Population genetics of American black bears in Georgia, USA

Michael J. Hooker[1,3], Bobby T. Bond[2], and Michael J. Chamberlain[1]

[1]*Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602, USA*
[2]*Georgia Department of Natural Resources, Wildlife Resources Division, Fort Valley, GA 31030, USA*

Abstract: There are 3 American black bear (*Ursus americanus*) populations in the state of Georgia, USA. We used multi-locus microsatellite genotypes derived from bear hair and tissue samples collected across these populations to assess levels of genetic diversity within and between populations. We used population assignment clustering to evaluate whether there has been recent immigration into the smallest of the 3 populations, the Central Georgia Bear Population. Compared with other bear populations in the United States, the North Georgia and South Georgia Bear Populations have relatively high rates of genetic diversity ($H_o = 0.72 \pm 0.02$, $A = 6.68 \pm 0.32$, and $H_o = 0.72 \pm 0.02$, $A = 6.82 \pm 0.35$, respectively). In contrast, the Central Georgia Bear Population has relatively low rates ($H_o = 0.46 \pm 0.03$, and $A = 3.96 \pm 0.20$). Fixation indices for pairings between Georgia bear populations indicated that the North Georgia Bear Population was more similar to the South Georgia Bear Population than either was to the Central Georgia Bear Population. Our findings suggest that the Central Georgia Bear population has experienced long-term genetic isolation and genetic drift. Of a sample of 365 bears from Central Georgia, we only detected 1 immigrant and no evidence of gene flow into the population. We recommend development and implementation of plans to encourage gene flow toward the Central Georgia Bear Population.

Key words: American black bear, genetic structure, Georgia, microsatellite, *Ursus americanus*

DOI: 10.2192/URSUS-D-18-00025.1 ***Ursus 29(2):134–146 (2019)***

Historically, American black bears (*Ursus americanus;* hereafter, black bears) were widely distributed across forested portions of North America (Pelton 2003). More recently, the range of the black bear receded to <70% of its historical extent (Pelton and van Manen 1994, Scheick and McCown 2014). Overharvest, persecution, and habitat alteration caused this reduction in bear abundance and distribution, especially in the southeastern United States (Pelton 2001). Maehr (1984) estimated that bears inhabited only 10% of their historical range in the Southeast as a result of habitat loss and historical overexploitation. A 1970 regional estimate of bear numbers across 11 southeastern states totaled <4,000 animals, with 4 of 11 states reporting <100 bears each (Pelton and Nichols 1972).

Concomitant with reduced bear abundance and range reductions in the Southeast was fragmentation of once contiguous bear populations into smaller ones. These populations became geographically isolated because of habitat fragmentation, habitat loss, and frustrated movements between populations (Pelton 1990, Hellgren and Maehr 1992). Habitat fragmentation, habitat loss, and geographic isolation of populations can cause reduced genetic diversity within populations (Sherwin and Moritz 2000), reduced (or eliminated) gene flow between populations (Vos et al. 2001), and ultimately lead to increased probability of extinction (Saccheri et al. 1998). Habitat fragmentation can frustrate movements and dispersal, contribute to lower abundance, and reduce population viability (Davies et al. 2001, Frankham et al. 2002). Moreover, habitat fragmentation can contribute to genetic isolation and declines in genetic diversity (Dixon et al. 2007). Loss of genetic diversity can be especially problematic for large carnivores because of their relatively low numbers, slow reproductive rates, and propensity to create conflicts with humans while attempting to move between habitat patches (Wayne et al. 1991, Roelke et al. 1993, Dunbar et al. 1996, Noss et al. 1996, Crooks 2002, Räikkönen et al. 2009).

The State of Georgia, USA, contains 3 bear populations representing 2 of the southeastern American black bear subspecies (Fig. 1; Hall 1981). The North Georgia Bear Population (NGP) and the Central Georgia Bear Population (CGP) are considered to be American black bear (*Ursus americanus americanus*), whereas the South Georgia

[3]email: hookerm@uga.edu

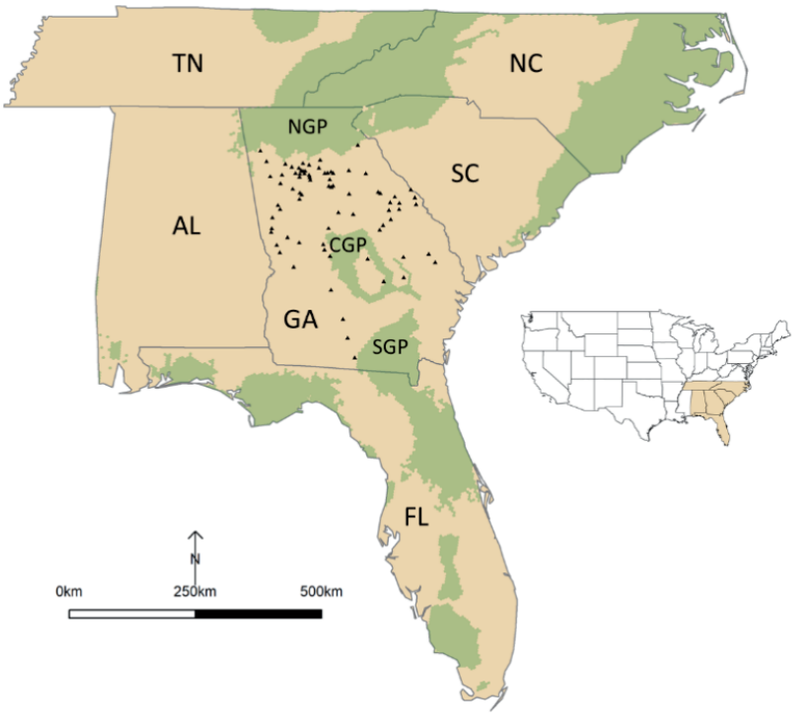

Fig. 1. Map of the state of Georgia (GA) and neighboring states of Alabama (AL), Florida (FL), North Carolina (NC), South Carolina (SC), and Tennessee (TN), with American black bear (*Ursus americanus*) distribution (green shading) and incidental, inter-population observations of bears (black triangles) between Georgia's 3 bear populations—the North Georgia Bear Population (NGP), Central Georgia Bear Population (CGP), and South Georgia Bear Population (SGP)— in Georgia, USA, 2006–2017. Bear distribution and observation data are modified and updated from Scheick et al. (2011) and Scheick and McCown (2014).

Bear Population (SGP) is considered to be the Florida black bear (*U. a. floridanus*). Collectively, these populations comprise roughly 5,100 bears, with the NGP being the most abundant and the CGP being the least abundant (Georgia Department of Natural Resources 2010, Hooker et al. 2015). Bears in the NGP occur in the northern counties of Georgia from the Georgia–Tennessee state line southward toward the suburbs north of Atlanta, and the Interstate-85 corridor between Atlanta and Greenville, South Carolina. The CGP is restricted primarily to 5 counties along the Ocmulgee River in Central Georgia southeast of Macon. The SGP is located in the south-central counties of Georgia along the Georgia–Florida state line, and is associated with the Okefenokee Swamp. The NGP is contiguous with the bear population in the mountains of southeastern Tennessee and western North and South Carolina. The SGP is contiguous with the Osceola bear population in northern Florida (Dobey et al. 2005). Conversely, the CGP has been considered demographically and genetically isolated from other bear populations in the recent past (Miller 1995, Sanderlin et al. 2009). Relatively low abundance and potential isolation from other bear populations makes conservation of the CGP of special concern (Hooker et al. 2015). Although there appears to be poor connectivity between bear populations in Georgia, reports of bears in areas between the NGP and CGP, or the CGP and the SGP, are seemingly increasing (see incidental, inter-population observations, black triangles in Fig. 1), necessitating research to evaluate levels of demographic and genetic separation among the 3 Georgia bear populations. Our objectives were to use microsatellite markers to assess genetic variation within and among the NGP, CGP, and SGP, and to determine whether there was evidence of gene flow into the CGP.

