GENETIC VARIATION IN BLACK BEAR POPULATIONS FROM LOUISIANA AND ARKANSAS: EXAMINING THE POTENTIAL INFLUENCE OF REINTRODUCTIONS FROM MINNESOTA

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Abstract: Using multilocus DNA fingerprinting, we assessed potential genetic effects that may have been caused by translocation of American black bears (Ursus americanus americanus) from Minnesota to Louisiana and Arkansas. The bear population in northeastern Minnesota exhibits less within-population genetic similarity (similarity within = 0.57) than bear populations in Louisiana and Arkansas (similarities within = 0.74) (P < 0.001). Populations in Louisiana and Arkansas are more closely related to each other (similarity between = 0.53) than they are to the population in Minnesota (similarity between = 0.34) (P < 0.001, Mann–Whitney test). Analysis of band-sharing data indicated that any genetic impacts that may have been caused by the translocations were not statistically significant.

Ursus 10:335-341

Key words: American black bear, Arkansas, DNA fingerprinting, Louisiana, Minnesota, population genetics, translocations, Ursus americanus.

The original range of the American black bear included most of North America, including all of Louisiana and Arkansas. Across this range, the species was divided into 16 subspecies (Hall 1981). The Louisiana black bear, U. a. luteolus, was originally described by Merriam (1893) on the basis of skull morphology. It historically occupied eastern Texas, all of Louisiana, southern Mississippi, and the southern portion of Arkansas. The American black bear occupied eastern and central North America, including central and northern Arkansas (Hall 1981).

Populations of both subspecies declined significantly in Louisiana and Arkansas during the 1800s and early 1900s due to unregulated harvest and substantial loss of forest habitat (Smith and Clark 1994). The bear hunting season was closed in Arkansas in 1927 due to concerns about low population levels (Smith and Clark 1994). In 1958, because bear populations remained low, the Arkansas Game and Fish Commission began a restocking program to increase populations to a level that would allow reopening hunting seasons (Smith and Clark 1994). In 1958, 40 bears (U. a. americanus) were captured in northeastern Minnesota (Lake and St. Louis counties) and released in Arkansas. Additional bears were captured in northeastern Minnesota and released in Arkansas during the summers of 1962–68. Release sites for approximately 254 bears included the Ozark National Forest (Pinney Creek and White Rock Wildlife Management Areas) and the Ouachita National Forest (Muddy Creek Wildlife Management Area). The precise number of bears released at each site cannot be determined due to incomplete documentation.

Similarly, the Louisiana Department of Wildlife and Fisheries recognized that black bear numbers were low within their state and began a restocking program in 1964. Adult bears and cubs were also trapped in northeastern Minnesota (Cook County), transported to Louisiana, and released in 2 areas. During 1964–67, approximately 130 bears were released in the Upper Atchafalaya River Basin. Approximately 35 bears were released in the Tensas River Basin during 1965–66 (Taylor 1971 cited in Pelton 1989).

The Arkansas bear populations increased considerably after restocking, to an estimated 2,500 bears in western and northern Arkansas, eastern Oklahoma, and southern Missouri (Smith and Clark 1994). With increasing population levels, the Arkansas Game and Fish Commission met its restocking objective and reopened black bear hunting in western and northern Arkansas in 1980 (Smith and Clark 1994). Hunting was still closed for a remnant population of native black bears near the White River National

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Wildlife Refuge in southeastern Arkansas. The current White River population is estimated at 170 bears, but the population may have reached a low of approximately 25 bears during the 1940s (Dellinger 1942 cited in Smith and Clark 1994).

Recovery records of released bears could not provide conclusive evaluation of the success of the restocking programs in Louisiana, and populations remain at notably low levels, as has the amount of suitable bear habitat. In 1981, the bear populations were estimated at 30–50 individuals in the Tensas River area, 30–50 individuals in the lower Atchafalaya Basin, with an unknown number of individuals in the upper Atchafalaya Basin (State Survey, 1981; Louisiana Department of Wildlife and Fisheries, cited in Pelton 1989).

