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American black bear population fragmentation detected with pedigrees in the transborder Canada–United States region

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Abstract: Population fragmentation is stressing wildlife species worldwide. In populations with minimal genetic structure across potential fractures, detecting fragmentation can be challenging. Here we apply a relatively unused approach, genetic pedigree analysis, to detect fragmentation in the American black bear (*Ursus americanus*) across 2 highway corridors that are bordered by large, contiguous populations. We compared our results with movements detected through Global Positioning System (GPS) telemetry of collared bears between 2005 and 2010. We used 20-locus microsatellite genotypes to identify 104 first-order relatives (parent–offspring or full siblings) within 383 black bears, sampled between 2002 and 2012. We compared numbers of pairs of immediate relatives found on either side of 2 highways—U.S. Highway 2 in northwestern Montana, USA, and BC Highway 3 in southeastern British Columbia, Canada—with an expected rate, the mean across 22 lines parallel to each highway at 1-km intervals. We found that over similar geographic scales, dispersal was lower across the transportation corridors than adjacent areas without a highway corridor. The observed number of migrants across Highway 2 was 3, well below the confidence interval of the expected number of 15.1 migrants/available bears (95% CI = 12.2–18.0). Highway 3 had 6 migrants, compared with the expected 13.1 bears (95% CI = 10.8–15.5). None of 16 black bears wearing GPS radiocollars for 1 year crossed Highway 2, yet 6 of 18 crossed Highway 3. These results suggest that even though 33% of radiocollared black bears crossed Highway 3, there appeared to be less dispersal across the transportation corridors than across other regions in the study area. Pedigree and telemetry results were more closely aligned in the Highway 2 system, with both methods suggesting more intense fragmentation than we found along Highway 3. Our results identified pedigree analysis as another tool for investigating population fragmentation, particularly in situations where genetic differentiation is too weak to determine migration rates using individual-based methods, such as population assignment.

Key words: American black bear, carnivore, connectivity, ecological genetics, microsatellites, pedigree, population fragmentation, transborder, *Ursus americanus*

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Fragmentation is one of the most important conservation issues of our times, threatening species' persistence and, thus, biodiversity (Wilcove et al. 1998, Fahrig 2003). Enhancing connectivity (the antithesis of fragmentation) was the most frequently recommended science-based strategy for managing natural systems in response to climate change in a recent review paper (Heller and Zavaleta 2009). Mitigating current fragmentation was the third most recommended strategy. Fragmentation

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interrupts ecological processes associated with movement, including gene flow (Frankham 2006), interpopulation dynamics (Moilanen and Hanski 2006), and demographic rescue (Martin et al. 2000, Peery et al. 2010). Several large mammals, including wolverine (*Gulo gulo;* Cegelski et al. 2006), mountain caribou (*Rangifer tarandus;* van Oort et al. 2011), pronghorn antelope (*Antilocapra americana;* Poor et al. 2012), bighorn sheep (*Ovis canadensis;* Epps et al. 2007), and grizzly bear (*Ursus arctos;* Proctor et al. 2005, 2012b) are affected by population fragmentation at the southern extent of their North American distributions.

To define fragmentation, we first define and conceptualize a population. Among several options, we favor an evolutionary definition of population, where interbreeding individuals occupy a space over time (see Waples and Gagiotti 2006). We recognize that in reality, populations may exist in a continuum of gene flow rates with neighboring assemblages of organisms ranging from totally isolated to reasonably connected. Although setting specific criteria that separate categories of populations across this continuum can be challenging, measuring those gene flow rates to assign categories can even be more challenging. Fragmentation therefore becomes the interruption of movements and breeding across space that limits gene flow and alters the degree of interbreeding between organisms in what was one interbreeding unit. We recognize that 'fragmentation' and the resulting reduction in gene flow may be incremental, or the first stages of what might lead to complete fragmentation or population isolation.

In many cases, where small or severely isolated populations exist, fragmentation can be detected by exploiting genetic differences between populations to assign individuals to natal populations, which can then be compared with capture locations to infer lifetime movement (Proctor et al. 2005, 2012b; Dixon et al. 2007). By contrast, when fragmentation is too recent for population differences to have accumulated, or where large population size limits the power of genetic drift to create differences between populations, these tools lack power (Paetkau et al. 2004). A lack of population differentiation also limits the power of indirect genetic tools for inferring population structure, including reduced heterozygosity (Keyghobadi et al. 2005), genetic distance measures, F_{ST} (Kyle and Strobeck 2001), or even individual-based methods, including genetic clustering (Benzecri 1973, Pritchard et al. 2000) or assignment methods (Paetkau et al. 2004, Proctor et al. 2012b).

In western North America there have been few investigations of fragmentation of American black bear populations (*U. americanus;* hereafter, 'black bear'). Cushman et al. (2006) found gene flow among black bears in 2 adjacent mountain ranges to be positively influenced by mid-elevation forest cover and possibly inhibited by forest roads. Their pairwise-genetic-similarity methods found no evidence of fragmentation across a wide settled rural river valley with a highway through it. Short Bull et al. (2011) used similar methods and found similar results over a broader landscape, but found variability in landscape features that favored or inhibited gene flow. Cushman et al. (2006) suggested that small sample sizes (154 bears), small numbers of nDNA loci (9), and lack of genetic differentiation related to slow genetic drift may have influenced their inferences. In the eastern United States, Coster and Kovach (2012) detected population structure in black bears across major highways using spatial autocorrelation and landscape genetic analyses.

Proctor et al. (2005, 2012b) detailed population-level fragmentation of grizzly bear populations in western North America, primarily using assignment methods (Benzecri 1973, Paetkau et al. 2004, Piry et al. 2004). However, when these methods were applied to a preliminary set of black bear genotypes in our study area (acquired during grizzly bear surveys), our findings (unpublished data) were consistent with Cushman et al. (2006); there was no evidence of population-level fragmentation of black bears across highway–settlement corridors that functioned as barriers for grizzly bear movement and gene flow (Proctor et al. 2005, 2012b, Kasworm et al. 2014, Kendall et al. 2016). One of our research goals was to compare ecological characteristics of grizzly with black bears, including population-level fragmentation. We therefore developed 2 inter-related research questions: were black bears fragmented by major highway corridors, and if so, might we detect that fragmentation using pedigree-related analysis?

