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Influence of Translocations on Eastern Wild Turkey Population Genetics in Texas

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ABSTRACT Between 1979 and 2006, over 7,000 eastern wild turkeys (*Meleagris gallopavo silvestris*) from 16 states were translocated to east Texas in an attempt to restore a stable, huntable population. Although current populations are stable in some areas and a spring male-only hunting season was opened in 1995, turkey density in the region remains low and large areas of apparently suitable habitat are not occupied. The long-term effects of the extensive translocations and current levels of connectivity among various populations are unknown. We used microsatellite DNA analysis to assess the influence of translocations on current genetic structure and gene flow in eastern wild turkeys. The influence of translocations was clearly evident and reflected historical contributions from the Midwest and southeastern United States. The east Texas population consisted of 3 distinct genetic clusters. Despite a lack of clear geographic barriers and nearly contiguous forest cover in much of the east Texas landscape, regional gene flow among clusters appeared to be limited. Diversity in the regional population remains high, but we recommend that regulations reflect the current population structure and that long-term efforts should be made to increase connectivity among wild turkeys in the region. © 2013 The Wildlife Society.

KEY WORDS genetic structure, *Meleagris gallopavo silvestris*, microsatellites, Texas, translocation, wild turkey.

Translocations and reintroductions have been used successfully to restore many wildlife populations to portions of their former range. If not carefully conducted, however, translocations can result in small, isolated populations because of poor survival of founder individuals or fragmentation of habitat (Leberg 1991, Stangel et al. 1992). The effects of an initial founder event may be exacerbated if the population remains small and isolated. Genetic drift and inbreeding can result in reduced diversity and inbreeding depression, which can negatively affect fitness and the long-term viability of the established population (Stangel et al. 1992, Reed and Frankham 2003, DeYoung and Honeycutt 2005). For game species, translocations frequently have been used to restock or supplement native populations depleted from overharvest or other factors. Often the fate and breeding success of translocated individuals are poorly recorded and translocation success is unknown (Fischer and Lindenmayer 2000). Population genetic analyses provide an effective tool to assess the success of past translocations and their influence on current populations (DeYoung and Honeycutt 2005).

During the mid to late 20th century, wild turkeys (*Meleagris gallopavo*) were translocated widely throughout the United States to reestablish local populations (Tapley et al. 2005). Overall, the translocations have been successful and the reestablishment of wild turkey populations is often cited as a triumph of modern wildlife management (Kennamer et al. 1992). In an effort to mitigate the long-term effects of small, isolated populations following translocation of wild turkeys, managers have employed block stocking, whereby groups of birds are released at several stocking sites in relatively close proximity in a management unit (Lopez et al. 2000). In theory, block stocking creates a network of connected subpopulations with elevated gene flow and maintenance of high genetic diversity (Allendorf 1983, Latch and Rhodes 2005). If high levels of gene flow occur among subpopulations, then the genetic signatures from source populations will eventually be obscured (Baker and Moeed 1987). On the other hand, in the absence of gene flow, isolated populations may retain these signatures for many generations (Kennedy et al. 1987, Williams et al. 2000, Latch and Rhodes 2005, Hicks et al. 2007).

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Although wild turkeys were never extirpated from eastern Texas, the population had been reduced to very low numbers (perhaps fewer than 100 individuals) in 5 isolated populations by the 1940s (Texas Game, Fish, and Oyster Commission 1945). In an attempt to restore the population, over 7,000 eastern wild turkeys (*M. g. silvestris*) were translocated into east Texas between 1979 and 2006, with the majority of translocations occurring between 1988 and 1999 (Suarez 2002; Texas Parks and Wildlife Department, unpublished data). Source stocks came from 16 states, but 5 states accounted for 77.5% of translocated individuals: Iowa, Wisconsin, South Carolina, Missouri, and Georgia (Seidel 2010; Texas Parks and Wildlife Department, unpublished data). These translocations were executed using a block stocking strategy in which 15–20 birds from multiple source populations were released at several stocking sites in close geographic proximity (Campo and Dickson 1990, Lopez et al. 1998, George et al. 2000). Information recorded for stocking events was highly variable, with limited information on source populations (often only the state of origin) and timing of translocations. These stocking attempts had mixed success, as some translocations produced successful population establishment and other sites suffered heavily from high mortality and poor recruitment (Hopkins 1981, Campo et al. 1984, Lopez et al. 1998, George et al. 2000, Kelly 2001, Feuerbacher et al. 2005). The current population size in the east Texas region is approximately 15,000 birds, but eastern wild turkeys remain at very low densities throughout the region and do not appear to be using significant areas of available habitat (Tapley et al. 2005).