Study area

We conducted research in all 3 bear populations in Georgia. The NGP occurred in northern Georgia, and was a trans-border population with North Carolina, South

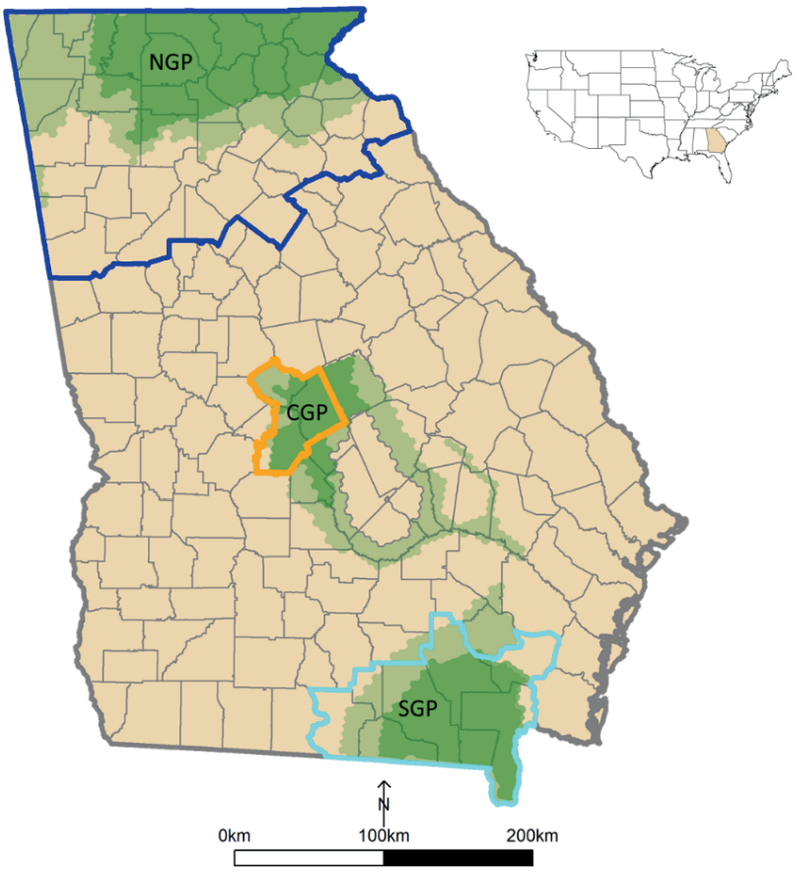

Fig. 2. State of Georgia counties with primary (dark green) and secondary (light green) ranges of the North Georgia Bear Population (NGP), Central Georgia Bear Population (CGP), and South Georgia Bear Population (SGP), and 3 Georgia bear hunting zones—the North Bear Zone (blue), the Central Bear Zone (orange), and the South Bear Zone (turquoise)—in Georgia, USA, 2006–2017. American black bear (*Ursus americanus*) distribution data from Scheick et al. (2011) and Scheick and McCown (2014).

Carolina, and Tennessee. The NGP was separated from the CGP by the city of Atlanta, and the considerable urban sprawl associated with the city. The CGP was separated from the NGP and SGP by >150 km, and was essentially restricted to 5 counties southeast of Macon, whereas the SGP was a trans-border population with Florida. Some of our samples were collected from hunter-harvested bears, especially those from the NGP and SGP; therefore, we placed emphasis on counties within Georgia's 3 bear-hunting zones (Fig. 2). These zones included 49 counties and encompassed most of the area within Georgia known to be occupied by bears.

The North Bear Zone (NBZ, 31,654 km^2), the largest of the 3 bear-hunt zones, consisted of Carroll, Fulton, DeKalb, Gwinnett, Walton, Barrow, Jackson, Madison, Hart, and all Georgia counties north of these. The South Bear Zone (SBZ, 10,442 km^2) included Brantley, Charlton, Clinch, Echols, Lanier, Lowndes, and Ware counties. The smallest zone, the Central Bear Zone (CBZ, 2,555 km^2), consisted of Bibb, Houston, and Twiggs counties. Adjacent to the CBZ were Bleckley and Pulaski counties, which were not within the bear hunt zone but were part of non-invasive sampling activities (see Methods) and location of several road-killed bears used in our analysis.

The NBZ encompassed extremes in terms of terrain, remoteness, and both human and bear densities. Many of the counties in the northeastern portion of the NBZ were mountainous, sparsely populated with humans, and had relatively high bear densities. These counties contained

large tracts of federally and state-owned forest land, some of which were roadless wilderness. Conversely, the southwestern portion of the NBZ contained metropolitan Atlanta (pop. 5,710,795 U.S. Census Bureau 2015). The NBZ contained portions of 4 physiographic provinces: Appalachian Plateau, Blue Ridge, Piedmont, and Valley and Ridge (Usery 2016).

The CBZ was in the Ocmulgee River drainage at the Fall Line, the boundary of the Piedmont and Coastal Plain physiographic provinces (Usery 2016). Predominant forest types in the CBZ were bottomland hardwood forests within the Ocmulgee River flood plain, and planted pine (*Pinus* spp.), natural pine, and mixed pine–hardwood in the uplands. Most forest land in the CBZ was privately owned and managed for timber production. Within this 3-county zone there was considerable difference among counties in terms of human density. Bibb County contained the city of Macon (pop. 91,234) and was estimated to contain 153,721 people, whereas neighboring Twiggs County had <9,000 residents (U.S. Census Bureau 2015).

The SBZ was in the lower Coastal Plain physiographic province (Usery 2016) along the Florida–Georgia boundary in the area of Okefenokee Swamp and Okefenokee National Wildlife Refuge. Okefenokee Swamp was one of the largest freshwater swamps in the United States and was typified by bay (e.g., loblolly-bay [*Gordonia lasianthus*], swamp-bay [*Persea palustris*], sweet-bay [*Magnolia virginiana*], black gum [*Nyssa sylvatica*], and cypress [*Taxodium* spp.]) forests. Private lands surrounding Okefenokee Swamp were predominantly managed slash pine (*Pinus elliottii*) forest, with low human population densities.

Methods

Sample collection

During 2012–2017, we collected samples from which DNA could be extracted (e.g., hair, tissue, and blood) from bears using a variety of methods. Within the CGP we used non-invasive sampling with hair snares (Woods et al. 1999, Sylvest 2014, Hooker et al. 2015), live capture of bears using modified Aldrich foot snares (Johnson and Pelton 1980), hunter-harvested bears, and investigations of vehicle–bear collisions and other bear mortalities. In North and South Georgia, we relied primarily on hunter-harvested bears as a source of samples. We collected samples from areas outside the 3 Georgia bear populations from road-killed bears or from bears being handled by Georgia Department of Natural Resources personnel as part of management actions. Our capture and handling methods were approved by the University of Georgia Institutional Animal Care and Use Committee (Protocol Number A2011 10-004-A1).

We placed all samples collected in central Georgia in #1 paper coin envelopes and stored them in a climate-controlled environment at room temperature. We checked hair snares on a weekly basis and, therefore, samples from hair snares had ≤7 days of environmental exposure before collection. We held tissue samples or blood swabs (i.e., samples with high moisture content) out of storage with other samples until samples were thoroughly desiccated. We collected samples from the NGP and SGP using TypiFix™ (IDnostics AG, Schlieren, Switzerland) single-use tissue sample collectors. As above, we inventoried these samples and stored them at room temperature. We then forwarded all samples to Wildlife Genetics International (Nelson, British Columbia, Canada) for DNA extraction and microsatellite genotyping.