We suspected that, because there were large numbers of bears on each side of these potential fractures, genetic drift would be acting very slowly, and genetic signals necessary to detect population structure would very likely not be detectable. We therefore turned to developing limited pedigrees or family relationships to attempt to detect fragmentation, if it were occurring. Pedigrees and family relationships have been used to estimate dispersal ([Grizzly bears, *U. arctos*] Proctor et al. 2004; [American black bears] Costello et al. 2008, Moore et al. 2014; [Scandinavian brown bears, *U. arctos*], Støen et al. 2005; [poplar, *Populus nigra*], Pospiskova and Salkova 2006). Taking pedigree methods to the next level, Kormann et al. (2014) used parsimonious pedigrees to assess levels of connectivity and fragmentation in capercaillie (*Tetrao*

urogallus) in Europe, whereas Kanno et al. (2014) used brook trout (*Salvelinus fontinalis*) pedigrees to assess level of connectivity among streams. Proctor et al. (2012a, 2018) used family pedigrees to monitor increased interpopulation connectivity in grizzly bears.

Our objectives were therefore to test whether the spatial patterns of close family members could reveal patterns of fragmentation (if it existed) where more traditional methods that relied on the development of genetic structure could not.

There are several reasons that made this black bear system an ideal test case for relationship-based insight into dispersal and fragmentation. From a simple logistical perspective, most of the DNA samples were collected as by-catch during projects that targeted grizzly bears, so samples were available. Furthermore, on account of the scale of the collections, we had access to genotypes from hundreds of individuals, which we expected to be necessary in order to identify enough relationships for the method to work. There is also a genuine need for more information on the sensitivity of black bears to population fragmentation as well to compare that sensitivity with that of grizzly bears in the same study area (Proctor et al. 2005, 2012b). Black bears have a promiscuous mating system (Schenk and Kovacks 1995; Onorato et al. 2004), overlapping home ranges (Garshelis and Pelton 1981), and male-biased dispersal (Rogers 1987, Schwartz and Franzmann 1992, Costello et al. 2008), which is similar to grizzly bears (McLellan and Hovey 2001, Proctor et al. 2004, Graves et al. 2014, Norman and Spong 2015), so females may be more easily fragmented than males, as in grizzly bears (Proctor et a. 2005, 2012b). Finally, there is growing evidence that the population dynamics of grizzly bears are influenced by the presence and abundance of black bears (McLellan 1994, Mattson et al. 2005), so we also sought to understand the function of this black bear system to inform efforts to recover several small threatened grizzly bear populations (Proctor et al. 2010).

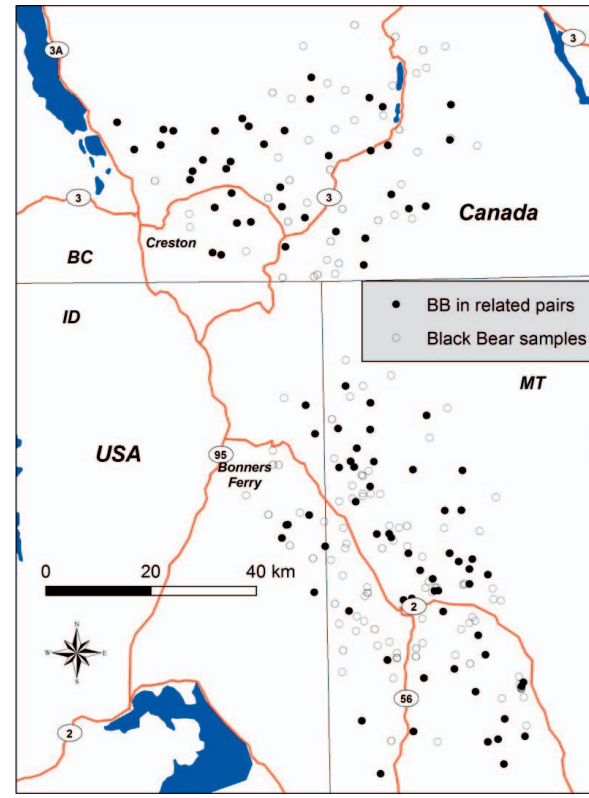

Fig. 1. American black bear (*Ursus americanus*) genetic samples adjacent to U.S. Highway 2 in northwestern Montana, USA, and Highway 3 in southeastern British Columbia, Canada, sampled between 2002 and 2012. Open circles are DNA sites where we sampled black bears (BB). Black circles are locations of black bears that were found to be in a first-order familial relationship.

Study area

Our study area encompassed the transborder area adjacent to both U.S. Highway 2 in northwestern Montana and northern Idaho, USA, which separates the Purcell and the Cabinet Mountains, and BC Highway 3 as it traverses the Purcell Mountains in southeastern British Columbia, Canada (Fig. 1). The area is mountainous throughout and is primarily coniferous forest, with occasional wetlands, avalanche paths, alpine areas above tree line, and other nonforested habitats. The region supports a timber industry and sporadic mining on both sides of the border that have created a network of resource-extraction roads. Mountain ranges are separated by valleys containing major highways and railways that connect urban centers and support a linear assemblage of rural landowners or communities along portions of their length.

Average summer traffic on U.S. Highway 2 is approximately 2,000–2,500 vehicles/day (vpd). A railroad with approximately 35 trains/day, and the Kootenay River, parallel most of its length within our study area. BC Highway 3 carries approximately 4,300 vpd in summer, parallels a railway with 6–16 trains/day, and follows the courses of small tributaries of the Kootenay River, including the Goat and Moyie rivers.

Data-based population estimates for black bears across our study area ranged from 130 to 230 bears/1,000 km^2 (Mace and Chilton-Radandt 2011; Supplemental

Material 1). Black bears were legally hunted across our study area, and topography was generally similar, with moderately rugged mountains with major valleys containing human settlement and highways.

Methods

Field techniques

We used genetic sampling and radiotelemetry for our data collection. A portion of our genetic and telemetry samples were collected specifically for fragmentation analysis, but most came from DNA sampling used to estimate population abundance and telemetry projects with other research goals. However, we subsampled these projects for samples within 25 km of our target highways. Our radiotelemetry sample was also collected with a bias toward bears captured closer to highways, in the hopes of collaring bears that might have crossed. Therefore, although these 2 methods may not cover the exact same areas adjacent to our target highways, they were reasonably similar except genetic sampling usually measures dispersal over many years and up to a lifetime, whereas telemetry is only for the time the collars were on the bears.

