran Junction entrance to Grand Teton National Park, the Bighorn Mountains, and the Medicine Bow Mountains (Fig. 1). The Tetons are a continuation of the central Rocky Mountains of Montana and Idaho with vegetation communities transitioning

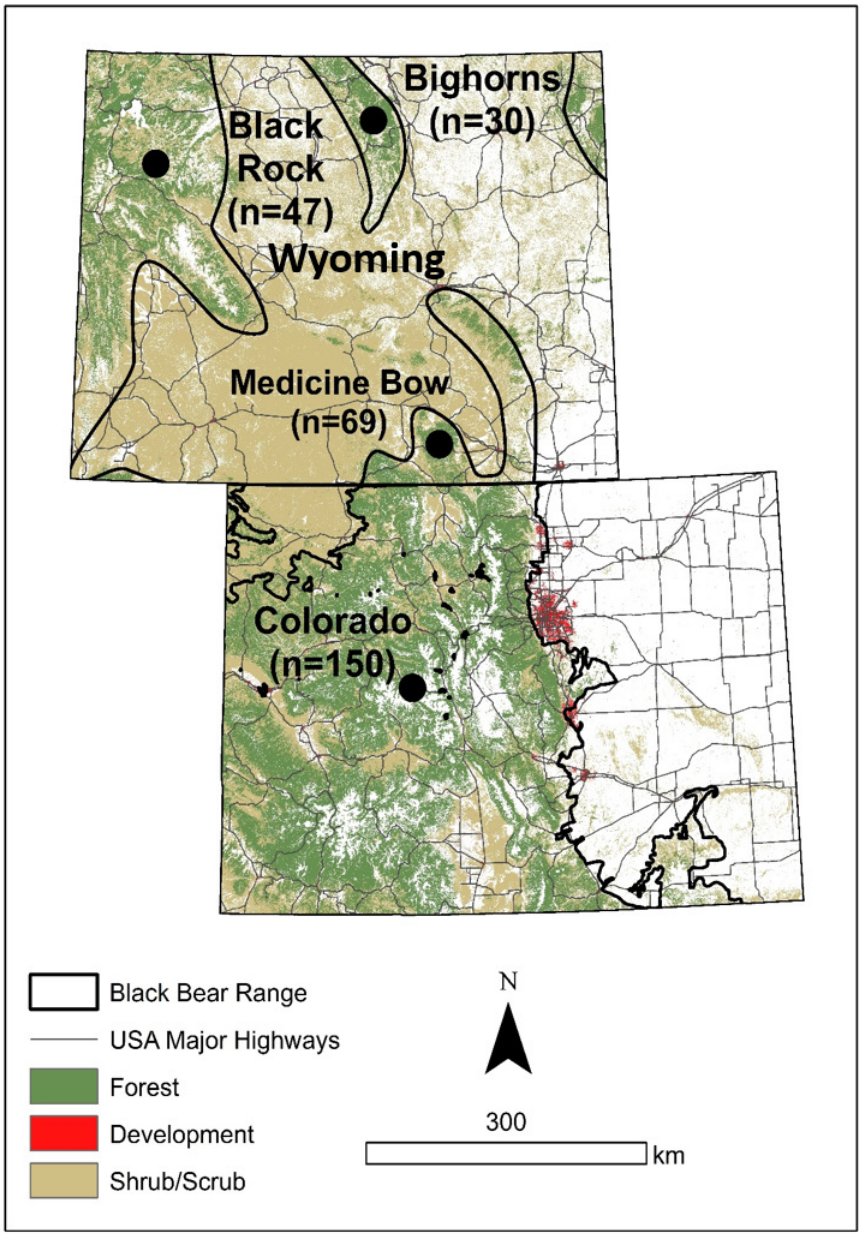

Figure 1 The geographic range of black bears across Wyoming (Buskirk 2016) and Colorado (Colorado Parks and Wildlife) with forest, shrub, and development land cover (Homer et al. 2015) and the major roadways (U.S. Interstates, State Highways, U.S. Routes; ESRI). Black bear range is delineated by the black line and sample locations are defined by the center point of each sample area in the Black Rock Mountains, Bighorn Mountains, Medicine Bow Mountains, and in Colorado. The area of shrub/scrub in central Wyoming represents the Wyoming Basin.