We extracted DNA from samples using QIAGEN's DNeasy Tissue kits, and amplified specific microsatellite loci using polymerase chain reaction. Detailed descriptions of laboratory methods used for our study have been previously described by Paetkau and Strobeck (1994, 1998) and Paetkau (2003, 2004). We genotyped all individuals sampled within the NBZ and SBZ, and samples from counties outside the bear hunt zones, for 22 microsatellite loci: CPH9, CXX20, CXX110, D1A, D123, G1A, G1D, G10B, G10C, G10H, G10J, G10L, G10M, G10P, G10U, G10X, MU23, MU50, MU59, MSUT-2, REN144 A06, and REN145 P07 (Paetkau and Strobeck 1994, Paetkau et al. 1995, Taberlet et al. 1997, Kitahara et al. 2000, Breen et al. 2001) and an amelogenin sex marker (Ennis and Gallagher 1994). We treated samples from the CBZ the same as above, but we analyzed only a subset of all CBZ samples at all 22 loci. Further error checking and quality control used in our study are described by Paetkau (2003).

Analysis

We tested for deviations from expected values of Hardy–Weinberg equilibrium using Program Genepop 4.5.1 (Raymond and Rousset 1995). We computed exact *P*-values using complete enumeration for loci with <4 alleles (Louis and Dempster 1987); otherwise, we used the Markov chain method (de-memorization 10,000, batches 20, iterations per batch 5,000 [Guo and Thompson 1992]). We also tested for linkage disequilibrium and nonrandom associations between alleles at different loci within populations using Markov chain methods (de-memorization 10,000, batches 200, iterations per batch 10,000 [Guo and Thompson 1992]), and again adjusted *P*-values for multiple comparisons using Bonferroni correction (Rice 1989).

As measures of genetic variation within each population, we calculated observed mean heterozygosity (H_o), expected mean heterozygosity (H_e), and mean number of alleles at each locus (A). We calculated genetic distance between all populations (global F_{st}) and between paired populations (pairwise F_{st}; Weir and Cockerham 1984).

To assess potential inter- and intra-population genetic structure, we initially conducted a factorial correspondence analysis (FCA) implemented in Program GENETIX 4.05 (Benzecri 1992, Belkhir 1999). The FCA involves no a priori assumptions regarding sampling location or population of origin for individuals, but rather, groups like individuals on multiple factorial axes (i.e., in multidimensional space) based on shared alleles (Haroldson et al. 2010). To reduce dimensionality, we plotted the first 2 dimensions of this data space in 2-dimension scatterplots, and visually inspected the plots for evidence of clustering relative to sampling location and known population of origin. We then used the results of FCA analyses to inform our structuring of data sets for subsequent analyses.

We used the population assignment test within Program STRUCTURE 2.3.4 to determine likely number of clusters (i.e., populations; K) within our data set of 10-locus genotypes based on allele frequencies (Pritchard et al. 2000). We used the 'admixture model' without the LOCPRIOR option. The LOCPRIOR option allows sampling location information to aid the clustering algorithm in cases with weak structure signals by assuming that animals sampled from like locations are more likely to share common ancestry (Porras-Hurtado et al. 2013). However, results of our FCA analysis indicated that structure signals between the 3 Georgia bear populations were not weak. Assuming that all 3 Georgia bear populations were historically part of a contiguous bear population, we used the correlated allele frequency model. We used a 100,000-step Markov-chain Monte Carlo (MCMC) for 20 runs following a 10,000-step burn-in to consider scenarios in which K ranged from a minimum of 1 to a maximum of 6 (i.e., our assumed no. of populations plus 3; [Evanno et al. 2005]). To mitigate issues of inherent stochasticity among the 20 MCMC runs (e.g., label-switching or multimodality [Stephens 2000, Jasra et al. 2005]) we used Program CLUMPP 1.1.2 (Jakobsson and Rosenberg 2007) implemented through the 'main pipeline' of CLUMPAK (Kopelman et al. 2015) to align and find agreement among results of the 20 runs. To determine the most appropriate value of K for our data, across $K = 1$–6, we used CLUMPAK to calculate and plot both the log probability of our data, $\ln \Pr(X \mid K)$ as suggested by Pritchard et al. (2000) and ΔK, the rate of change of K using the method of Evanno et al. (2005) across $K = 2$–5.

We were specifically interested in detection of immigrants, or offspring of immigrants, within the CGP; therefore, we used the USEPOPINFO model in STRUCTURE 2.3.4 to analyze our data set (Pritchard et al. 2000). Within the USEPOPINFO model, it is possible to indicate the number of generations back within which to consider (GENSBACK) where GENSBACK = 0 represents an individual being a migrant and GENSBACK = 1 indicates an individual is the offspring of a migrant parent and so on. We limited our analysis to a maximum of GENSBACK = 3 because of the decreasing power to detect immigrants as GENSBACK increases (Pritchard et al. 2000). We ran models with $v = 0.05$, where v is the probability that an individual is an immigrant to the population from which it was sampled, or has some level of immigrant ancestry, and $1 - v$ is the probability the individual is purely from the population from which it was sampled (Pritchard et al. 2000). We used a 100,000-step MCMC for 20 runs following a 10,000-step burn-in, and based on the results of the above clustering analysis, limited the number of clusters considered to $K = 3$ (i.e., 1 cluster representing each of the 3 Georgia bear populations).

Results

From 2012 through 2017, we developed microsatellite genotypes for 507 individual black bears. Based on sample collection location, the NGP, CGP, and SGP yielded 84, 362, and 54 genotypes, respectively (Fig. 3a). We derived the remaining 7 genotypes from samples collected outside any of the 3 Georgia bear populations. Of these 7, we derived 2 genotypes from samples collected along the southern periphery of the NGP, 1 from a sample collected on the western periphery of the CGP, and the remaining 4 from samples collected well outside the range of any of the 3 Georgia bear populations.

A plot of the 2 primary dimensions from a preliminary FCA of all 507 individuals genotyped at 10 common loci revealed 3 defined clusters corresponding to the genotypes derived from samples collected within each of the 3 populations (Fig. 3b). The 2 samples from the periphery of the NGP (male bears N15M and N16M) clustered with the NGP group. Two of the 4 samples collected well outside any population (male bears C42M and C60M) clustered with the CGP group and the remaining 2 (male bears C5M and C367M) clustered with the SGP group. The sample collected along the western periphery of the CGP (male bear C51M) clustered with the SGP. Subsequent FCA analyses considering populations