DNA sampling. We obtained genetic samples from the roots of hair from black bears live-captured for research or from DNA-based population surveys designed for estimation of population size or fragmentation of grizzly bears. In the United States, we obtained black bear DNA samples from 2 surveys, one carried out by Montana Fish, Wildlife & Parks (MFWP) to estimate abundance of black bear populations in spring and early summers between 2002 and 2009 (Mace and Chilton-Radandt 2011), and another carried out in 2012 to estimate grizzly bear population size (Woods et al. 1999, Kendall et al. 2016). The Mace and Chilton-Radandt (2011) surveys sampled bears in a one-time grid of 5-km × 5-km cells (1 sampled site/cell) over 2 weeks where hunter kills were used as recaptures. The Kendall et al. (2016) survey was designed for grizzly bears and sampled for 9, 2-week sessions over a 5-km × 5-km grid that also included rub-tree sampling. Also, we obtained a portion of our samples from hunter-killed black bears through MFWP. In Canada, we used samples from 2 DNA-based population surveys on grizzly bears carried out in 25-km^2 cells (1 sample site/cell) across 4, 2-week sessions in spring and early summer of 2004 and 2005 (Proctor et al. 2007) and samples from live-trapped bears captured while radiocollaring between 2004 and 2010.

We stored hair samples at room temperature in paper envelopes. Tissue samples from live-captured bears were dried, frozen, or placed in lysis buffer prior to analysis. After extracting DNA from snagged hair follicles and tissues, we used microsatellite analysis to identify individuals (Woods et al. 1999, Paetkau 2003). We georeferenced samples obtained through DNA surveys or live captures (the vast majority of samples) with a Global Positioning System (GPS) unit. We randomly selected one location for bears that were sampled at >1 location if they all were on the same side of their relative highway system (Highway 2 or 3). Bears sampled on both sides of a highway were reported separately. We identified location of hunter-killed samples in Montana to the accuracy scale of a watershed (approx. 100 km^2).

Radiotelemetry. We deployed GPS-telemetry collars on 16 black bears in the U.S. Highway 2 area and 18 bears in the BC Highway 3 area between 2005 and 2010. We captured bears with Aldrich foot snares and occasionally with culvert traps. In Canada, our bear handling procedures were in accordance with the Canada Council on Animal Care Standards. In the United States, methods were similar to those described by Jonkel (1993) and were in accordance with the University of Montana Institutional Animal Care and Use Committee (protocol identification number is 007-06CSFWB-040106). We primarily used Telonics Inc. (Mesa, Arizona, USA) Spread Spectrum radiocollars allowing periodic remote data downloads (and occasionally store-on-board collars), and occasionally used collars from Lotek (Newmarket, Ontario, Canada). We examined movement data by displaying location data derived from radiocollars on maps within a Geographic Information System (GIS).

We focused our collaring effort on an area approximately within 25–30 km north and south of each highway to maximize the chance of collaring a bear that might cross either highway. We captured most bears in May or June and monitored them for 1–2 years. We programmed collars to collect bear locations every 1–4 hours, depending on collar size (smaller bears carried smaller collars with less battery life) and age of bears (subadult bears carried collars designed to drop off earlier, so as to not interfere with neck growth). Our actual fix success rate yielded a location approximately every 3 hours, or 8 locations/day. We were interested in movement data that might take a bear across 1 of the 2 monitored highways; therefore, we did not ascertain whether there were any fix-success biases associated with particular habitat types (Frair et al. 2004, Proctor et al. 2015). We filtered our GPS telemetry data, only using locations that had a Positional Dilution of Precision (PDOP) value <10 (Lewis et al. 2011, Proctor et al. 2015). The resulting data set had a mean PDOP value of 3.3. We report the average number of days collars were active per bear and the average number of locations per bear.

Genetic analysis

We carried out genetic analyses at the Wildlife Genetics International lab in Nelson, British Columbia. We extracted DNA using DNeasy columns (Qiagen Inc., Mississauga, Ontario, Canada) and initially identified individuals with 6 or 7 microsatellite loci (Paetkau et al. 1998, Woods et al. 1999). We then genotyped 1 sample/individual to 20 loci (21 including sex) to allow sufficient power to assign parentage and identify full siblings. To eliminate genotypes created through genotyping error (Gagneux et al. 1997, Goossens et al. 1998, Taberlet et al. 1999, Paetkau 2003), we further scrutinized 20-locus genotypes for close mismatches. We reanalyzed the mismatching markers of all pairs of samples that mismatched at 1, 2, or 3 loci to confirm the genotype or resolve errors (Paetkau 2003, Kendall et al. 2009). We also reanalyzed the markers at which alleles were not shared for all pairs of individuals that shared an allele at all but 1 or 2 of 20 microsatellite markers, to correct errors between parent and offspring. We used the following markers: G1A, G10B, G10C, G1D, G10H, G10J, G10L, G10M, G10P, G10U, G10X, MU23, MU50, MU 51, MU59, CXX20, CXX110, P07, Msut2, and CPH9 (Ostrander et al. 1993, Taberlet et al. 1997, Paetkau et al. 1998, Kitahara et al. 2000, Breen et al. 2001, Proctor et al. 2002). We determined genotypes on Applied Biosystems 377 and 3100 automated sequencers, and scored genotypes with the help of Genotyper software (Applied Biosystems, Foster City, California, USA). We distinguished grizzly from black bear samples using a species-specific microsatellite marker (G10J; Paetkau 2003) and determined sex according to protocols detailed by Ennis and Gallagher (1994).

We estimated expected (H_E) and observed (H_O) heterozygosity using the software program GENETIX (Belkhir 1996–2004). We tested for conformance to Hardy–Weinberg Equilibrium and linkage equilibria within Genepop 4.2 (Raymond and Rousset 1995, Rousset 2008), adjusting critical values using the Dunn–Sidak experiment-wise error rate (Sokal and Rohlf 1995). We tested for F_{ST} values between sample sets across each highway system within Genepop 4.2. We used a multidimensional Factorial Correspondence Analysis (FCA; Benzecri 1973, She et al. 1987) in the program GENETIX (Belkhir 1996–2004) to look for evidence of population structure or fragmentation. The FCA is a special case of principal components analysis that provides an objective exploration into groupings of similar genotypes with no a priori assumptions of group membership. Using individual genotype data, GENETIX develops a multidimensional hyperspace, with 1 dimension (axis)/allele for all loci. Values measured are the sharing of alleles, with 3 states for every allele: absent, 1 copy (heterozygous), or 2 copies (homozygous). The more alleles shared by multiple individuals, the more they will cluster. The multidimensional hyperspace is ultimately reduced to the principal dimensions that capture the main axes of differences in clusters. An algorithm seeks the direction of a dimension to maximize the distance between clusters.