Studies on wild turkey populations show that translocations can leave genetic signatures for decades (Leberg et al. 1994, Latch and Rhodes 2005) and exhibit reduced genetic variability compared to the source populations (Mock et al. 2001, 2004; Latch and Rhodes 2005). Our goals in this research were to use microsatellite loci to examine the extent to which historical translocations are reflected in the current genetic structure of wild turkeys in east Texas. To do this, we attempted to determine the expected genetic structure in the population based on translocation records and then compared this to the existing structure. We also examined the issue of whether ongoing gene flow throughout the region has been sufficient to obscure the genetic signature of these translocations and compared the genetic diversity of east Texas turkeys to native populations in other regions.

STUDY AREA

We conducted this study in 24 east Texas counties reflecting the approximate historical distribution of eastern wild turkeys in Texas. The area spanned 4 ecoregions (Diggs et al. 2006), including parts of 18 counties (3,100,000 ha) in the Pineywoods ecoregion, parts of 9 counties (767,000 ha) in the Post Oak Savannah, parts of 6 counties (500,000 ha) in the Blackland Prairie, and parts of 2 counties (139,000 ha) in the Cross Timbers (Fig. 1). The elevation in the study area ranged from 30 m to 518 m and the annual average rainfall was 69–127 cm (Texas Forest Service 2008). The primary ecoregion was the Pineywoods, which is characterized by extensive forests of shortleaf pine (*Pinus echinata*), longleaf pine (*P. palustris*), loblolly pine (*P. taeda*), and non-native slash pine (*P. elliottii*) on uplands (Texas Forest Service 2008). Interspersed within these pine forests were areas of upland hardwoods, mixed pine-hardwood forests, and bottomland hardwood forests (Texas Forest Service 2008).

METHODS

Sample Collection

To characterize wild turkey population structure, we used a combination of feather samples from hunter-harvested turkeys throughout the region and blood samples from captured wild turkeys. We obtained feather samples from hunters at mandatory Texas Parks and Wildlife Department (TPWD) check stations during the 2008 and 2009 spring turkey hunting season (1–30 Apr; Fig. 1). We provided sampling kits at check stations that included disposable scissors, 2 15-ml plastic tubes prefilled with 10 ml of 70% ethyl alcohol, and a card with instructions and blanks to record data about the sampled bird. We asked hunters to remove 10 feathers from the sides of the body, use the scissors to cut 1.3–2.7 cm from the feather base, and deposit these tips in the tube of alcohol. The tubes were stored at room temperature and picked up at the conclusion of the season in each year.

We obtained blood samples from wild turkeys captured with cannon nets at selected private and public land sites in Nacogdoches, Angelina, Jasper, and Red River counties during 2007 and 2008 as part of an ongoing movement and nesting study (Fig. 1; Isabelle 2010). All of these sites had relatively stable wild turkey populations for at least 10 years prior to our sampling efforts. We obtained at least 3 ml of whole blood via brachial venipuncture from each captured turkey and stored the samples at room temperature in 15-ml tubes filled with 10-ml of lysis buffer (Longmire et al. 1997). Wild turkey capture and handling procedures were in accordance with the Stephen F. Austin State University Animal Care and Use Committee (protocol no. TECMW10-08-07).

To examine genetic origin of wild turkeys in east Texas, we used reference samples from states that contributed large numbers of turkeys to historical translocation efforts. A comprehensive review of TPWD records indicated that Iowa ($n = 3,843$), Wisconsin ($n = 790$), South Carolina ($n = 330$), Missouri ($n = 453$), and Georgia ($n = 453$) contributed 77.5% of birds translocated into east Texas since 1979. We obtained reference samples from a tissue and DNA collection used in previous studies (Mock et al. 2002, Latch and Rhodes 2005, Latch et al. 2006*a*).