from aspen (*Populus tremuloides*) and Douglas fir (*Pseudotsuga menziesii*) to ponderosa pine (*Pinus ponderosa*) and subalpine tundra at higher elevations. The Bighorn Mountains are an isolated range in north-central Wyoming separated from the Tetons by sagebrush (*Artemesia* spp.) shrubland. In southeastern Wyoming, the

Medicine Bow Mountains are an extension of the Front Range of the Colorado Rocky Mountains, consisting of subalpine tundra, coniferous forests mixed with aspen, ponderosa pine, and pinyon-juniper (*Juniperus* spp.) at lower elevations (Knight et al. 2015). The Wyoming Basin, which stretches from northeastern to southwestern Wyoming, is comprised of shrub-steppe habitat which is dominated by sagebrush, grassland, and intermixed with short-grass prairie. The basin limits the dispersal of forest-obligate bird and mammal species (Findley and Anderson 1956) and similarly may limit dispersal between black bears in northern and southern Wyoming, leading to genetic differentiation between subpopulations (McDonald et al. unpubl. data).

Materials and Methods

We extracted deoxyribonucleic acid (DNA) from intact follicles from the Colorado and Wyoming bears following standard procedures using a QIAGEN DNeasy Blood and Tissue Extraction Kit (QIAGEN, Valencia, CA). We genotyped bears using four microsatellite loci: G1A, G10C, G1D, and G10L (Paetkau and Strobeck 1994). Microsatellites were amplified under the following conditions: initial denaturing at 94˚C for 2 min; 33 cycles of amplification at 94˚C for 30 s, 56˚C for 30 s, 72˚C for 1 min; final elongation of 72˚C for 5 min; incubation at 4˚C. The total reaction volume was 12 µl and contained 7.5µl of d2H2O, 1.25x PCR buffer, 0.25 mM of deoxynucleoside triphosphate, 0 to 1.56 mM of MgCl2, 0.33 µg/µl of Bovine Serum Albumen, 1 U of Taq DNA polymerase, 0.33 µm of fluorescently labeled forward primer and reverse primer, and 1.5 to 2.0 ng/µl of DNA. Fragment sizes for the Colorado bears were determined using an ABI 3730 DNA Analyzer (Applied Biosystems) and scored in GeneMapper (Applied Biosystems). The alleles from the Wyoming bears were initially scored using electrophoresis on a 25-cm, 7% polyacrylamide gel. We used a 350-bp genetic ladder on a Li-Cor 4200-S automated DNA sequencer to assess allele sizes and genotyped individuals using GeneImagIR™, version 3.0 software. To test whether allelic scoring of the Colorado bears and of the Wyoming bears was consistent, we randomly selected 20 DNA samples of the genotyped bears from Wyoming, amplified, and scored these samples following the conditions described above for the Colorado bears. We adjusted the alleles from the Wyoming bears based on observed allele frequency distributions per locus as described in a previous study of black bears (Paetkau 1997; Csiki et al. 2003). Alleles at locus G1A and at locus G10C aligned with the published base pair sizes and were not adjusted; we decreased alleles at G1D by one base pair, and increased alleles at G10L by one base pair if they were 171 base pairs or less, or by two base pairs if they were greater than 171 base pairs.