We also looked for population structure within the software Structure (Pritchard et al. 2000), which iteratively assigns individuals to one of several populations based on allele frequencies, but requires no a priori group membership. We assumed that bears sampled on each side of our 2 highway systems made up a 'population' on each side, and the program developed a probability of assignment to each 'population.' We ran this Markov chain Monte Carlo clustering routine assuming admixture and correlated allele frequencies using 100,000 burn-in runs (no data collected) and 400,000 iterations where probabilities of ancestry (qhat) were accumulated and developed.

Density estimation of black bears within Canada

We also estimated the density and abundance of black bears in the Canadian Yahk Mountains and the area north of BC Highway 3 to help provide a conservation context to our fragmentation analysis. Details of the Methods can be viewed in Supplemental Material 1. Density estimates for the U.S. populations have been previously estimated and reported elsewhere (Mace and Chilton-Radandt 2011).

Pedigree analysis

We identified 3 types of related groups, family triads (mother–father–offspring), parent–offspring dyads, and full sibling dyads. We identified family groups where allele matching patterns were consistent with those of a mother, father, and offspring using the parentage program PARENTE (Cercueil et al. 2002). In a mother–father–offspring triad, the offspring holds one allele from each parent. A perfect match with this pattern for both parents at 20 loci is a powerful indicator that the family relationship is real. Second, we considered all dyads that shared an allele at all 20 loci to be potential parent–offspring pairs. In reality, some portion of these may be full siblings. And third, we used our 20-locus microsatellite genotypes within ML-Relate (Kalinowski et al. 2006) to estimate relatedness (r) using maximum likelihood estimation. Both parent–offspring and full siblings (siblings with the same parents) have r-value distributions with a mean of 0.5 (Ivy and Lacy 2010). We are trying to identify first-order relatives (parent–offspring pairs and full siblings); therefore, we were not concerned that some pairs in our

parent–offspring group may have been full siblings. To minimize the number of half siblings in our sample, we chose 0.4 as our threshold between first-order relatives and other pairs, reducing the chance of including half siblings. The mean *r*-value for all pairwise combinations of individuals in our data set was 0.04.

We then mapped all 3 types of putative related pairs in a GIS to determine the spatial relationship of capture locations. We identified paired relationships and drew a line between their sample locations.

Estimating fragmentation

We estimated the level of fragmentation across each highway system by comparing the observed number of first-order pairs of related bears pairs on opposite sides of a highway with an expected number developed from adjacent areas not fragmented by the highway. We calculated the observed number of migrants by summing the number of lines connecting related pairs that spanned each highway. To develop an expected value, we created sets of lines parallel to each highway at 1-km intervals between 2 and 12 km—one set of 11 lines to the north and one set of 11 to the south of each highway. We then summed the number of first-order pairs of related bears that spanned each line in the same way as we tabulated relative pairs across the highways. We limited our expected lines to ±12 km from each highway because of limited sampling effort, such that the resulting sample density approached zero beyond 12 km. Our expected number of migrants was the mean number of first-order pairs of related bears per line, computed across all 22 parallel lines adjacent to each highway.

The number of possible related pairs that might span a highway (or parallel line) is a function of the numbers of bears in related pairs on each side of that line, so we applied a correction factor to standardize the numbers of related pairs spanning a line, such that our expected values were not skewed lower simply because of a line being on the periphery of our sampling area. We multiplied the number of first-order pairs that spanned any parallel line by Equation 1 below, which appropriately corrects for proportions of total number of possible related pairs across any parallel line relative to the total number of bears in related pairs across the highway being considered.

$$\text{Standardizing correction factor} = \frac{\text{No. of possible related pairs spanning highway of interest}^{i}}{\text{No. of possible related pairs spanning parallel line of interest}^{j}} \quad \text{(Eq. 1)}$$

Table 1. Expected (H_E) and observed (H_O) heterozygosity of American black bears (*Ursus americanus*) north and south of U.S. Highway 2 and BC Highway 3 in our transborder study area of northwestern Montana, USA, and southeastern British Columbia, Canada, across 20 microsatellite loci sampled between 2002 and 2012 (per locus values can be viewed in Supplemental Material 2).

Highway	*n*	H_E	H_O
Hwy 2 North	96	0.75	0.74
Hwy 2 South	103	0.77	0.78
Hwy 3 North	106	0.75	0.76
Hwy 3 South	78	0.74	0.73

i, product of number of bears in related pairs north and south of the highway being considered.

j, product of number of bears in related pairs north and south of any parallel line.

The numerator also adjusts outputs to be in the same range as the observed migrant values. For example, there were 25 bears in first-order relative pairs south, and 46 bears north, of Highway 3. Therefore there were 1,150 (25×46) possible related pairs that might span the highway. If a parallel line had 15 and 57 bears on the south and north side, respectively, there were 840 possible related pairs that might span that line. Clearly, the location of the line through the sample area dictates the likelihood of observing (or expecting) a relative migrant, hence the need for this correction factor. To complete the example, if there were 10 related pairs spanning that line, we multiply 10 by 1,150/840, or 1.37. We calculated our expected number of migrants for each highway by taking the mean of the standardized number of related pairs spanning all 22 parallel lines on both sides of each highway. We also report the number of recaptures of the same individual that spanned either U.S. Highway 2 and BC Highway 3 relative to the number of recaptures with >1 location.