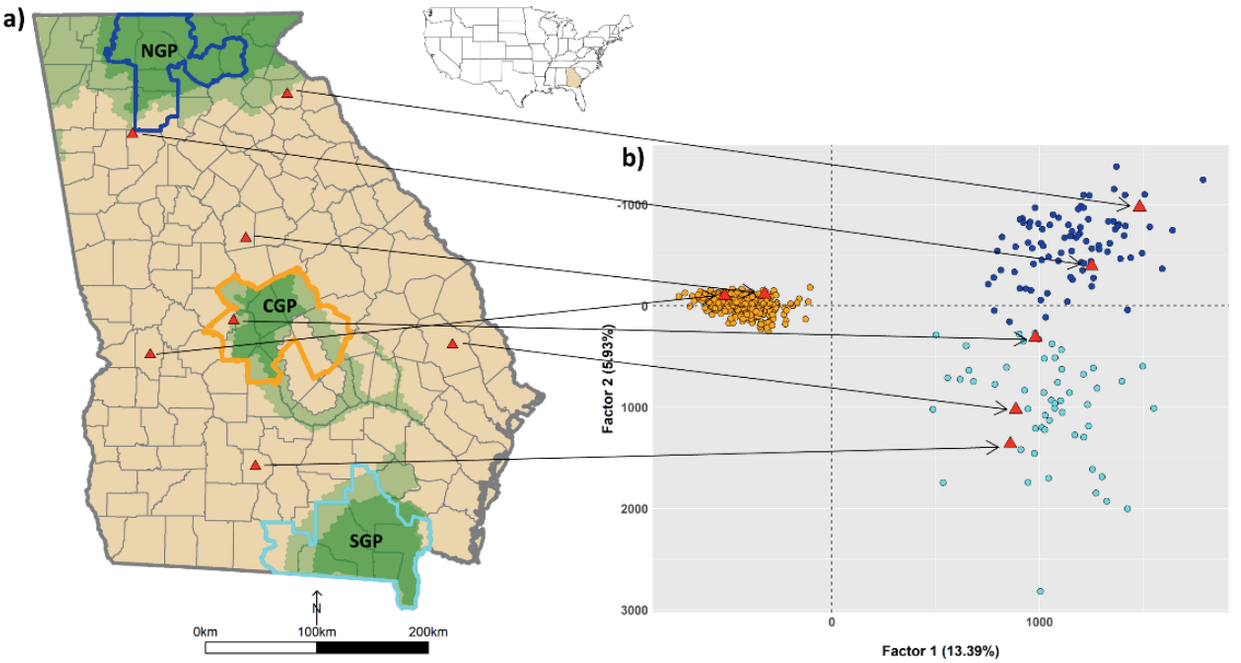

Fig. 3. (a) State of Georgia counties with primary (dark green) and secondary (light green) ranges of the North Georgia Bear Population (NGP), Central Georgia Bear Population (CGP), and South Georgia Bear Population (SGP); counties from which American black bear (*Ursus americanus*) genotypes were derived within the NGP (blue, $n = 84$), the CGP (orange, $n = 362$), and the SGP (turquoise, $n = 54$); and the locations of black bear genotypes that were sampled from outside known bear range (red triangles, $n = 7$) Georgia, USA, 2006–2017. Bear distribution data from Scheick et al. (2011) and Scheick and McCown (2014). (b) Factorial correspondence analysis of 507 American black bear, 10-locus, microsatellite genotypes derived from bears sampled within or between 3 Georgia, USA, bear populations: North Georgia Bear Population (NGP), Central Georgia Bear Population (CGP), and South Georgia Bear Populations (SGP), during 2012–2016. Parenthetical percentages are variance accounted for by respective factor.

individually confirmed the clustering of N15M and N16M with the NGP group and C42M and C60M with the CGP group. However, C51M was a strong outlier from the SGP group and both C5M and C367M were on the outer edge of the SGP cluster, indicating uniqueness relative to the other bears in the SGP (Fig. 4). Further investigation, conducted by Wildlife Genetics International personnel, into the possible population of origin of bears C51M, C5M, and C367M revealed that C51M was likely a bear from the Apalachicola Bear Population in North Florida, and bears C5M and C367M appeared to be crosses of SGP bears and bears from Florida bear populations (D. Paetkau, Wildlife Genetics International, personal communication [8 Jul 2016]).

We compiled 2 data sets based on the number of loci in the genotype of each individual. One data set consisted of individuals from the populations and genotyped at 22 loci. We used this data set to calculate population genetics statistics and compare the 3 Georgia bear populations. Not all individuals from the CGP were genotyped at 22 loci, so we compiled a second data set containing all individuals sharing 10 common loci in their genotype, 10 being the lowest number of loci used to identify individuals in the CGP. The probability of identity (PIsibs) for the 10-locus data sets for each of the 3 populations was 1.8×10^{-4}, 1.8×10^{-3}, and 1.7×10^{-4} for the NGP, CGP, and SGP, respectively. This represents a 1 in approximately 5,556, 1 in approximately 556, and 1 in approximately 5,882 probability of 2 related individuals sharing the same genotype at the same markers within the NGP, CGP, and SGP, respectively. We used our 10-locus data set to investigate the CGP for the presence of immigrants and evidence of gene flow in to the CGP.

After Bonferroni correction, 1 of 22 loci (4.5% [REN144 A06]) failed to adhere to assumptions of Hardy–Weinberg equilibrium within each of the Georgia

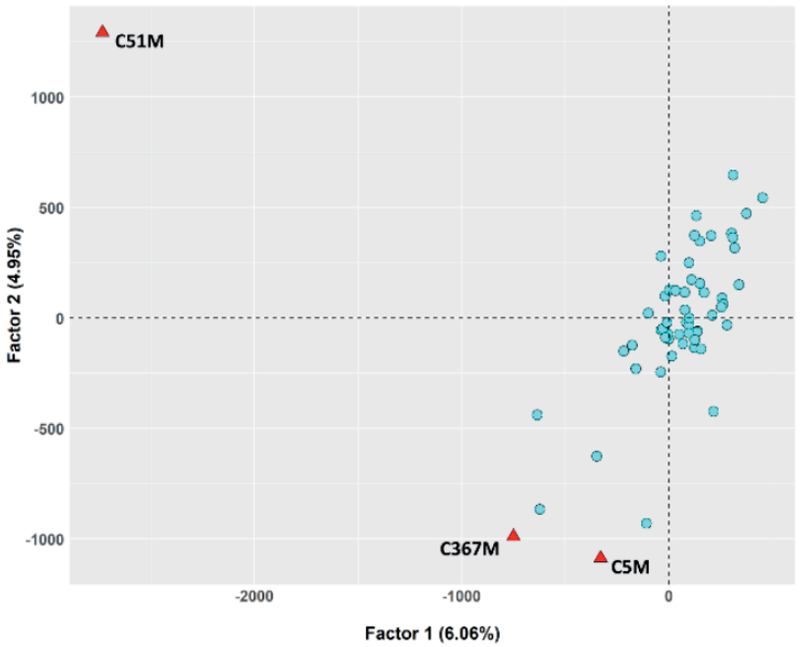

Fig. 4. Factorial correspondence analysis of American black bear (*Ursus americanus*) 10-locus, microsatellite genotypes derived from bears sampled within the South Georgia Bear Population (turquois circles, $n = 54$), and 3 bears sampled outside the South Georgia Bear Population (red triangles, $n = 3$) in Georgia, USA, during 2012–2017. Parenthetical percentages are variance accounted for by respective factor.

bear populations ($P < 0.05$). An additional 4 of 22 (18.2% [G10B, MU50, G10X, CPH9]) failed within the CGP. Our test for non-random loci pairings indicated no departures from randomness among all pairings within the SGP. Only 1 of 231 (0.4% [G10X-MSUT2]) loci pairings within the NGP failed the linkage disequilibrium test, whereas 5 of 231 (2.2% [CPH9-G10U, G10B-G10P, G10X-MSUT2, REN144 A-G10J, REN145 P07-CXX110]) failed within the CGP. The NGP and the SGP were similar in mean number of unique alleles per loci and heterozygosity levels, whereas the CGP was considerably lower than either of those populations (Table 1). The degree of genetic separation between the 3 GA bear populations (F_{st}) was greater between the CGP and either the NGP or the SGP, than between the NGP and the SGP, in spite of the NGP and SGP having the greatest geographic separation (Table 2). In estimating the most likely number of clusters (K) within our 10-locus data set, using the algorithm within Program STRUCTURE, there was agreement between the method of Pritchard et al. (2000) and the method of Evanno et al. (2005) that there were 2 clusters (Fig. 5). One cluster consisted solely of individuals from the CGP, and the second consisted of a combination of the NGP and SGP (Fig. 6).

The results of our testing the 10-locus data set for migrants, or descendants of migrants, within the 3 Georgia bear populations flagged only 1 bear (female C87F) as having a <1 probability of ancestry purely from the population from which she was sampled, the CGP. This female was estimated to have a 0.17 probability of full CGP ancestry in spite of having been sampled from within the CGP. Relative to the NGP and SGP, female C87F had

Table 1. Measure of genetic variation within 3 populations of American black bears (*Ursus americanus*) based on 196, 22-locus microsatellite genotypes including the mean number of alleles per locus (*A*), observed heterozygosity (H_o), expected heterozygosity (H_e), and number of genotypes (n), during 2012–2016, Georgia, USA.