We calculated allele frequencies, observed (H_O) and expected heterozygosity (H_E; GENEPOP v. 4.2), and the polymorphism information content (CERVUS v. 3.0.7; Kalinowski et al. 2007) and tested for departures from Hardy-Weinberg equilibrium and genotypic linkage equilibrium (GENEPOP v. 4.2) for the Colorado and Wyoming populations separately (Raymond and Rousset 1995), applying a Bonferroni correction (Rice 1989). We tested for genetic differentiation between populations using pairwise F_{ST} (Weir and Cockerham 1984) values for each locus separately and for all loci combined. To further assess the genetic structure of bears in Colorado and Wyoming, we tested for isolation by distance with a Mantel test (Rousset 2008) with genetic distance expressed as $F_{ST}/(1 - F_{ST})$ and geographic distance expressed as the natural logarithm of the distance in kilometers between populations. We defined the geographic location of the three populations in Wyoming using the center point of each of the three sample areas. Due to the broad distribution of black bears in Colorado, we represented the Colorado sample area with the bear capture site that was geographically closest to Wyoming. We

calculated the straight-line distance between each population (ArcGIS version 10.4.1, Environmental Systems Research Institute). We then evaluated the influence of habitat type, defined broadly as forest and shrub/scrub habitat, which is dominated by shrubs and trees less than five meters tall (Homer et al. 2015; Jonkel and Miller 1970), on black bear population structure. We calculated the proportion of forest and shrub land cover along the straight-line distance between sites using 2011 National Landcover Data and weighted the simple distances between sites by the estimated proportions (Geospatial Modeling Environment version 0.7.2, Spatial Ecology). We then estimated isolation by distance through forest and shrubland habitat types.

To cluster individuals by genotype in the absence of geographic information, we used STRUCTURE version 2.3.4 (Pritchard et al. 2000). We performed ten independent runs of $K = 1 – 10$, where K indicates the number of populations based on genotypic similarity, with and without population gene flow at 50,000 Markov chain Monte Carlo repetitions and a burn-in period of 5,000. We used the admixture model due to expected gene flow among the populations. The final K value was selected by plotting K ($K = 1 – 10$) versus the ΔK ($\Delta K = m([L'' K])/s[L(K)]$ where $L(K) = Ln\ P(D)$) and selecting the best fit (Evanno et al. 2005).

Results

All four loci, G1A, G10C, G1D, and G10L, were polymorphic, with average observed heterozygosity ranging from 0.38 in Wyoming to 0.50 in Colorado (Table 1). The Black Rock population and the Medicine Bow populations departed from Hardy-Weinberg equilibrium and one pair of loci (G1A and G10L) exhibited linkage disequilibrium ($P = 0.002$).

Gene flow was highest between the Bighorn and Black Rock populations ($F_{ST} = 0.023$, weighted distance = 132.73 km) and between the Colorado and Medicine Bow populations ($F_{ST} = 0.029$, weighted distance = 63.21 km) and lowest between the Black Rock and Medicine Bow populations ($F_{ST} = 0.279$, weighted distance = 339.08 km; Table 2). Tests of isolation by distance indicated genetic structure between the bears at the four study sites. Isolation by the straight-line distance between sites showed a positive but non-significant relationship ($r^2 = 0.58$, $P = 0.08$). Isolation by distance of forest and shrub cover between sites were positive and significantly related ($r^2 = 0.72$, $P = 0.03$; Fig. 2).

Population assignment tests revealed two genetically distinct populations because ΔK reached the maximum value ($\Delta K = 12.7$) at $K = 2$. When we used our four sampling locations as predefined populations, STRUCTURE clustered 79% of the bears

Table 1. Allelic richness (A_r), base pair size (BP), observed (H_O) and expected (H_E) heterozygosity, and polymorphism information content (PIC) for Colorado ($n = 150$) and Wyoming ($n = 146$) black bear populations at 4 microsatellite loci (G1A, G10C, G1D, and G10L).