Results

All bears within each sample area conformed to Hardy–Weinberg Equilibrium and all loci were in linkage equilibria after alpha was corrected by the Dunn–Šidák method (Sokal and Rohlf 1995). Mean H_E and H_O across the 20 loci we used to genotype the 383 black bears in our genetic samples (Fig. 1) north and south of U.S. Highway 2 and BC Highway 3 were relatively similar and relatively diverse (Table 1; per locus H_E and H_O can be viewed in Supplemental Material 2). Using traditional population metrics, we failed to detect significant population structure across each of the highway systems we

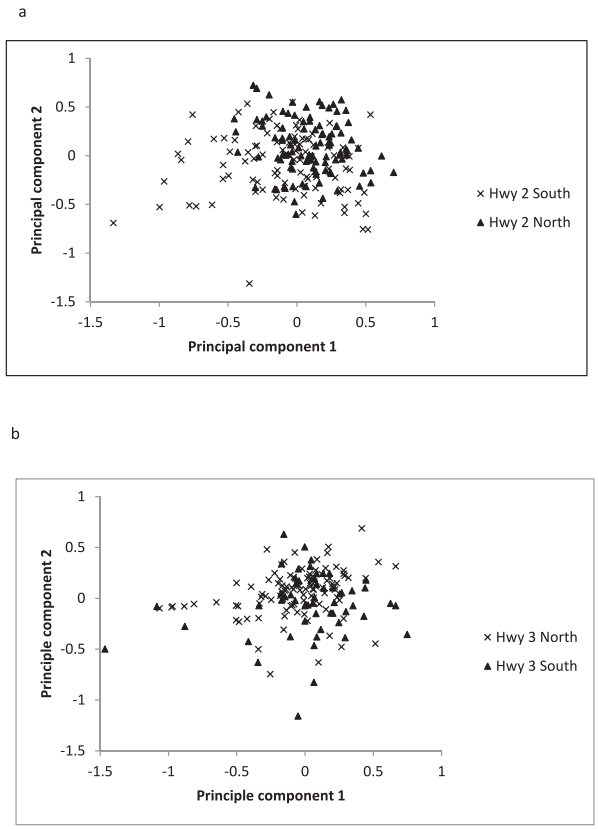

Fig. 2. (a) First and second principal components from a genotype-based factorial correspondence analysis (Program GENETIX) of population genetic structure of American black bears (*Ursus americanus*) sampled north and south of U.S. Highway 2 in northwestern Montana, USA, between 2002 and 2012. Plot demonstrates no genetic signal as a result of minimal genetic drift across this highway; and (b) Program GENETIX plot of black bear population structure across Highway 3 in southeastern British Columbia, Canada, also exhibiting no genetic structure.

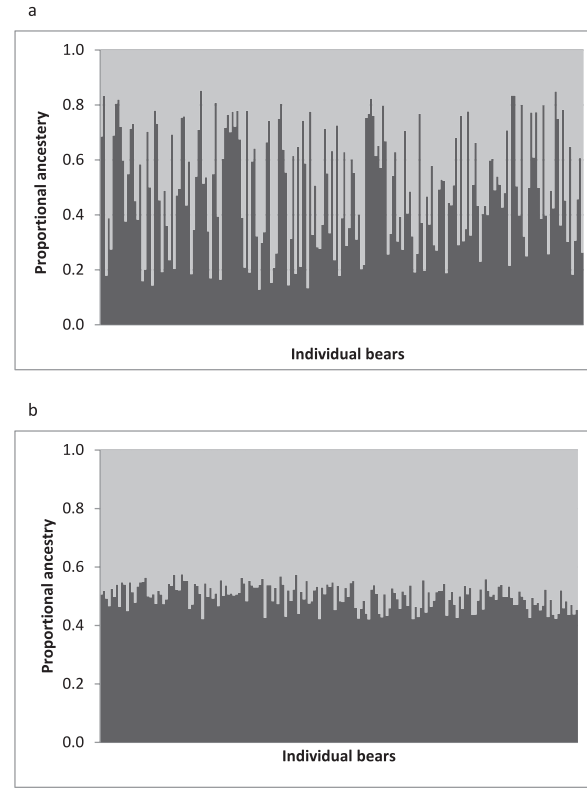

Fig. 3. (a) Program Structure bar plot of the proportional ancestry of American black bears (*Ursus americanus*) north and south of U.S Highway 2 in northwestern Montana, USA, sampled between 2002 and 2012, suggesting no genetic structure. F_{ST} between these groups of bears was 0.008. (b) A similar plot of black bears north and south of BC Highway 3 in southeastern British Columbia, Canada, suggesting no genetic structure across the highway. F_{ST} between these groups of bears was 0.007. The comparison of proportional ancestry across each highway system suggests a slight structuring developing along U.S. Highway 2, where the variance of proportional ancestry was 0.043 compared with 0.002 for BC Highway 3.

examined. Even with this relatively genetically diverse population, we could not detect individual migrants because of the similarity of population genetic metrics in each sample area. F_{ST} values were similarly low across both highways—0.008 for F_{ST} across U.S. Highway 2 and 0.0074 for BC Highway 3. Multifactorial correspondence analysis revealed that bears across each highway system appeared to come from one panmictic population (Fig. 2). Program Structure yielded a similar result, although the difference in variances in the assignment of proportional ancestry suggested the beginnings of population structure in the U.S. Highway 2 system (Fig. 3). The variances were 0.043 for U.S. Highway 2 and 0.002 for BC Highway 3 (Fig. 3). Using pedigrees, we identified 9 family triads with a perfect allele match, with offspring sharing an allele from each of the mother and father, representing 18 parent–offspring relationships (9 mother–offspring and 9 father–offspring). All probabilities of these triad family relationships and the dyads reported below were >0.95, except one dyad had an 80% probability. We did not accept any family relationships that did not have perfect allele-sharing patterns because we verified their genotypes. None of the parents or their offspring were

Table 2. Parent–offspring and full sibling pairs of American black bears (*Ursus americanus*) in northwestern Montana, USA, and southeastern British Columbia, Canada, sampled between 2002 and 2012. The number of related bears across each highway are in parentheses (migrants).

	Highway 2	Highway 3	Total
Related pairs	No. of bear (migrants)	No. of bear (migrants)	No. of bear (migrants)
Triad parent–offspring pairs	6 (0)	12 (0)	18 (0)
Parent–offspring pairs	30 (1)	18 (1)	48 (2)
Full siblings	19 (2)	20 (5)	38 (7)
Totals	55 (3)	50 (6)	104 (9)

sampled from opposite sides of either highway. We also identified 48 pairs that shared ≥1 allele at all 20 loci for our putative parent–offspring group and 38 more pairs with relatedness (r) values >0.4, for our putative full siblings (Table 2). From this set of 104 likely first-order relatives, we found 3 migrants (observed) across U.S. Highway 2 within our study area (Table 2; Fig. 4). The observed number of 3 migrants was in contrast to, and well below, the 95% Confidence Interval of the standardized expected number of 15.1 migrants (95% CI = 12.2–18.0; Table 3). We detected 6 migrants (observed) across BC Highway 3. The observed number of 6 migrants was also below the standardized expected rate of 13.1 bears (95% CI = 10.8–15.5; Table 3). There were 10 bears in 5 first-order relationships that were shared between the 2 highway systems (Fig. 3). Of those families with a migrant, we often do not know which individual within each dyad was the migrant; therefore, we cannot determine the exact sex ratio of our migrant sample. However, 88% of

Table 3. Observed versus expected numbers of American black bear (*Ursus americanus*) migrants per available bears and the number of bears wearing Global Positioning System (GPS) radiocollars that crossed U.S. Highway 2 in northwestern Montana, USA, and Highway 3 in southeastern British Columbia, Canada, sampled between 2005 and 2010.