Population	*A*	H_o	H_e	*n*
NGP[a]	6.68 ± 0.32	0.72 ± 0.02	0.73 ± 0.01	72
CGP[b]	3.96 ± 0.20	0.46 ± 0.03	0.47 ± 0.03	70
SGP[c]	6.82 ± 0.35	0.72 ± 0.02	0.71 ± 0.02	54

[a]North Georgia Bear Population.
[b]Central Georgia Bear Population.
[c]South Georgia Bear Population.

Table 2. Fixation index (F_{st}) between pairings of 3 American black bear (*Ursus americanus*) populations in Georgia, USA, during 2012–2016.

Population 1	Population 2	F_{st}	*P*
SGP[a]	NGP[b]	0.14	<0.01
SGP	CGP[c]	0.32	<0.01
NGP	CGP	0.28	<0.01

[a]South Georgia Bear Population.
[b]North Georgia Bear Population.
[c]Central Georgia Bear Population.

a 0.00 probability of being a migrant from either the NGP or SGP and a 0.05, 0.29, and 0.45 probability of being a first, second-, and third-generation descendant of a NGP bear, respectively.

Discussion

Population persistence is influenced by combinations of deterministic (e.g., habitat loss and overexploitation) and stochastic (e.g., demographic and genetic) factors (Shaffer 1981), and small populations tend to have decreased rates of persistence due to stochastic demographic processes (MacArthur and Wilson 1967, Shaffer 1987, Lande 1993). Furthermore, smaller populations are prone to negative impacts of stochastic genetic processes, such as fixation of deleterious alleles, genetic drift, and inbreeding depression (Mills 2012). These negative impacts come in 2 forms: reduced genetic diversity and inability to adapt to environmental change, and inbreeding with subsequent deleterious effects on survival and reproduction (Frankham et al. 2002, Keller and Waller 2002). Additionally, population persistence can be affected by a population's spatial juxtaposition (pattern) and functional relationship (process) to neighboring populations (Hanski 2005). Hellgren and Vaughan (1994) identified alleviation of negative demographic and genetic consequences caused by habitat loss and fragmentation as conservation and management priorities for southeastern bear populations.

We observed patterns of heterozygosity and allelic richness within the CGP suggestive of a genetic bottleneck and genetic drift, likely a function of low population abundance and isolation from neighboring bear populations (Nei et al. 1975, Frankham et al. 2002, Hooker et al. 2015). We recognize that comparing levels of genetic diversity across studies can be problematic

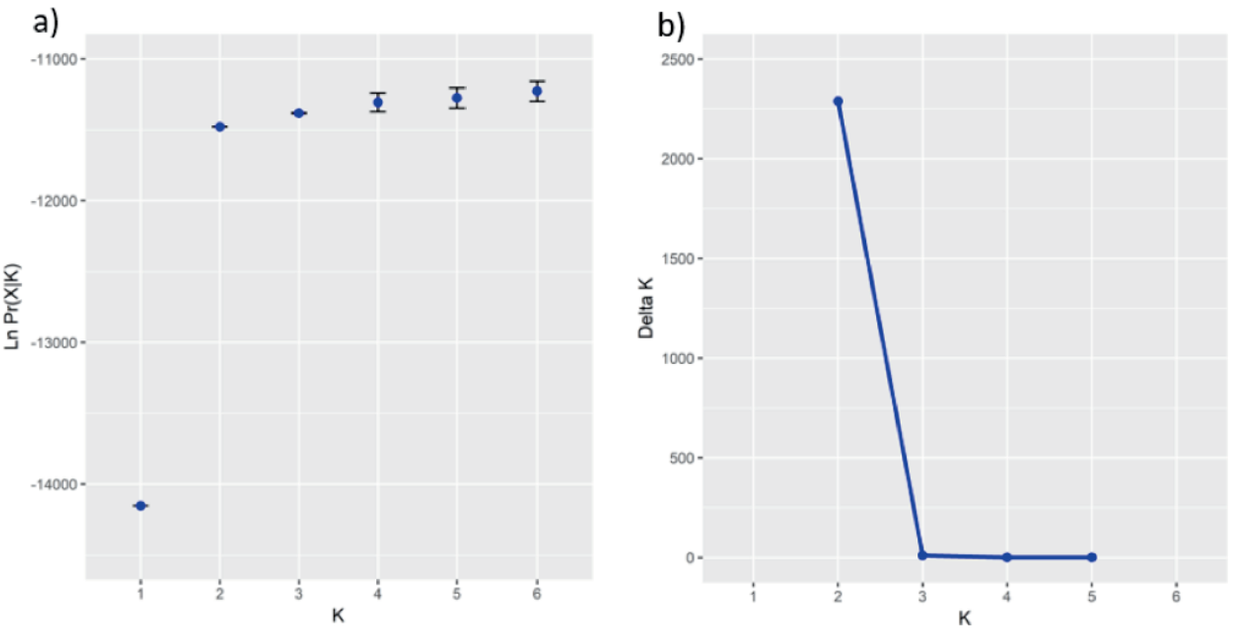

Fig. 5. The number of clusters (*K*) in a data set of 504 American black bear (*Ursus americanus*) 10-locus microsatellite genotypes (sampled from 3 populations in GA, USA, during 2012–2016) estimated by (a) the log probability of the data given *K* (mean of 20 iterations at each level of *K* ± standard deviation; Pritchard et al. 2000), and (b) the second-order rate of change in the likelihood function across levels of *K* (Δ*K*; Evanno et al. 2005).

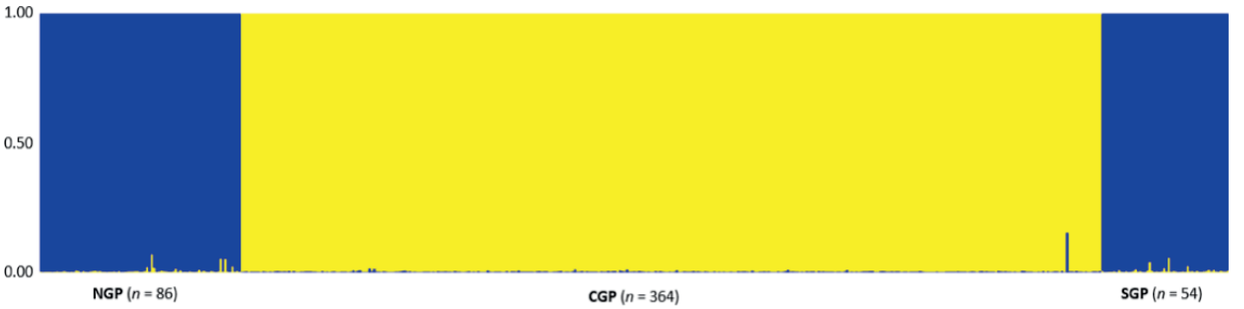

Fig. 6. Bar graph depicting cluster ($K = 2$) assignment of 504 American black bear (*Ursus americanus*) 10-locus microsatellite genotypes sampled from 3 Georgia, USA, populations—North Georgia Bear Population (NGP), Central Georgia Bear Population (CGP), and South Georgia Bear Populations (SGP)—during 2012–2016. Narrow vertical bars represent an individual bear. X-axis labels indicate population of origin, based on sampling location and factorial correspondence analysis, for individuals with sample size (*n*) in parenthesis. Y-axis and colors represent each bear's estimated proportion of membership in each of the 2 clusters.

because of variability in number of loci used, the specific loci used, and variability in mutation rates for loci (Conner and Hartl 2004). Nevertheless, previous studies using similar microsatellite markers to those in our study observed heterozygosity levels of >0.70 for American black bear populations in areas with expansive habitat and little impedance to gene flow (Paetkau and Strobeck 1998; Woods et al. 1999; Schwartz et al. 2006; Pelletier et al. 2012, 2017). Conversely, similar studies of American black bears from small, isolated populations reported heterozygosities of <0.50 (Boersen et al. 2003, Csiki et al. 2003, Brown et al. 2009, Clark et al. 2010, Hooker 2010, Lowe 2011, Troxler 2013, Pelletier et al. 2017), which places the CGP among the populations with the poorest values (Table 3; Dixon et al. 2007).