DNA Extraction

We extracted DNA from all samples using DNeasy 96 Blood and Tissue kits (Qiagen, Inc., Valencia, CA). We extracted DNA from the blood samples following the manufacturer's protocol for purification of total DNA from animal blood or cells (spin-column protocol) with 4 modifications: 1) we increased the amount of blood used from 5–10 μl to 200 μl, 2) we increased the incubation period from 10 minutes to

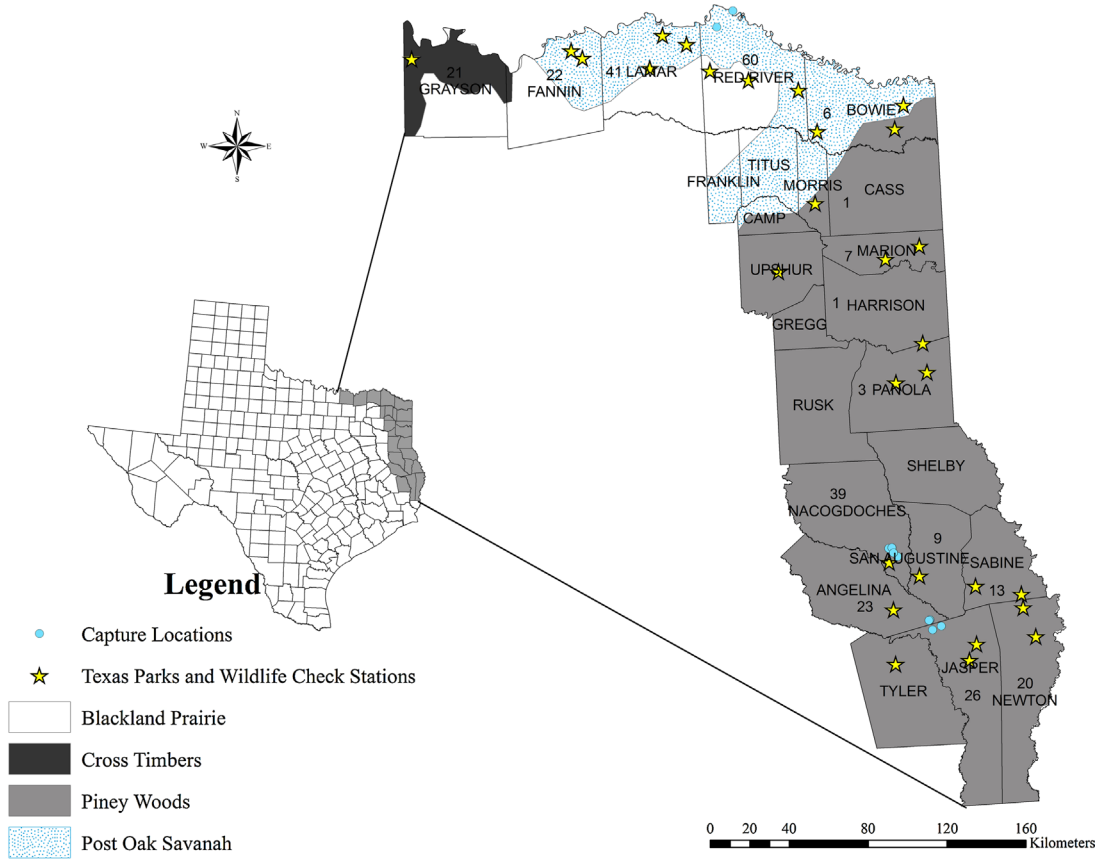

Figure 1. Capture locations and Texas Parks and Wildlife mandatory check stations in east Texas where blood and feather samples were obtained from eastern wild turkeys from 2007 to 2009. Numbers indicate the total number of samples in each county.

30–60 minutes, 3) we used 100 µl of buffer AE instead of 200 µl, and 4) we increased the second incubation from 1 minute to 10 minutes. We extracted DNA from the feathers using the manufacturer's protocol for purification of total DNA from animal tissue (spin-column protocol) with 2 modifications: 1) we used 100 µl of buffer AE instead of 200 µl, and 2) we increased the second incubation from 1 minute to 10 minutes.