Category	Highway 2	Highway 3
Pedigree analysis		
Observed no. of migrants	3	6
Expected no. of migrants	15.1	13.1
95% CI	12.2–18.0	10.8–15.5
GPS telemetry		
Telemetry bears	16	18
Telemetry migrants	0	6

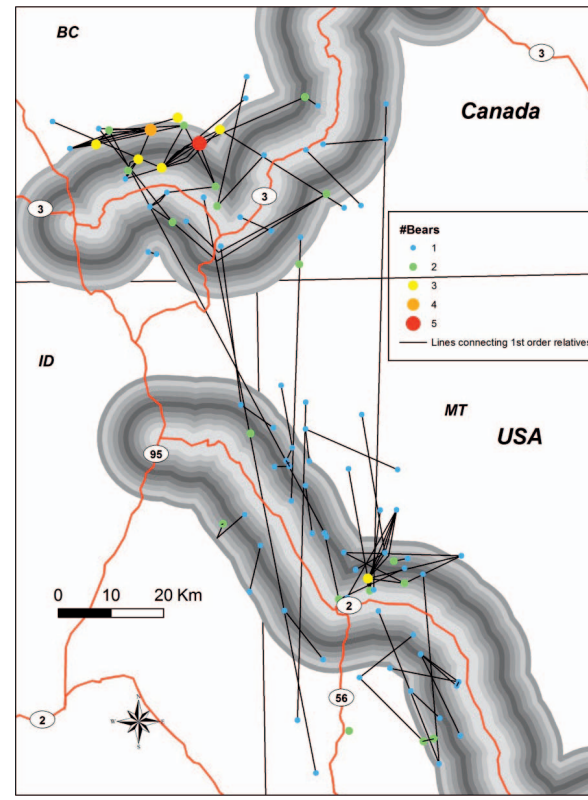

Fig. 4. Sampling locations of parent–offspring and full sibling related pairs of American black bears (*Ursus americanus*) in the U.S. Highway 2 region of northwestern Montana, USA, and the BC Highway 3 region of southeastern British Columbia, Canada, sampled between 2002 and 2012. Lines connect first-order relatives. For each highway system, we compared the observed number of migrants with an expected number from adjacent areas not fragmented by the highway (see text for details). Inputs for the observed rate came from the number of first-order relative pairs spanning each highway. Similarly, the expected rate input came from the number of first-order relatives spanning the parallel lines adjacent to each highway. Parallel lines are depicted with shade changes, created in Geographic Information System using buffers to the highways at 1-km intervals between 2 and 12 km adjacent to each highway.

all individuals within families where one individual was a migrant, were males. We sampled 1 male bear on both sides of BC Highway 3 of 33 recaptures in our sample within that system, and sampled no bears across U.S. Highway 2 of 21 recaptures within that system.

We radiocollared 16 black bears (10 M, 6 F) in the U.S. Highway 2 region, and none of them crossed the highway–railroad–river corridor; however, 2 males

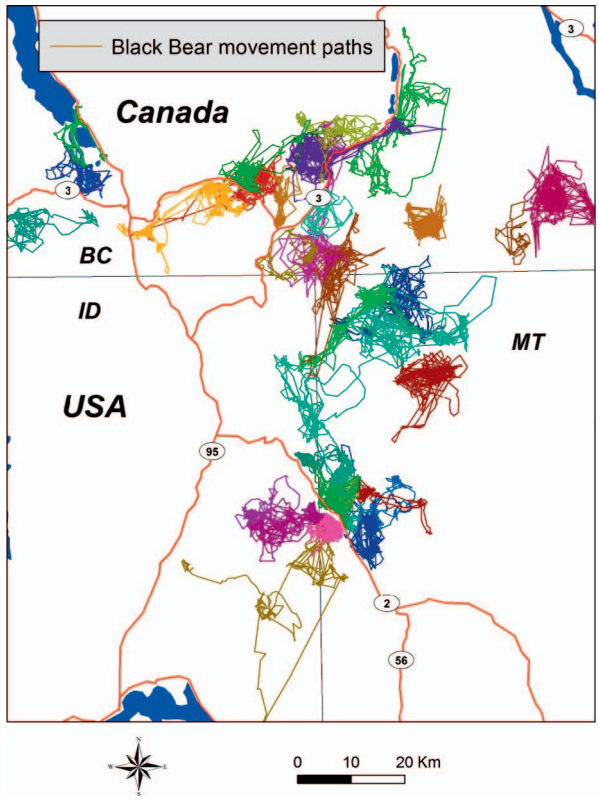

Fig. 5. Global Positioning System telemetry-derived movement paths for American black bears (*Ursus americanus*) along U.S. Highway 2 in northwestern Montana, USA, and BC Highway 3 in southeastern British Columbia, Canada, radiocollared between 2005 and 2010. Each line color connects sequential locations of individual bears. No radiocollared bear crossed the Highway 2 corridor (although 2 crossed the highway, but not the railroad and river in the valley bottom), whereas 6 crossed the BC Highway 3 corridor.

crossed the highway but not the railroad and river in the valley bottom (Fig. 5; Table 3). Collars stayed active on Highway 2 bears on average 121 days, yielding on average 1,540 locations/bear. Of the 18 collared bears (17M, 1F) in the BC Highway 3 area, 6 males crossed that highway–railroad–river corridor (Fig. 5; Table 3). Collars were active 143 days on average, delivering 1,458 locations/bear on average.