Out of a sample of 363 bears from within or along the periphery of the CGP, only 1 bear (C51M) was a migrant from outside the CGP, and 1 bear (C87F) displayed evidence of distant ancestry outside the CGP. The presence of C51M along the periphery of the CGP is encouraging because it demonstrates that immigration from outside bear populations into the CGP is possible. However, C51M was killed in a vehicle collision and, at 2 years of age, likely did not breed before dying, thus representing immigration but not gene flow.

Black bears exhibit inbreeding avoidance behavior, by which young males disperse from their natal area and young females tend to stay within or near their natal range (Alt 1978, Rogers 1987, Beck 1991, Schwartz and Franzmann 1992, Costello 2010). Black bears are capable of long-distance movements (Rogers 1987, Elowe and Dodge 1989, Beck 1991, Lee and Vaughan 2003) necessary for inter-population exchange among disjunct populations. Previous authors have noted that long-distance

Table 3. Genetic diversity metrics for American black bear populations in the southeastern United States with observed heterozygosity (H_o), expected heterozygosity (H_e), and mean number of alleles per loci (A).

Population (*n*)	H_o	H_e	A	State	Citation
South Georgia (54)	0.72	0.71	6.82	GA	This project
North Georgia (72)	0.72	0.73	6.68	GA	This project
Osceola (41)	0.71	0.71	6.67	FL	Dixon et al. 2007
Apalachicola (40)	0.69	0.71	5.92	FL	Dixon et al. 2007
St. Johns (40)	0.65	0.66	5.75	FL	Dixon et al. 2007
Big Cypress (41)	0.64	0.65	5.50	FL	Dixon et al. 2007
Eglin (40)	0.61	0.54	4.08	FL	Dixon et al. 2007
Ocala (40)	0.58	0.61	4.75	FL	Dixon et al. 2007
Aucilla (40)	0.57	0.59	5.00	FL	Dixon et al. 2007
Central Georgia (70)	0.46	0.47	3.96	GA	This project
Highlands/Glades (28)	0.33	0.38	2.75	FL	Dixon et al. 2007
Southwestern Alabama (19)	0.32	-	2.80	AL	Edwards 2002
Chassahowitzka (29)	0.29	0.27	2.25	FL	Dixon et al. 2007

movements may result following translocation events (Rogers 1973), whereas others have noted such movements may simply be associated with dispersal from natal ranges (Maehr et al. 1988, Stratman et al. 2001). Regardless, various factors contribute to infrequent and potentially unreliable interchange, such as habitat fragmentation, habitat loss, and anthropogenic activities such as highways and other infrastructure that degrade habitat (McCown et al. 2004, Latham et al. 2011). Collectively, these factors appear to be inhibiting gene flow into the CGP.

Management implications

Although the NGP and SGP are both potential sources of immigrants into the CGP, we only detected one recent immigrant (from neither the NGP nor the SGP) in the CGP, and no evidence of recent gene flow into the CGP. Given the level of genetic diversity we documented within the CGP, and the apparent continued genetic isolation between the CGP and surrounding bear populations, we encourage managers to consider options for the introduction of novel genetic material (i.e., bears from populations other than the CGP) into the CGP. This introduction of novel genetic material could be accomplished by corridor development and natural dispersal of bears, by translocation of bears into the CGP, or a combination. Translocations would likely result in the most rapid increase in gene flow into the CGP, and have been used to reestablish extirpated bear populations, augment existing populations, and create 'stepping-stone' populations between extant but demographically and genetically separate subpopulations in the southeastern United States (Eastridge and Clark 2001, Wear et al. 2005, Benson and Chamberlain 2007). In doing so, translocations facilitate genetic connectivity between otherwise isolated populations (Laufenberg and Clark 2014). We also caution against reduction of the CGP in the absence of efforts to alleviate the population's isolation. Reducing the population in its current state has potential to further erode its genetic diversity and make long-term conservation less tenable.

Acknowledgments

We appreciate funding provided by the Georgia Department of Natural Resources - Wildlife Resources Division, and the Warnell School of Forestry and Natural Resources at the University of Georgia. We are indebted to K. Kramer, R. Wood, R. Jones, T. Shover, A. Hammond, and G. Nelms (all of the Georgia Department of Natural Resources) for their logistic support within our Central Georgia study area and for collecting samples for this project in northern and southern Georgia. We extend the highest gratitude to D. Paetkau and the staff of Wildlife Genetics International for their diligent work processing samples and being tolerant of many issues. We thank Weyerhaeuser (formerly Plum Creek Timber Company, Inc.), for granting access to their forested land in Central Georgia. Specifically, we thank K. Cheynet of Plum Creek for assisting us with locating tracts of land in Central Georgia and for being patient during the process of defining our land access agreement. We are also indebted to many private land owners, too many to list individually. We thank A. Ashley, B. Bennett, R. Clark, M. Foster, J. Gentry, H. Glasko, C. Gray, M. Miller, E. Mitchell, J. Reese, J. Sylvest, and J. Wilson for their efforts conducting field work. Lastly, we extend our appreciation to the Associate Editor and anonymous reviewers for their constructive comments.

Literature cited

ALT, G.L. 1978. Dispersal patterns of black bears in northeastern Pennsylvania—A preliminary report. Proceedings of the Eastern Workshop on Black Bear Management and Research 4:186–199.

BECK, T.D.I. 1991. Black bears of west-central Colorado. Colorado Division of Wildlife Technical Publication 39, Fort Collins, Colorado, USA.

BELKHIR, K., P. BORSA, L. CHIKHI, N. RAUFASTE, AND F. BONHOMME. 1999. GENETIX 4.05, logiciel sous Windows TM pour la génétique des populations. Laboratoire Génome, Populations, Interactions, Université de Montpellier II, Montpellier, France. [In French.]

BENSON, J.F., AND M.J. CHAMBERLAIN. 2007. Space use, survival, movements, and reproduction of reintroduced Louisiana black bears. Journal of Wildlife Management 71:2393–2403.

BENZECRI, J.-P. 1992. Correspondence analysis handbook. Mercel Dekker, New York, New York, USA.

BOERSEN, M.R., J.D. CLARK, AND T.L. KING. 2003. Estimating black bear population density and genetic diversity at Tensas River, Louisiana using microsatellite DNA markers. Wildlife Society Bulletin 31:197–207.

BREEN, M., S. JOUQUAND, C. RENIER, C.S. MELLERSH, C. HITTE, N.G. HOLMES, A CHERON, N. SUTER, F. VIGNAUX, A.E. BRISTOW, C. PRIAT, E. MCCANN, C. ANDRE, S. BOUNDY, P. GITSHAM, R. THOMAS, W.L. BRIDGE, H.F. SPRIGGS, E.J. RYDER, A. CURSON, J. SAMPSON, E.A. OSTRANDER, M.M. BINNS, AND F. GALIBERT. 2001. Chromosome-specific single locus FISH probes allow anchorage of an 1,800 marker integrated radiation-hybrid/linkage map of the domestic dog (*Canis familiaris*) genome to all chromosomes. Genome Research 11: 1784–1796.

BROWN, S.K., J.M. HULL, D.R. UPDIKE, S.R. FAIN, AND H.B. ERNEST. 2009. Black bear population genetics in California: Signatures of population structure, competitive release, and historical translocation. Journal of Mammalogy 90: 1066–1074.

CLARK, J.D., R. EASTRIDGE, AND M.J. HOOKER. 2010. Effects of exploitation on black bear populations at White River National Wildlife Refuge. Journal of Wildlife Management 74:1448–1456.