Under the Endangered Species Act of 1973, Congress defined species to include "any subspecies of fish or wildlife or plants, and any distinct population segment of any species or vertebrate fish or wildlife which interbreeds when mature" (emphasis added). Hence, any subspecies or distinct population segment of *U. americanus* found to warrant protection because of low numbers could be protected; protection did not have to be justified at the species level. With an increasing concern over loss of black bear habitat and notably low bear populations, the U.S. Fish and Wildlife Service (USFWS) listed the Louisiana black bear as "threatened" in January of 1992 (57 Federal Register 588).

During the listing process, questions were raised about the potential genetic impacts of the bears introduced into Louisiana from Minnesota during the 1960s (Pelton 1991, Smith and Clark 1994). This introduction of *U. a. americanus* bears into Louisiana could have altered the putatively unique gene pool of *U. a. luteolus*. In making the listing decision, the USFWS consulted the report by Pelton (1989) that assembled preliminary genetic and morphological analyses of black bears from Louisiana, Tennessee, West Virginia, Virginia, Arkansas, and Minnesota. Genetic marker frequency data, including protein electrophoresis and mitochondrial DNA (mtDNA) data, failed to reveal significant inter-population differentiation, excepting data from 2 isozyme loci suggesting that Minnesota populations may be distinct from other populations (Johns et al. 1989, Zimmerman 1989). However, the sample sizes for studies reported in Pelton (1989) were small (approximately 3 bears/population), limiting the strength of conclusions. Any genetic impacts of the introduced bears on the *U. a. luteolus* genome were unknown at the time of listing. The objective of this study, therefore, was to assess any genetic effects of translocated bears from Minnesota on bear populations in Arkansas and Louisiana.

We thank the U.S. Fish and Wildlife Service and the National Council of the Paper Industry for Air and Stream Improvement, Inc. for funding this research. We also thank the following individuals and agencies for assistance in collecting blood and tissue samples: D. Garshelis, Minnesota Department of Forestry and Wildlife; D. Goad, Arkansas Game and Fish Commission; M. Hurdle and N. Hunter, White River National Wildlife Refuge (NWR); H. Jacobson and T. White, Mississippi State University; T. Edwards, Tensas River NWR; M. Pelton and personnel, University of Tennessee; R. Pace, Louisiana State University; and K. Shropshire, Mississippi Department of Wildlife, Fisheries, and Parks. S. Fain, USFWS National Fish and Wildlife Forensics Laboratory, provided access to unpublished laboratory methods and data. In addition, we thank B. Lubinski and J. Allen, Virginia Polytechnic Institute and State University, (VPISU) for laboratory assistance, S. Miller, VPISU, and T. Eason, University of Tennessee, for field assistance, and J. Kasbohm, VPISU, for his guidance and assistance collecting samples. We also thank an anonymous reviewer for helpful comments.

**METHODS**

**Sample Collection**

We collected blood and tissue samples from 7 black bear populations in Arkansas, Louisiana, and Minnesota (Fig. 1). Bears were trapped and immobilized for blood collection using standard procedures (Kasbohm and Vaughan 1993); this introduction of *U. a. americanus* bears into Louisiana could have altered the putatively unique gene pool of *U. a. luteolus*. In making the listing decision, the USFWS consulted the report by Pelton (1989) that assembled preliminary genetic and morphological analyses of black bears from Louisiana, Tennessee, West Virginia, Virginia, Arkansas, and Minnesota. Genetic marker frequency data, including protein electrophoresis and mitochondrial DNA (mtDNA) data, failed to reveal significant inter-population differentiation, excepting data from 2 isozyme loci suggesting that Minnesota populations may be distinct from other populations (Johns et al. 1989, Zimmerman 1989). However, the sample sizes for studies reported in Pelton (1989) were small (approximately 3 bears/population), limiting the strength of conclusions. Any genetic impacts of the introduced bears on the *U. a. luteolus* genome were unknown at the time of listing. The objective of this study, therefore, was to assess any genetic effects of translocated bears from Minnesota on bear populations in Arkansas and Louisiana.