Discussion

Our results suggest that dispersal across these highway–railway–river corridors was less than expected, but not completely absent. We found the black bear population around U.S. Highway 2 corridor was more fragmented than the population traversed by BC Highway 3, as measured by both genetic and telemetry data sets. This pattern was consistent with the levels of grizzly bear fragmentation across these 2 highway systems, where the Cabinet Mountain grizzly bears south of U.S. Highway 2 were completely isolated from the Yaak population (Proctor et al. 2012b) and males still occasionally crossed BC Highway 3 in the Purcell Mountains (Proctor et al. 2005, 2012b). The fragmentation of grizzly bears in these systems creates a greater conservation risk because it results in a small number of grizzly bears in the Yaak separated from a small number of grizzlies in the Cabinets. In contrast, black bears have a lower conservation risk because the black bear population sizes were an order of magnitude larger than the grizzly population in these fragmented areas. Estimates of abundance in the U.S. Cabinet population range between 600 and 900 black bears (210/1,000 km^2, Mace and Chilton-Radandt 2011) and 22–24 grizzly bears (Kasworm et al. 2014; 95% CI = 20–30 or 3.8/1,000 km^2, Kendall et al. 2016). The U.S. Yaak area potentially contains approximately 650–850 black bears (150/1,000 km^2, Mace and Chilton-Radandt 2011) and only 18–22 grizzly bears (Kasworm et al. 2014; 95% CI = 15–23 or 5.5/1,000 km^2, Kendall et al. 2016).

Applying these densities, we estimated that our survey area in the Canadian portion of the Yahk contained approximately 351 (95% CI = 243–504) black bears (130 black bears/1,000 km^2). Conversely, Proctor et al. (2007) estimated that the area supports approximately 20 (95% CI = 16–24) grizzly bears (7 grizzly bears/1,000 km^2). In the area north of BC Highway 3 in the Purcell Mountains, our estimated black bear density was 226 bears/1,000 km^2 and the grizzly bear density was estimated at 14 bears/1,000 km^2 (Proctor et al. 2007). So although the fragmentation we report here may not reveal an urgent conservation threat to black bears (due to the large population sizes), it does corroborate fragmentation reported for grizzly bears and suggests that other mammal species may be also experiencing population-level fragmentation from these highway settlement corridors in this mountainous ecosystem. Also, whereas there have been no extensive explorations of black bear fragmentation at the regional scale, we assumed that black bears in this study are part of regionally contiguous occupied habitat.

Ideally, wildlife and land use managers make management decisions at the ecosystem and regional scale informed with multispecies data. We realize this is a challenge because of the paucity of fragmentation studies for

many species. Our results add another large carnivore species to the short list of species for which we have fragmentation data in our study region. We also used data that were collected for grizzly bear surveys to yield an analysis of black bear fragmentation, demonstrating the potential value of data collected inadvertently.

Our results only hint at what might be the causes of black bear fragmentation. Proctor et al. (2012b) demonstrated an association between fragmentation of grizzly bear populations and patterns of human settlement, human-caused mortality along highway corridors, and vehicle traffic volume. It is logical that these same factors contributed to partial fragmentation of black bears in our study area. Black bear conflicts with people result in many dead black bears, and black bears are involved in the vast majority of bear-related conflicts in our study area (Province of British Columbia 2001, Annis 2013). Interestingly, summer traffic volumes on U.S. Highway 2 (2,000–2,500 vpd) are less than those on BC Highway 3 (4,300 vpd), yet fewer black bears cross Highway 2 than Highway 3. Both highways have few settlements and a railroad running parallel along their length. However, the railroad paralleling Highway 2 has twice as much train traffic as the railroad along Highway 3 (35 trains/day along Hwy 2 vs. 16/day along Hwy 3). In addition, much of the train traffic along Highway 2 is at night, when black bear and grizzly bear movements are more likely (Waller and Servheen 2005). Large amounts of train traffic were demonstrated to be a significant mortality risk factor for grizzly bears in a study of a similar combined Highway 2 and train corridor approximately 200 km east of our study area (Waller 2005, Waller and Servheen 2005). The same level and timing of train traffic reported by Waller and Servheen (2005) also occurs in our study area. Another difference between Highway 3 and Highway 2 is that Highway 2 also has the relatively large Kootenay River along much of its length. In addition to the highway traffic and human settlements affecting both corridors, we speculate that the larger amount of rail traffic and the presence of the Kootenay River may combine to impede black bear dispersal more in the Highway 2 region than in Highway 3. The topography of the study area has minor differences in ruggedness, but we found no evidence that ruggedness influenced bear movements in our telemetry data. The valley bottoms that bears are not crossing are the most mellow and easiest to traverse.

Although there have been several efforts to identify black bear crossing locations or corridors across major highways regionally, few have documented fragmentation of black bear populations or causes of fragmentation. Cushman et al. (2006) explored landscape resistance to potential barriers to gene flow and investigated connectivity routes (Cushman et al. 2008, 2013), but did not report fragmentation of black bear populations. Our results do not conform to those found by Cushman et al. (2006), who found no fragmentation across a larger settled adjacent valley with a highway and larger river, but with no railroad. Lewis et al. (2011) predicted crossing locations for black bears along one highway in northern Idaho near our study area, but provided no evidence for fragmentation. Using telemetry, Serrouya (1999) found that black bears crossed a major highway–railway–river corridor (similar to U.S. Highway 2) less than expected in Banff National Park, Alberta, Canada. Their highway had approximately 15,000 vpd in summer and 30–35 trains/day, but almost no human settlement, except for the town of Banff, which is a tightly contained settlement of approximately 7,500 inhabitants within the national park. Dixon et al. (2006) demonstrated population fragmentation in the black bears in Florida, USA, between populations separated by 50–300 km of unoccupied habitat, where significant genetic differentiation existed, allowing the effective use of genetic distance and individual-based assignment tests. McCoy (2005) found that age cohort, sex, and level of conditioning to human foods influenced highway crossing-rate variation of black bears in western Montana. Food-conditioned bears, adult females, and subadult males crossed more often than male or non–food-conditioned bears, but higher crossing rates were accompanied by an increase in mortality risk. McCoy (2005) found that highways partially fragmented populations of non–food-conditioned bears, but not those that were food-conditioned.

Although we could not determine the exact sex ratio of our migrant sample, our results suggest that it was likely male-biased. This result was not unexpected because black bears are known to have male-biased dispersal (Costello et al. 2008, Costello 2010, Moore et al. 2014, Vitale et al. 2018). Several researchers have reported dispersal among a small portion of female black bears (Costello et al. 2008, Moore et al. 2014). The tendency for female black bears to display philopatry, or very limited dispersal (Costello 2010, Vitale et al. 2018), reduces our expectation that female bears would disperse across human-settled valleys with major highways.