Location	Locus	A_r	BP	H_O	H_E	PIC
Colorado	G1A	6	201-216	0.50	0.50	0.68
	G10C	3	114-120	0.52	0.48	0.30
	G1D	6	186-200	0.49	0.51	0.73
	G10L	11	158-191	0.48	0.52	0.87
Wyoming	G1A	6	197-211	0.27	0.73	0.74
	G10C	6	114-126	0.43	0.57	0.45
	G1D	8	186-198	0.43	0.57	0.77
	G10L	17	154-193	0.39	0.61	0.91

Table 2. Pairwise FST and distance (both straight-line and weighted) between black bear sampling locations in the Black Rock Mountains in northwestern Wyoming (n = 47); Colorado (n = 150), the Medicine Bow Mountains in south-central Wyoming (n = 69), and the Bighorn Mountains in northern Wyoming (n = 30).

	F_{ST}	Straight-line Distance (km)	Distance Weighted by Forest and Shrub (km)
Black Rock/Bighorns	0.023	236.62	132.73
Colorado/Medicine Bow	0.029	77.68	63.21
Colorado/Bighorns	0.158	404.72	253.41
Black Rock/Colorado	0.198	443.95	411.14
Medicine Bow/Bighorns	0.234	344.09	241.56
Black Rock/Medicine Bow	0.279	419.82	339.08

from Colorado and 86% of the bears from the Medicine Bow Mountains into one population and 92% of the bears from the Black Rock Mountains and 94% of the bears from the Bighorn Mountains into another. Without predefined populations, 87% of the bears from Colorado and 91% of the bears from the Medicine Bow Mountains were clustered into one population and 98% of the bears from the Black Rock Mountains and 100% of the bears from the Bighorn Mountains were clustered into the other (Fig. 3).

Discussion

Although bears possess strong dispersal power, black bears in the southern Rocky Mountains can be separated into two

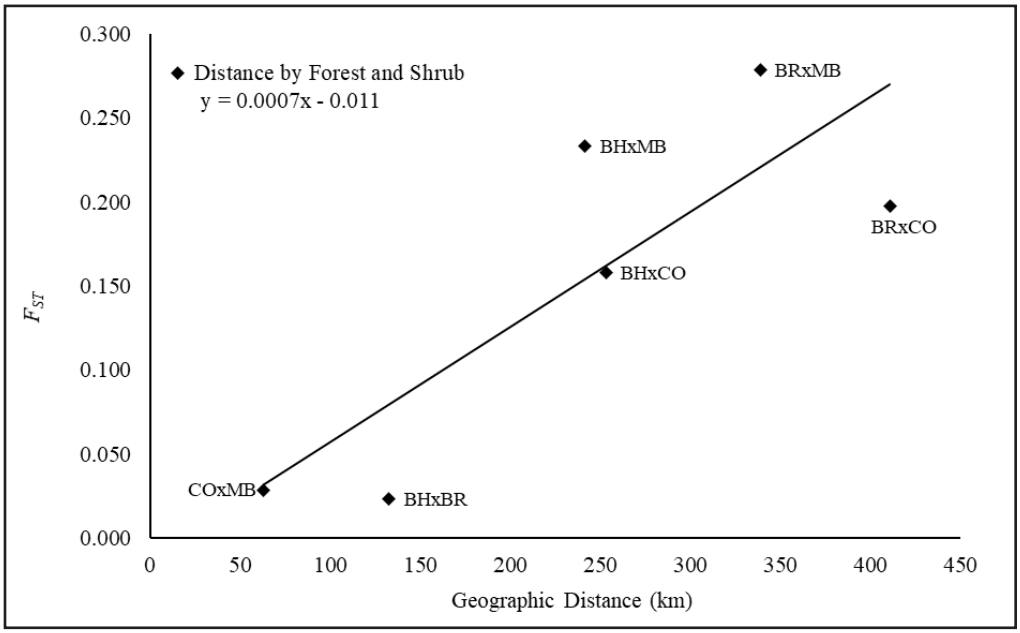

Figure. 2 Results of isolation by distance analysis showing distance weighted by the proportion of forest and shrubland between populations (Medicine Bow Mountains = MB, Black Rock Mountains = BR, Bighorn Mountains = BH, Colorado = CO) compared to the pairwise genetic distance (FST). The FST between Medicine Bow and Black Rock Mountains and between Medicine Bow and the Bighorn Mountains each are higher than expected given the distance through bear habitat between populations indicating that the Wyoming Basin may limit dispersal between these populations.