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**METHODS**

**Sample Collection**

We collected blood and tissue samples from 7 black bear populations in Arkansas, Louisiana, and Minnesota (Fig. 1). Bears were trapped and immobilized for blood collection using standard procedures (Kasbohm and Vaughan 1993); additional tissue samples were collected from hunter-killed and road-killed bears. Blood and tissue samples were stored at -60°C or mixed with a sodium dodecyl sulphate buffer for storage at ambient temperatures (Kirby 1992).

**DNA Fingerprinting**

We extracted whole genomic DNA from blood and tissue using standard proteinase K digestion and phenol/chloroform extraction techniques (Sambrook et al. 1989). Purified DNA was digested using the restriction enzyme *Hinfl*, and the DNA samples were subjected to TBE agarose gel electrophoresis according to Sambrook et al. (1989). We used lambda DNA cut with *BstEII* (New England Biolabs, Beverly, Mass.), placed in several lanes across each gel, as a molecular weight marker. DNA fragments were transferred from the agarose gel to a Magnagraph nylon membrane (MSI, Westboro, Mass.)
via Southern blotting (Southern 1975). We hybridized Southern blots using Jeffreys’ minisatellite probe 33.15 (Jeffreys et al. 1985) tagged with chemiluminescent agents (Cellmark Diagnostics, Germantown, Md.). After hybridization using the specific protocol established by Cellmark Diagnostics, we exposed each membrane to Kodak XAR5 X-omat X-ray film (Rochester, N.Y.). The hybridized regions on each membrane were observed as banding patterns on the autoradiograph.

Interpretation and Analysis of DNA Fingerprints

We quantified the degree of relatedness between any 2 individual bears in terms of the number of bands of equal electrophoretic mobility exhibited by both individuals in the 2.3–7.2 kilobase range of molecular weights. A measure of phenotypic similarity, S, was calculated for all pairings of individuals, allowing for comparisons within and between populations examined on the same autoradiograph (Bruford et al. 1992). We calculated S as:

\[ S = \frac{2n_y}{n_x + n_y} \]

where

- \( n_y \) = the number of bands exhibited by both individuals,
- \( n_x \) = the total number of bands exhibited by individual x, and
- \( n_y \) = the total number of bands exhibited by individual y.

Median similarity values of S were compared within and between Arkansas, Louisiana, and Minnesota populations. Because data were non-normally distributed, we used median instead of mean values and non-parametric statistical procedures. Mann–Whitney tests were performed to determine significant differences.

RESULTS

We screened genetic variability among DNA samples of 103 bears from 7 populations using DNA fingerprinting techniques (Table 1). Median estimated similarity values within populations (reported along the diagonal of Table 2) ranged from 0.57 (Cook County, Minn.) to 0.81 (White River NWR). Median estimated similarity values between populations ranged from 0.19 (White River NWR versus Ouachita National Forest) to 0.70 (White River NWR versus Tensas NWR) (Table 2, Fig. 1).

Within-population similarity values (0.57 versus 0.74) within the Minnesota and Arkansas–Louisiana populations were different (P < 0.001, Mann–Whitney test). Among the 3 Arkansas populations, estimated genetic similarity was higher (P < 0.001, Mann–Whitney test) within White River NWR (0.81) than within the Ozark and Ouachita National Forest populations (0.63 pooled) (Table 2). Among the 3 Louisiana populations, estimated genetic similarity was lower (P < 0.001, Mann–Whitney test) within the Upper Atchafalaya Basin (0.67) than within the Tensas River NWR and Lower Atchafalaya Basin populations (0.78 pooled).