Here we focused on individual-based methods to assess fragmentation of black bears in northwestern Montana and southeastern British Columbia. Following the fates of individuals allows inferences to current ecological conditions and potential conservation issues. It also provides a measure of 'direct' evidence between the metric and

the inference, as opposed to less direct measures based on deviations in Hardy–Weinberg Equilibrium, linkage equilibrium, or *F*-statistics. In reality, bear populations are not likely to show perfect random mating or perfect linkage equilibrium. Therefore, it might be a challenge to make inferences based on nuances of these metrics, which might also reflect imperfect power of these tests. Therefore, we wanted to use more direct methods of inference that were more closely linked to following the fates of individuals. Nonetheless, there are promising techniques using linkage disequilibrium to estimate effective population size (N_e). In recent examples, simulations demonstrated relatively accurate detection of early fragmentation into smaller units (England et al. 2010), and the re-establishment of connectivity in a recovering system (Kopatz et al. 2017). This method may not be well-suited to our study area because the populations of bears on each side of our studied fractures are rather large (see above). Another method of detecting fine-scale structure (or fragmentation) and their driving landscape variables involves the use of spatial autocorrelation (similarity in pairwise genetic distance) and landscape genetic analyses. This method relates genetic similarity to resistance surfaces of correlated landscape variables (Coster and Kovach 2012). Our analysis did not provide fine-scale 'explanatory' insights, although the highway settlement corridors are certainly implicated as causes of the fragmentation.

The use of pedigrees to assess population fragmentation offers a unique view into spatial structure in systems with no or very little genetic differentiation. Its value is that it renders fragmentation detectable if there has been insufficient time for, or when the rate of ongoing movements is sufficient to prevent, the development of genetic differentiation, which can provide early warning of population fragmentation (Paetkau et al. 2004). It is the lack of gene flow over time that allows fragmentation of a population (using an evolutionary definition that includes interbreeding individuals in time and space) to be detected. In the initial stages of human-caused fragmentation, these genetic signals may not be developed enough to allow measurement using measures that relate to gene flow.

One challenge in using pedigrees is the need to identify a sufficient number of first-order relatives to allow patterns to be detected. In large populations, many individuals are not closely related; therefore, one needs a reasonably large sample size to detect an adequate sample of first-order relatives. For example, in the evolution of this study, we originally sampled 50 individuals on each side of our 2 highway systems. Although our results were similar, the sample sizes were too small to provide confidence. We subsequently doubled our sample size to include approximately 100 animals on each side of our 2 highways and that increased the number of detectable relatives considerably, from 36 to 104 first-order relatives, improving the quality of our inferences at the population level. Use of pedigrees for ecological inference is increasing as genetic tools become more accessible and common, and have been used in a variety of studies including dispersal (Moore et al. 2014), kin-related social structure (Støen et al. 2005), habitat connectivity (Hogg et al. 2006, Kanno et al. 2014, Proctor et al. 2018), and to assess the genetic viability of a reintroduced species (Vonholdt et al. 2008).

All parent–offspring pairs we identified, including those high-confidence relationships in perfectly matched genotype triads and others that shared ≥1 allele at all loci, had *r* values ≥0.5. Therefore, our use of $r \geq 0.4$ for a full sibling threshold also identified parent–offspring relationships.

In the context of identifying first-order relatives that were captured on opposite sides of our target highways, both parent–offspring and full siblings are functionally equivalent because each would constitute a movement across a highway corridor away from their birth area. One value of using genetic samples to assess dispersal events is that they can detect events over a longer timeframe than 1 or 2 seasons of telemetry, as well as often sampling a larger number of animals through remote genetic sampling, as we employed. Furthermore, movement is not always associated with breeding, so movements detected through telemetry do not always reflect gene flow and both techniques can miss dispersal events.

PARANTE (Cercueil et al. 2002) assumes that sample areas are in Hardy–Weinberg and linkage equilibrium, which all our sample areas were, and that alleles are identical by descent. We used PARANTE to identify allele sharing patterns within familial triads (mother–father–offspring) or dyads (parent–offspring or siblings). We did not rely on the probabilities generated that are reliant on the above-mentioned assumptions. Rather, we used ML-Relate (Kalinowski et al. 2006) to estimate probabilities of relatedness of dyads with the relevant allele sharing patterns determined through PARANTE. ML-Relate assumes that individuals are not inbred, and that a population is closed (i.e., migrants with different allele frequencies are not entering the system). We have reasonable confidence that the individuals in our study were not likely inbred because they are part of populations in a large continuous geographic area with hundreds of individuals and black bears have sex-biased dispersal, evolved to reduce risk of inbreeding (Costello et al. 2008). These

populations are not closed, but part of a larger population with individuals with similar allele frequencies, not immigrants from a distinct population. By far the most likely potential for errors in these analyses are from genotyping errors. Realizing this potential, we applied the extra effort to assess close genotypes (rerun until errors are resolved; Paetkau 2003) not only for individual identification, but for all individuals that were genetically close to being in family relationships.

We envision future efforts to use pedigrees and family relationships to identify new interpopulation migrants in populations that are managed for connectivity, particularly after a period of anthropogenic fragmentation (Proctor et al. 2018). Pedigrees would be particularly useful in documenting gene flow (genetic connectivity) and even demographic rescue (demographic connectivity) by detecting breeding events after immigration into a beleaguered, fragmented, or previously isolated population (Proctor et al. 2018).

Concluding remarks

Our results identify pedigree analysis as another tool for investigating population fragmentation, particularly in situations where genetic signals of differentiation are too weak to determine migration rates using individual-based methods, such as population assignment. Our results also demonstrated that other large carnivores besides grizzly bears are being fragmented by transportation–settlement corridors in the Canada–United States transborder region of western North America. In that regard, we found that neither highway system we studied was causing complete fragmentation. Variation existed in the level of black bear population fragmentation between our 2 highway systems; Highway 2 in northwestern Montana was more fragmented than Highway 3 in southern British Columbia.

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Supplemental material

1. Spatial capture–recapture population estimate of Canadian black bears (*Ursus americanus*)

2. Expected and observed heterozygosity of black bear loci north and south of U.S. Hwy 2 and BC Highway 3