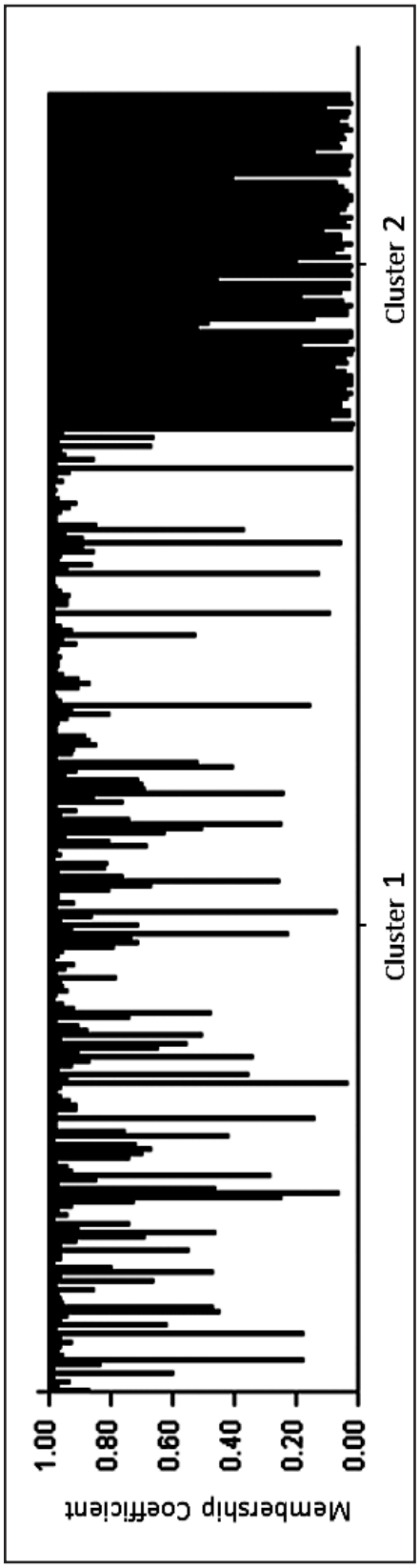

Figure. 3. The proportional membership of each individual black bear in the two clusters STRUCTURE identified without predefined populations. The white segment represents Cluster 1 (Colorado and Medicine Bow Mountains) and the black segment represents Cluster 2 (Black Rock Mountains and Bighorn Mountains).

discrete genetic populations. Black bears in northern Wyoming (Black Rock and the Bighorn Mountains) clustered into one distinct population and bears in southern Wyoming and Colorado clustered into another. These results reveal the origin of bears throughout a heretofore unsampled region within their distributional range; in particular, that black bears along the southern part of Wyoming belong to the previously described southern genetic group extending from Colorado south through New Mexico, while black bears in north and central Wyoming belong to the northern clade that ranges from Montana into Canada. The level of divergence we detected between northern Wyoming and the southern Wyoming/Colorado complex was within the range of F_{ST} values reported by other studies on black bear population structure. The divergence we observed was lower compared to black bear populations in Louisiana, where populations were augmented with bears from Minnesota and formed two distinct populations (F_{ST} = 0.206; Triant et al. 2004). On the other hand, the level of divergence we observed was much greater than those reported for populations sampled elsewhere in relatively contiguously forested regions and originating from the same phylogenetic cluster (Puckett et al. 2015) in eastern North America. In Ontario, black bears displayed weak structure (F_{ST} = 0.06) resulting from isolation by distance across much of their distribution with the exception of a geographically isolated population (Pelletier et al. 2012). Similarly, in New Hampshire black bears exhibited low levels of genetic structure (F_{ST} = 0.014) despite increasing anthropogenic pressures (Coster and Kovach 2012) and bears sampled in the forests of South Carolina are considered to be one population (F_{ST}= 0.023; Drewry et al. 2012). Our estimated F_{ST} were most similar to those observed in the highly fragmented forests of Florida (F_{ST} = 0.224; Dixon et al. 2006) and

southeast Arizona (F_{ST} = 0.112; Atwood et al. 2011). Altogether, our findings suggest that the amount of forest cover between populations, which facilitates dispersal in black bear populations elsewhere (Cushman et al. 2006; Bull et al. 2011), is the primary driver of genetic structure when comparing bears in the northern clade (Black Rock and Bighorns) to those in the southern Rocky Mountains (Colorado and Medicine Bow).