The estimated median genetic similarity between the Cook County, Minnesota population and each population from Louisiana and Arkansas was 0.34 (5 inter-population comparisons). The estimated median genetic similarity between the Louisiana and Arkansas populations was 0.53 (6 inter-population comparisons) (Table 3). These 2 between-population similarity values were different (P < 0.001, Mann–Whitney test).

DISCUSSION

Genetic Variation within Populations

Band-sharing data indicated that the bear population in Cook County, Minnesota exhibited more genetic diversity than bear populations from Louisiana and Arkansas. The Minnesota population is much larger than the isolated Louisiana or Arkansas populations (Jonkel 1978), and larger populations tend to show more genetic variation than smaller, isolated populations (Allendorf and Leary 1986, Hartl 1988).

Among the 3 populations in Arkansas, the White River NWR population exhibited the highest within-population genetic similarity. Even though the White River NWR population may have declined to approximately 25 individuals in the 1940s (Dellinger 1942 cited in Smith and Clark 1994), this population was not part of the restocking program in Arkansas. The population remains at a low number relative to the Ozark and Ouachita NF populations (Smith and Clark 1994), and the White River NWR population may have lost genetic variation due to a genetic bottleneck and associated random genetic drift (Allendorf 1986, Hartl 1988). Smith and Clark (1994) estimate that approximately 2,500 bears now inhabit western and northern Arkansas and portions of eastern Oklahoma and southern Missouri. Restocking efforts may have reduced any effects of random genetic drift and be partly responsible for the higher genetic diversity within the Ozark and Ouachita NF populations. The rapid recovery from any genetic bottleneck may have minimized associated losses of genetic diversity (Nei et al. 1975).

Among the 3 black bear populations in Louisiana, the Tensas River NWR and Lower Atchafalaya Basin populations showed less genetic variation. This may be due to
Table 1. DNA fingerprint banding sharing patterns within black bear populations in Minnesota, Arkansas, and Louisiana (HinfI restriction digests, Jeffreys' 33.15 probe). Due to the non-normality of the data, values are given as medians, with ranges given in parentheses. Sample sizes (n) given refer to the number of bears sampled/population. A shared band is one exhibited by all individuals sampled within a given population; a polymorphic band is one not exhibited by all individuals in a given population.

<table>
<thead>
<tr>
<th>Populationa (n)</th>
<th>Bands/individual (range)</th>
<th>Shared bands (range)</th>
<th>Polymorphic bands (range)</th>
<th>Total bands (range)</th>
</tr>
</thead>
<tbody>
<tr>
<td>COOK (31)</td>
<td>22.0 (14–33)</td>
<td>3.0 (1–6)</td>
<td>46.5 (28–55)</td>
<td>49.5 (32–56)</td>
</tr>
<tr>
<td>OZAR (8)</td>
<td>27.0 (23–33)</td>
<td>9.0 (6–12)</td>
<td>39.0 (31–47)</td>
<td>48.0 (43–53)</td>
</tr>
<tr>
<td>OUAC (8)</td>
<td>27.0 (21–32)</td>
<td>10.0 (9–11)</td>
<td>35.5 (28–43)</td>
<td>45.5 (39–52)</td>
</tr>
<tr>
<td>WRIV (17)</td>
<td>26.0 (20–38)</td>
<td>12.0 (11–23)</td>
<td>25.0 (19–27)</td>
<td>38.0 (31–48)</td>
</tr>
<tr>
<td>TENS (16)</td>
<td>19.5 (10–26)</td>
<td>9.0 (5–13)</td>
<td>15.5 (13–37)</td>
<td>27.5 (20–42)</td>
</tr>
<tr>
<td>UATC (12)</td>
<td>25.0 (15–33)</td>
<td>5.0 (2–8)</td>
<td>37.0 (27–40)</td>
<td>42.5 (29–47)</td>
</tr>
<tr>
<td>LATC (11)</td>
<td>14.5 (12–27)</td>
<td>7.0 (5–9)</td>
<td>23.0 (18–28)</td>
<td>30.0 (23–37)</td>
</tr>
</tbody>
</table>