Microsatellite Amplification and Analysis

We amplified 10 microsatellite loci in wild turkey blood and tissue samples, including TUM50, WT32, TUM23, TUM6, WT30-2 (Huang et al. 1999), WT54, WT38-2, WT75, WT90-2, and WT10 (Latch et al. 2002). The 10-µl amplification reactions consisted of 1.5–2 µl of template DNA, 2–5 pmol of forward primer, 2–5 pmol of reverse primer, 2.9–3.46 µl of H_2O, and 5 µl of AmpliTaq Gold PCR Master Mix (Applied Biosystems, Inc., Carlsbad, CA). We amplified all loci with 1.5 mM $MgCl_2$ except for locus WT90-2, which used 2.5 mM. We amplified the loci according to the following thermocycler conditions: 1) a 10-minute initial denaturation step at 95° C; 2) 30–35 cycles of 30 seconds at 95° C, 30 seconds at the locus-specific annealing temperature, and 30 seconds at 72° C; 3) a final extension for 10 minutes at 72° C; and 4) a 45-minute soak at 60° C. The thermalcycler conditions for locus WT90-2 were 1) a 10-minute initial denaturation step at 95° C; 2) 10 cycles of 30 seconds at 95° C, 30 seconds at 60° C (decreasing 1 every cycle to 50° C), and 30 seconds at 72° C; 3) 30 cycles of 30 seconds at 95° C, 30 seconds at 50° C, and 30 seconds at 72° C; 4) a final extension for 10 minutes at 72° C; and 5) a 45-minute soak at 60° C. We used a 3130 × 1 Genetic Analyzer (Applied Biosystems, Inc.) for separation and detection of alleles. We determined the allele sizes for each locus using GeneMapper v4.0 (Applied Biosystems, Inc.). To reduce chances of scoring errors, we reamplified any genotypes with low intensity (<100 as determined by GeneMapper) chromatographs. If a sample had >3 loci missing despite repeated attempts at DNA extraction and amplification, we deemed the sample unusable and removed it from the dataset. To assess genotyping error, we selected 38 samples (approx. 10% of the 376 useable samples) to reanalyze and produced duplicate genotypes. We then compared the duplicate genotypes and calculated mean error rates per allele and per locus (Pompanon et al. 2005).

Data Analysis

Prior to analyzing the microsatellite data, we used translocation records to describe the population structure that reflected translocation history for the region. Records of translocations in east Texas are very inconsistent, with some records lacking essential information like numbers of birds or source state. We used only records that included at least the

county of release, the source state, and the number of turkeys released and based our analysis at the county level.

Assignment method: origin.—We used the program STRUCTURE (version 2.3.2; Pritchard et al. 2000) to identify the genetic signature of source populations (e.g., Latch and Rhodes 2005). By defining a source population with the USEPOPINFO model, STRUCTURE can assign unknown individuals to 1 or more predefined populations based on allele frequencies. Other programs and methods exist that will assign unknown individuals to a sampled population; however, STRUCTURE has high accuracy (71.5% when the accuracy threshold is 0.95) even at low levels of differentiation ($F_{ST} = 0.03$; Maudet et al. 2002). Consequently, we used this method to determine which potential source population had the closest genetic affiliation with east Texas birds.

To verify that the reference samples grouped by state and that there was a detectable genetic difference among the states, we completed 5 runs of STRUCTURE (100,000 burn-in period and 200,000 Markov Chain Monte Carlo [MCMC] replications after burn-in). We assumed 1–7 genetic clusters ($K = 1$–7) and used the no admixture model and default settings. We determined the most likely number of clusters using the change in mean likelihood value for each cluster, with the largest change indicating the likeliest cluster number (Evanno et al. 2005). Individuals were assigned to clusters by 5 iterations at 100,000 burn-in and 500,000 MCMC replications after burn-in at the inferred *K*. We identified individuals with mixed ancestry using the average q (the probability that an individual belongs to a given cluster); an individual was defined as admixed if $q < 0.80$ in every cluster. We evaluated inbreeding within each source population with the inbreeding coefficient (F_{IS}; Nei 1987) as calculated in the program GENEPOP (version 4.1.4; Raymond and Rousset 1995). Hardy–Weinberg equilibrium (Guo and Thompson 1992) was assessed with ARLEQUIN (version 3.1; Excoffier et al. 2005) using the observed and expected heterozygosities (1,000,000 MCMC steps and 100,000 dememorization steps).

We used reference samples from Iowa, Wisconsin, South Carolina, Missouri, and Georgia to characterize each potential source population using the USEPOPINFO model in STRUCTURE. In our initial runs to assign Texas samples to source populations, we used the admixture model and default settings, including allowing the program to infer the admixture coefficient (α) from the genetic data. STRUCTURE infers α from all available data, including both reference and source populations, which can produce unusually large values for α and create difficulty in assignment of any individuals to source clusters (Pritchard et al. 2000). In this case, it caused STRUCTURE to infer a very high alpha (approx. 7) and no individual was assigned to any source population. Taken separately, east Texas individuals and reference samples both had similar low α values ($\alpha \leq 0.08$). Therefore, we used a fixed $\alpha = 0.08$, determined from the reference samples by averaging from 5 iterations at 100,000 burn-in and 500,000 MCMC replications. We then assigned the Texas samples to potential source populations with 5 runs of STRUCTURE (100,000 burn-in period and 500,000 MCMC reps after burn-in) using the admixture model and a fixed $\alpha = 0.08$. An individual was defined as admixed if it had an average $q < 0.80$ in all groups.