CONNER, K., AND D.L. HARTL. 2004. Primer of ecological genetics. Sinauer Associates, Sunderland, Massachusetts, USA.

COSTELLO, C.M. 2010. Estimates of dispersal and home-range fidelity in American black bears. Journal of Mammalogy 91:116–121.

CROOKS, K.R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology 16:488–502.

CSIKI, I., C. LAM, A. KEY, E. COULTER, J.D. CLARK, R.M. PACE III, K.G. SMITH, AND D.D. RHOADS. 2003. Genetic variation in black bears in Arkansas and Louisiana using microsatellite DNA markers. Journal of Mammalogy 84: 691–701.

DAVIES, K.F., C. GASCON, AND C.R. MARGULES. 2001. Habitat fragmentation: Consequences, management, and future research priorities. Pages 81–97 in M.E. SOULE AND G.H. ORIANS, editors. Conservation biology: Research priorities for the next decade. Island Press, Washington, DC, USA.

DIXON, J.D., M.K. OLI, M.C. WOOTEN, T.H. EASON, J.W. MCCOWEN, AND M.W. CUNNINGHAM. 2007. Genetic consequences of habitat fragmentation and loss: The case of the Florida black bear (*Ursus americanus floridanus*). Conservation Genetics 8:455–464.

DOBEY, S., D.V. MASTERS, B.K. SCHEICK, J.D. CLARK, M.R. PELTON, AND M.E. SUNQUIST. 2005. Ecology of Florida black bears in the Okefenokee–Osceola ecosystem. Wildlife Monographs 158:1–41.

DUNBAR, M.R., M.W. CUNNINGHAM, J.B. WOODING, AND R.P. ROTH. 1996. Cryptorchidism and delayed testicular descent in Florida black bears. Journal of Wildlife Diseases 32: 661–664.

EASTRIDGE, R., AND J.D. CLARK. 2001. Evaluation of 2 soft-release techniques to reintroduce black bears. Wildlife Society Bulletin 29:1163–1174.

EDWARDS, S.A. 2002. Ecology of the black bear (*Ursus americanus floridanus*) in southwestern Alabama. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

ELOWE, K.D., AND W.E. DODGE. 1989. Factors affecting black bear reproductive success and cub survival. Journal of Wildlife Management 53:962–968.

ENNIS, S., AND T.F. GALLAGHER. 1994. A PCR-based gender-determination assay in cattle based on the bovine amelogenin locus. Animal Genetics 25:425–427.

EVANNO, G., S. REGNAUT, AND J. GOUDET. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. Molecular Ecology 14:2611–2620.

FRANKHAM, R., J.D. BALLOU, AND D.A. BRISCO. 2002. Introduction to conservation genetics. Cambridge University Press, Cambridge, England, UK.

GEORGIA DEPARTMENT OF NATURAL RESOURCES. 2010. Black bear fact sheet. Georgia Department of Natural Resources, Wildlife Resources Division, Social Circle, Georgia, USA.

GUO, S.W., AND E.A. THOMPSON. 1992. Performing the exact test of Hardy–Weinberg proportion for multiple alleles. Biometrics 48:361–372.

HALL, E.R. 1981. The mammals of North America. Volume 2. John Wiley and Sons, New York, New York, USA.

HANSKI, I. 2005. Metapopulation ecology. Oxford University Press, Oxford, England, UK.

HAROLDSON, M.A., C.C. SCHWARTZ, K.C. KENDALL, K.A. GUNTHER, D.S. MOODY, K. FREY, AND D. PAETKAU. 2010. Genetic analysis of individual origins supports isolation of grizzly bears in the Greater Yellowstone Ecosystem. Ursus 21:1–13.

HELLGREN, E.C., AND D.S. MAEHR. 1992. Habitat fragmentation and black bears in the eastern United States. Proceedings of the Eastern Black Bear Workshop on Management and Research 11:154–165.

———, AND M.R. VAUGHAN. 1994. Conservation and management of isolated black bear populations in the southeastern coastal plain of the United States. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 48: 276–285.

HOOKER, M.J. 2010. Estimating population parameters of the Louisiana black bear in the Tensas River Basin, Louisiana, using robust design capture–mark recapture. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

———, J.S. LAUFENBERG, A.K. ASHLEY, J.T. SYLVEST, AND M.J. CHAMBERLAIN. 2015. Abundance and density estimation of the American black bear population in Central Georgia. Ursus 26:107–115.

JAKOBSSON, M., AND N.A. ROSENBERG. 2007. CLUMPP: A cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. Bioinformatics 23:1801–1806.

JASRA, A., C.C. HOLMES, AND D.A. STEPHENS. 2005. Markov chain Monte Carlo methods and the label switching problem in Bayesian mixture modeling. Statistical Science 20: 50–67.

JOHNSON, K.G., AND M.R. PELTON. 1980. Prebaiting and snaring techniques for black bear. Wildlife Society Bulletin 8:46–54.

KELLER, L.F., AND D.M. WALLER. 2002. Inbreeding effects in wild populations. Trends in Ecology and Evolution 17: 230–240.

KITAHARA, E., Y. ISAGI, Y. ISHABASHIS, AND T. SAITOH. 2000. Polymorphic microsatellite DNA markers in the Asiatic black bear *Ursus thibetanus.* Molecular Ecology 9: 1661–1686.

KOPELMAN, N.M., J. MAYZEL, M. JAKOBSSON, N.A. ROSENBERG, AND I. MAYROSE. 2015. CLUMPAK: A program for identifying clustering modes and packaging population structure inferences across *K*. Molecular Ecology Resources 15:1179–1191.

LANDE, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142:911–927.

LATHAM, A. D.M., M.C. LATHAM, M.S. BOYCE, AND S. BOUTIN. 2011. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. Ecological Applications 21:2854–2865.

LAUFENBERG, J.S., AND J.D CLARK. 2014. Population viability and connectivity of the Louisiana black bear (*Ursus americanus luteolus*). U.S. Geological Survey Open-File Report 2014-1228. http://dx.doi.org/10.3133/ofr20141228. Accessed 15 Dec 2018.

LEE, D.J., AND M.R. VAUGHAN. 2003. Dispersal movements by subadult American black bears in Virginia. Ursus 12: 162–170.

LOUIS, E.J., AND E.R. DEMPSTER. 1987. An exact test for Hardy–Weinberg and multiple alleles. Biometrics 43: 805–811.

LOWE, C.L. 2011. Estimating population parameters of the Louisiana black bear in the Upper Atchafalaya River Basin. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

MACARTHUR, R.H., AND E.O. WILSON. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

MAEHR, D.S. 1984. Distribution of black bears in eastern North America. Distribution of black bears in eastern North America. Proceedings of the Eastern Black Bear Workshop 7:74.

———, J.E. LAYNE, E.D. LAND, J.W. MCCOWN, AND J. ROOF. 1988. Long distance movements of a Florida black bear. Florida Field Naturalist 16:1–6.

MCCOWN, J.W., P.S. KUBILIS, T.H. EASON, AND B. SCHEICK. 2004. Black bear movements and habitat use relative to roads in Ocala National Forest. Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida, USA.

MILLER, D.A. 1995. Systematic classification of black bears in the Southeastern United States. Thesis, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.

MILLS, L.S. 2012. Conservation of wildlife populations: Demography, genetics, and management. John Wiley and Sons, West Sussex, England, UK.

NEI, M., T. MARUYAMA, AND R. CHAKRABORTY. 1975. The bottleneck effect and genetic variability in populations. Evolution 29:1–10.

NOSS, R.F., H.B. QUIGLEY, M.G. HORNOCKER, T. MERRILL, AND P.C. PAQUET. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conservation Biology 10:949–963.

PAETKAU, D. 2003. An empirical exploration of data quality in DNA-based population inventories. Molecular Ecology 12:1375–1387.

———. 2004. The optimal number of markers in genetic capture–mark–recapture studies. Journal of Wildlife Management 68:449–452.