a genetic bottleneck with associated random genetic drift (Hartl 1988), given that these populations were each estimated to have only 30–50 bears in 1981 (State Survey, 1981, Louisiana Department of Wildlife and Fisheries cited in Pelton 1989). Even though approximately 35 bears were translocated to the Tensas River NWR population during the restocking program, Nowak (1986 cited in Pelton 1989) speculated that none of the released bears survived or remained in the area. The Lower Atchafalaya Basin population was not part of the restocking program. The Upper Atchafalaya Basin exhibited the most within-population genetic variation; restocking efforts may have reduced the impacts of random genetic drift (Hartl 1988) and be partly responsible for the higher genetic diversity. The possibility that translocated black bears may have affected the U. a. luteolus gene pool, therefore, cannot be excluded.

Genetic Variation between Populations

Bear populations in Louisiana and Arkansas are more closely related to each other than they are to the population in Minnesota. Estimated genetic similarities between black bear populations in Louisiana and Arkansas were higher than the estimated genetic similarities between the Cook County, Minnesota, population and each population in Louisiana and Arkansas (P < 0.001, Mann–Whitney test). Although restocking efforts may have influenced levels of genetic variability within certain Louisiana and Arkansas bear populations, any genetic impacts caused by these translocations were not significant enough to alter the overall genetic similarity between populations.

Within Arkansas, the White River NWR population was more similar to the Ozark NF population than to the Ouachita NF population. Bears use narrow river corri-

Table 2. Matrix of median band-sharing values for genetic similarities of black bear populations in Minnesota, Arkansas, and Louisiana (HinfI restriction digests, Jeffreys' 33.15 probe). Values along the diagonal represent estimated genetic similarities within populations; values below the diagonal represent estimated genetic similarities between populations. Asterisks indicate absence of similarity estimates for pairs of populations for which DNA fingerprints were not observed on the same Southern blot.

<table>
<thead>
<tr>
<th>Populationa</th>
<th>COOK</th>
<th>OZAR</th>
<th>OUAC</th>
<th>WRIV</th>
<th>TENS</th>
<th>UATC</th>
<th>LATC</th>
</tr>
</thead>
<tbody>
<tr>
<td>COOK</td>
<td>0.57</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>OZAR</td>
<td>0.30</td>
<td>0.63</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>OUAC</td>
<td>0.23</td>
<td>0.43</td>
<td>0.635</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>WRIV</td>
<td>0.39</td>
<td>0.405</td>
<td>0.19</td>
<td>0.81</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TENS</td>
<td>0.41</td>
<td>****</td>
<td>****</td>
<td>0.70</td>
<td>0.78</td>
<td></td>
<td></td>
</tr>
<tr>
<td>UATC</td>
<td>0.29</td>
<td>****</td>
<td>****</td>
<td>****</td>
<td>0.56</td>
<td>0.67</td>
<td></td>
</tr>
<tr>
<td>LATC</td>
<td>****</td>
<td>****</td>
<td>****</td>
<td>****</td>
<td>****</td>
<td>0.50</td>
<td>0.78</td>
</tr>
</tbody>
</table>

Fig. 1. Median band-sharing values for genetic similarities within and between black bear populations in Minnesota, Arkansas, and Louisiana (HinfI restriction digests, Jeffrey’s 33.15 probe). Numbers enclosed in circles are arbitrary and represent populations, numbers enclosed in triangles represent genetic similarities within populations, and numbers enclosed in rectangles represent genetic similarities between populations.

...dors for dispersal or migration (Pelton 1989) and potentially can travel between the Ozark NF and White River NWR (approximately 250 km) using the White River corridor, providing a means for gene flow between these 2 populations. In contrast, travel between the Ouachita NF and White River NWR (approximately 175 km) may be limited by migration barriers, possibly including the Arkansas River, the city of Little Rock, and several major interstates.