Assignment method: genetic structure.—Within east Texas, we used the Bayesian clustering algorithm implemented in STRUCTURE to calculate the likelihood of various numbers (*K*) of genetic clusters (where *K* is specified by the user) and to group east Texas samples into clusters that minimized linkage disequilibrium and deviations from Hardy–Weinberg equilibrium. This approach is ideal for admixed data because the program does not require a priori knowledge of population substructure. It can detect cryptic genetic structure, even when no clear barriers to gene flow are apparent (e.g., Latch et al. 2008) and it can detect the correct number of clusters even at low levels of differentiation ($F_{ST} = 0.03$; Latch et al. 2006*b*).

To estimate the most likely number of east Texas clusters, we ran STRUCTURE (100,000 burn-in period and 200,000 MCMC replications after burn-in) assuming 1–7 genetic clusters ($K = 1$–7). We performed 5 iterations for each value of *K*. We allowed the allele frequencies to be correlated among clusters and we used the admixture model which allows individuals to be from >1 cluster. We determined the most likely number of clusters using the change in mean likelihood value for each cluster, with the largest change indicating the likeliest cluster number (Evanno et al. 2005). Individuals were assigned to clusters by 5 iterations at 100,000 burn-in and 500,000 MCMC replications after burn-in at the inferred *K*. An individual was defined as admixed if $q < 0.80$ in every cluster.

To determine genetic differentiation among clusters, we placed all non-admixed ($q \geq 0.80$) individuals into appropriate clusters based on the STRUCTURE results. Then, we used the program ARLEQUIN to calculate pairwise F_{ST} statistics (Weir and Cockerham 1984) for all genetic clusters. We assessed the genetic variability of the STRUCTURE clusters using allelic richness (El Mousadik and Petit 1996) as calculated in ADZE (version 1.0; Szpiech et al. 2008).

If spatial autocorrelation exists in a discontinuously sampled population, the STRUCTURE algorithm can produce spurious results suggesting genetic structure (Schwartz and McKelvey 2009). Because our captured wild turkeys were clustered in relatively small areas and we were dependent on hunter harvest for the remaining samples, we used the spatial genetic autocorrelation analysis in program GENALEX 6.41 (Peakall and Smouse 2006) to examine our data for evidence of autocorrelation. We used home range centroids as geographic locations for captured turkeys and the most precise location available (generally a road intersection) as reported by the hunter for hunter-harvested turkeys.

Genetic diversity.—We used the program CONVERT (version 1.31; Glaubitz 2004) to prepare the input files for the software used. We assessed genetic diversity in the wild turkey population at the county level, prior to clustering according to the STRUCTURE algorithm. We excluded

counties with fewer than 10 samples to reduce the potential bias due to small sample size. Specifically, we calculated F_{IS} (Nei 1987) within each county using the program GENEPOP. We also calculated allelic richness by county with ADZE and average number of alleles using ARLEQUIN. We assessed genetic variability and Hardy–Weinberg equilibrium using the observed and expected heterozygosities as calculated in ARLEQUIN with 1,000,000 steps and 100,000 dememorization steps. We tested for linkage disequilibrium (Slatkin and Excoffier 1996) in ARLEQUIN by generating 20,000 randomly permuted samples. To characterize overall genetic variation among the counties in east Texas, we calculated pairwise F_{ST} for all pairs of counties in ARLEQUIN.

RESULTS

After removing 9 unusable samples, we had 294 wild turkey samples in east Texas from 2007 to 2009 (Fig. 1). Most were from hunter-harvested turkeys ($n = 244$) and our sample represents approximately 45% of the eastern wild turkeys harvested legally in Texas in 2008 and 2009 (Texas Parks and Wildlife Department, unpublished data). We received 2 unsolicited samples from Wharton County, which was outside the original study area; however, we included the samples in the analysis because records suggest eastern wild turkeys were translocated into that area. The number of wild turkeys sampled in each county ranged from 1 (Harrison and Cass Counties) to 60 (Red River County) and the numbers generally reflected Texas Parks and Wildlife harvest numbers for these counties (Fig. 1). We amplified all 10 microsatellite loci and used them to discern the genetic structure in east Texas. All the loci had less than 3% missing data except for WT 75 (25%) and WT 90-2 (8.3%). Among the 294 samples, 199 (68%) were typed at all 10 loci, 73 (25%) were missing 1 locus, 17 (6%) were missing 2 loci, and 5 (2%) were missing 3 loci.