———, W. CALVERT, I. STIRLING, AND C. STROBECK. 1995. Microsatellite analysis of population structure in Canadian polar bears. Molecular Ecology 4:347–354.

———, AND C. STROBECK. 1994. Microsatellite analysis of genetic variation in black bears. Molecular Ecology 4: 347–354.

———, AND ———. 1998. Ecological genetic studies of bears using microsatellite analysis. Ursus 10:299–306.

PELLETIER, A., M.E. OBBARD, M. HARNDEN, S. MCCONNELL, E.J. HOWE, F.G. BURROWS, B.N. WHITE, AND C.J. KYLE. 2017. Determining causes of genetic isolation in a large carnivore (*Ursus americanus*) population to direct contemporary conservation measures. PLoS ONE 12:e0172319. doi:10.1371/journal.pone.0172319.

———, ———, K. MILLS, E.J. HOWE, F.G. BURROWS, B.N. WHITE, AND C.J. KYLE. 2012. Delineating genetic groupings in continuously distributed species across largely homogeneous landscapes: A study of American black bears (*Ursus americanus*) in Ontario, Canada. Canadian Journal of Zoology 90:999–1014.

PELTON, M.R. 1990. Black bears in the Southeast: To list or not to list. Proceedings of the Eastern Black Bear Workshop 10:155–161.

———. 2001. American black bear. Pages 224–233 in J.G. DICKSON, editor. Wildlife of southern forests habitat and management. Hancock House Publishers, Blaine, Washington, USA.

———. 2003. Black bear. Pages 547–555 in G.A. FELDHAMER, B.C. THOMPSON, AND J.A. CHAPMAN, editors. Wild mammals of North America. John Hopkins University Press, Baltimore, Maryland, USA.

———, AND R.G. NICHOLS. 1972. Status of the black bear (*Ursus americanus*) in the Southeast. Proceedings of the Eastern Black Bear Workshop 1:18–23.

———, AND F.T. VAN MANEN. 1994. Distribution of black bears in North America. Proceedings of the Eastern Black Bear Workshop 12:133–138.

PORRAS-HURTADO, L., Y. RUIZ, C. SANTOS, C. PHILLIPS, Á. CARRACEDO, AND M. LAREU. 2013. An overview of STRUCTURE: Applications, parameter settings, and supporting software. Frontiers in Genetics 4:98. doi: 10.3389/fgene.2013.00098.

PRITCHARD, J.K., M. STEPHENS, AND P. DONNELLY. 2000. Inference of population structure using multilocus genotype data. Genetics 155:945–959.

RÄIKKÖNEN, J., J.A. VUCETICH, R.O. PETERSON, AND M.P. NELSON. 2009. Congenital bone deformities and inbred wolves (*Canis lupus*) of Isle Royale. Biological Conservation 142:1025–1031.

RAYMOND M., AND F. ROUSSET. 1995. Genepop (Version-1.2) population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248–249.

RICE, W.R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

ROELKE, M.E., J.S. MARTENSON, AND S.J. OBRIEN. 1993. The consequences of demographic reduction and genetic depletion in the endangered Florida panther. Current Biology 3:340–350.

ROGERS, L.L. 1987. Factors influencing dispersal in the black bear. Pages 75–84 in B.D. CHEPKO-SADE AND Z.T. HALPIN, editors. Mammalian dispersal patterns: The effects of social structure on population genetics. University of Chicago Press, Chicago, Illinois, USA.

ROGERS, M.J. 1973. Movements and reproductive success of black bears introduced into Arkansas. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 27:307–308.

SACCHERI, I., M. KUUSSAARI, M. KANKARE, P. VIKMAN, W. FORTELIUS, AND I. HANSKI. 1998. Inbreeding and extinction in a butterfly metapopulation. Nature 392:491–494.

SANDERLIN, J.S., B.C. FAIRCLOTH, B. SHAMBLIN, AND M.J. CONROY. 2009. Tetranucleotide microsatellite loci from the black bear (*Ursus americanus*). Molecular Ecology Resources 9:288–291.

SCHEICK, B.K., AND W. MCCOWN. 2014. Geographic distribution of American black bears in North America. Ursus 25:24–33.

———, ———, AND M. ORLANDO. 2011. Updated distribution of black bears in North America. Proceedings of the Eastern Black Bear Workshop 20:30–35.

SCHWARTZ, C.C., AND A.W. FRANZMANN. 1992. Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. Journal of Wildlife Management 56:426–431.

SCHWARTZ, M.K., S.A. CUSHMAN, K.S. MCKELVEY, J. HAYDEN, AND C. ENGKJER. 2006. Detecting genotyping errors and describing American black bear movement in northern Idaho. Ursus 17:138–148.

SHAFFER, M.L. 1981. Minimum population sizes for species conservation. BioScience 31:131–134.

———. 1987. Minimum viable populations: Coping with uncertainty. Pages 69–86 in M. E. SOULE, editor. Viable populations for conservation. Cambridge University Press, Cambridge, England, UK.

SHERWIN, W.B., AND C. MORITZ. 2000. Managing and monitoring genetic erosion. Pages 9–34 in A.G. YOUNG AND G.M. CLARKE, editors. Genetics, demography and viability of fragmented populations. Cambridge University Press, Cambridge, England, UK.

STEPHENS, M. 2000. Dealing with label switching in mixture models, Journal of the Royal Statistical Society: Series B 62:795–809.

STRATMAN, M.R., C.D. ALDEN, M.R. PELTON, AND M.E. SUNQUIST. 2001. Long distance movement of a Florida black bear in the southeastern coastal plain. Ursus 12: 55–58.

SYLVEST, J.T. 2014. Abundance and density estimation of the Central Georgia black bear population. Thesis, University of Georgia, Athens, Georgia, USA.

TABERLET, P., J.J. CAMARRA, S. GRIFFIN, E. UHRES, O. HANOTTE, L.P. WAITS, C. DUBOIS-PAGANON, T. BURKE, AND J. BOUVET. 1997. Noninvasive genetic tracking of the endangered Pyrenean brown bear population. Molecular Ecology 6:869–876.

TROXLER, J.C. 2013. Population demographics and genetic structure of black bears in coastal Louisiana. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

U.S. CENSUS BUREAU. 2015. Quick facts. http://www.census.gov/quickfacts. Accessed 28 Aug 2016.

USERY, E.L. 2016. Geographic regions of Georgia: Overview. New Georgia encyclopedia. http://www.georgiaencyclopedia.org/. Accessed 26 Aug 2016.

VOS, C.C., A.G. ANTONISSE-DE JONG, P.W. GOEDHART, AND M.J.M. SMULDERS. 2001. Genetic similarity as a measure for connectivity between fragmented populations of the moor frog (*Rana arvalis*). Heredity 86:598–608.

WAYNE, R.K., N. LEHMAN, D. GIRMAN, P.J.P. GOGAN, D.A. GILBERT, K. HANSEN, R.O. PETERSON, U.S. SEAL, A. EISENHAWER, L.D. MECH, AND R.J. KRUMENAKER. 1991. Conservation genetics of the endangered Isle Royale gray wolf. Conservation Biology 5:41–51.

WEAR, B.J., R. EASTRIDGE, AND J.D. CLARK. 2005. Factors affecting settling, survival, and viability of black bears reintroduced to Felsenthal National Wildlife Refuge, Arkansas. Wildlife Society Bulletin 33: 1363–1374.

WEIR, B.S., AND C.C. COCKERHAM. 1984. Estimating F-statistics for analysis of population structure. Evolution 38:1358–1370.

WOODS, J.G., D. PAETKAU, D. LEWIS, B.N. MCLELLAN, M. PROCTOR, AND C. STROBECK. 1999. Genetic tagging of free-ranging black and brown bears. Wildlife Society Bulletin 27:616–627.

Received: October 20, 2018
Accepted: May 18, 2017
Associate Editor: E. Bellemain