Given that Colorado has a higher human population density and greater anthropogenic development (Table 3), our findings that Colorado bears exhibited greater connectivity compared to bears at the three study sites in Wyoming may be unexpected. However, development does not necessarily act as a barrier to bear movement (Coster and Kovach 2012) and can increase foraging availability (Kirby et al. 2016) and enhance survival (Beckmann and Berger 2003). In addition to a higher housing density, Colorado features twice as much forested area compared to Wyoming (United States Forest Service 2016), which may support panmixia of black bears. Our findings support the notion that habitat connectivity via forest cover plays a dominant role, rather than anthropogenic development, in black bear connectivity and regional genetic structure.

We propose that the biological mechanisms behind our finer-scale findings that bear genetic structure is explained by patterns of habitat connectivity, not only simple distance between subpopulations, is a consequence of colonization, habitat associations, and historic competitive interactions. The current distribution of black bears is explained by patterns of dispersal out of glacial refugia (Puckett et al. 2015) and the divergence we observed between bears in northern and southern Wyoming appears to have resulted from this historic pattern of colonization. We propose that this historic structure has been reinforced by the strong association between black bears and forest cover throughout their distributional range. Forested habitats confer abundant food resources (Jonkel and Cowan 1971), enhanced denning opportunities (Johnson et al. 1978), and increased vegetative cover for movement and dispersal (Herrero 1972). The absence of contiguous forest across large regions of Wyoming may limit bear dispersal between northern and southern Wyoming, strengthening historic patterns of genetic structure in this region. In addition, black bear use of forested habitats is enhanced in areas where they are sympatric with brown bears. Such behavior has been observed near the Black Rock study site, where black bears selected for forest and avoided open habitats in the presence of brown bears (Holm 1998; Schwartz et al. 2002). The presence of brown bears in northwestern Wyoming likely restricts black bears to forested areas and decreases gene flow between populations separated by open habitat, particularly across the Wyoming Basin, resulting in the structure we observed. Since brown bears occur in open habitats more often than forested areas (Herrero 1972; McLellan and Hovey 2001), it is unlikely that brown bears were common in Colorado forests, leading to the sort of panmixia found in black bears in Canada (Pelletier et al. 2012). The extirpation of brown bears elsewhere in North America has altered black bear habitat use and distribution through competitive release: in Labrador, black bears expanded habitat use into the tundra (Veitch and Harrington 1996) and in California, black bears colonized the central coast, creating a population distinct from

Table 3. The population density, housing density, and total road density, including primary, secondary, and rural roads (United States Census Bureau 2012), per square kilometer in Colorado and Wyoming.

Location	Population	Housing Units	Roads
Colorado	18.7	8.21	1.09
Wyoming	2.22	1.03	0.98

other neighboring populations (Brown et al. 2009). While it is difficult to disentangle habitat-mediated competition from the various habitat requirements of black bears across their range, we believe that both are important factors reinforcing the historic population structure of bears in this region. Our study reveals the phylogenetic origin of black bears in the southern Rocky Mountains and the importance of historic colonization events, habitat associations, and competition in shaping the current population genetic structure of bears in this region. Our findings identify that biological mechanisms, not merely distance, can structure populations of a highly vagile carnivore. Understanding the drivers of population structure is important for the long-term conservation and management of large carnivores, particularly in increasingly altered landscapes, where a suite of novel conditions is impacting carnivore population connectivity.

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