Estimated genetic similarity between the White River NWR, Arkansas, and Tensas River NWR, Louisiana, populations was high (0.70), suggesting gene flow between these 2 populations (Pelton 1989). Given the small sizes of the White River NWR and Tensas River NWR populations, sufficient migration would be necessary to keep the 2 populations from diverging genetically due to random genetic drift; the actual divergence of the populations would be a function of the number of migrants per generation and of means and variances of allele frequencies (Allendorf and Phelps 1981).

Statistical Considerations

Population data collected with DNA fingerprinting do not provide a complete characterization of genetic varia-
tion in terms of allele frequency distributions because neither the number of loci nor the locus affiliation of alleles is directly observable (Scott and Williams 1994). Use of certain traditional population genetic statistics was not found defensible in the context of small bear populations subject to restocking.

Inferences regarding average heterozygosity and genetic distance based on DNA fingerprinting data require 2 assumptions beyond those required for single-locus data (Jin and Chakraborty 1994). First, the Hardy–Weinberg rule is assumed for each population, but the assumption that migration is unimportant clearly is violated in a small population subject to reintroduction. Imprecision in estimating band frequencies due to sampling error also compromises tests based on Hardy–Weinberg assumptions. Second, co-migration of bands from distinct minisatellite loci and the assumption that they represent the same allele has an unknown effect on estimation of population genetic statistics.

Band-sharing data often are analyzed in the genetics literature using classical statistical procedures that assume normal data (Gilbert et al. 1990, Westneat 1990, Wayne et al. 1991, Triggs et al. 1992). However, non-parametric procedures should be used when data do not come from a normal distribution (Hollander and Wolfe 1973). Median values provide a more reliable representation of non-normal distributions than mean values; therefore, we used median values and non-parametric tests for differences in our analysis.

Given the pair-wise nature of the similarity index calculation, band-sharing data from each DNA fingerprint represent a collection of non-independent data points (Wayne et al. 1991). Under the Mann–Whitney test, however, data points are assumed to be independent. Although the independence assumption is violated, the current genetics and statistics literature offer no alternative statistical methods for handling dependent data. Although the robustness of the Mann–Whitney test to non-independence is unknown, after consultation with statisticians and geneticists, we chose to use the non-parametric procedures discussed for data analysis.

Lynch (1990) provided a method for partitioning the similarity index into within- and between-population components, but generous assumptions are needed to make the transition. Stephens et al. (1992) presented a method for calculating average heterozygosity using band-sharing data, provided that allele frequencies can be inferred from such data. Hence, these 2 statistical methods were not used in this study due to questions regarding the satisfaction of the underlying assumptions each required.

Conclusions

Any genetic impacts that may have been caused by the translocations were not statistically significant. The bear population of northeastern Minnesota exhibits less within-population genetic similarity than bear populations in Louisiana and Arkansas, and populations in Louisiana and Arkansas are more closely related to each other than they are to the population in Minnesota.

LITERATURE CITED


CITATION


Table 3. Median band-sharing values for genetic similarities of black bear populations in Minnesota, Arkansas, and Louisiana

<table>
<thead>
<tr>
<th>Population</th>
<th>Median band-sharing</th>
</tr>
</thead>
<tbody>
<tr>
<td>Within individual populations: (P &lt; 0.001)</td>
<td></td>
</tr>
<tr>
<td>Minnesota (n = 31)</td>
<td>0.57</td>
</tr>
<tr>
<td>Louisiana–Arkansas (n = 72)</td>
<td>0.74</td>
</tr>
<tr>
<td>Between individual populations: (P &lt; 0.001)</td>
<td></td>
</tr>
<tr>
<td>Minnesota vs. Louisiana–Arkansas (n = 77)</td>
<td>0.34</td>
</tr>
<tr>
<td>Louisiana–Arkansas (n = 56)</td>
<td>0.53</td>
</tr>
</tbody>
</table>