We obtained 82 source population reference samples from Iowa, Wisconsin, South Carolina, Missouri, and Georgia. These included 17–20 representative samples from most states; however, we had 6 samples from Iowa. We amplified 8 loci (TUM 6, TUM 23, TUM 50, WT 10, WT 30-2, WT 32, WT 38-2, and WT 54) in the reference samples. We were unable to amplify loci WT 75 and WT 90-2 in a sufficient number of reference samples to use these loci; therefore, we did not use these loci in any analyses involving the reference samples. We removed 18 unusable samples from the reference dataset and all the loci had <5% missing data except for WT 32 (20.7%). Based on the 38 duplicate genotypes, the mean error rates were 0.008 per allele and 0.016 per locus.

Assignment Methods: Region of Origin

The reference samples did not cluster by state, but by region (Midwestern and Southeastern). Therefore, we grouped the reference samples from Iowa, Missouri, and Wisconsin into the Midwestern region ($n = 42$) and grouped Georgia and South Carolina to characterize the Southeastern region ($n = 40$). These source regions were genetically distinct ($F_{ST} = 0.045$). The F_{IS} values were 0.05 for Georgia, 0.057 for Wisconsin, −0.115 for Iowa, 0.076 for Missouri, and 0.089 for South Carolina. Only 1 locus (WT30-2) in South Carolina and Missouri significantly deviated from Hardy–Weinberg equilibrium ($P < 0.05$).

Based on translocation records, 67% of wild turkeys translocated into Texas were from the Midwest (i.e., from Iowa, Missouri, or Wisconsin) and 10% were from the Southeast (Georgia or South Carolina). We also documented numerous translocations within Texas (often from areas previously stocked) and from various other states (Fig. 2A, see Table S1, available online at www.onlinelibrary.wiley.com). At the county level, turkeys of Midwestern origin dominated translocations into most counties; however, this was particularly true for counties north of Interstate 20, where none of Fannin, Lamar, Red River, or Bowie counties received any turkeys from the Southeast. Counties in the southwestern portion of the region (Angelina, Nacogdoches) received the greatest number of turkeys from the Southeast. Translocations within Texas and from other (or unknown) states were most prevalent in Newton and Jasper counties in the southeastern portion of the region.

Approximately 33% of the east Texas turkeys were assigned ($q > 0.80$) to the Midwestern region and 4% of the samples grouped with the Southeastern region. The majority of turkeys (63%) were classified as admixed, which included turkeys that were affiliated with states not represented in the reference samples and, possibly, turkeys primarily descended from native Texas birds. The majority of the turkeys that grouped with the Southeastern samples were from Jasper and nearby counties, whereas only 4 of these samples were from counties along the Red River (Fig. 2B, see Table S1, available online at www.onlinelibrary.wiley.com).

Assignment Methods: Genetic Structure

Based on the largest change in mean likelihood value (ΔK; Evanno et al. 2005) for each cluster, we concluded that the most likely number of clusters in east Texas was 3 (Table 1). We refer to these genetic groupings as clusters 1–3. The largest number of the 294 samples (26%) came from cluster 1, whereas 20% were from cluster 2, 19% were from cluster 3, and 35% were admixed (see Table S2, available online at www.onlinelibrary.wiley.com). Almost 95% of turkeys in cluster 1 were sampled from counties along the Red River (Bowie, Fannin, Grayson, Red River, and Lamar) in northeast Texas. Approximately 68% of turkeys in cluster 2 were from Newton, Sabine, Jasper, and San Augustine counties in the southeast portion of the region (Fig. 3). Finally, most (80%) of the turkeys in cluster 3 were in Angelina and Nacogdoches counties in the southwest (Fig. 3). Cass, Harrison, and Panola counties were almost entirely comprised of admixed individuals, but all of these counties had small sample sizes ($n < 4$).

Pairwise F_{ST} values for the east Texas clusters as genetically defined by STRUCTURE were significant ($P < 0.05$) and ranged from 0.056 to 0.078. The F_{ST} value between cluster 2 and 3 ($F_{ST} = 0.078$) was greater than the F_{ST} value between

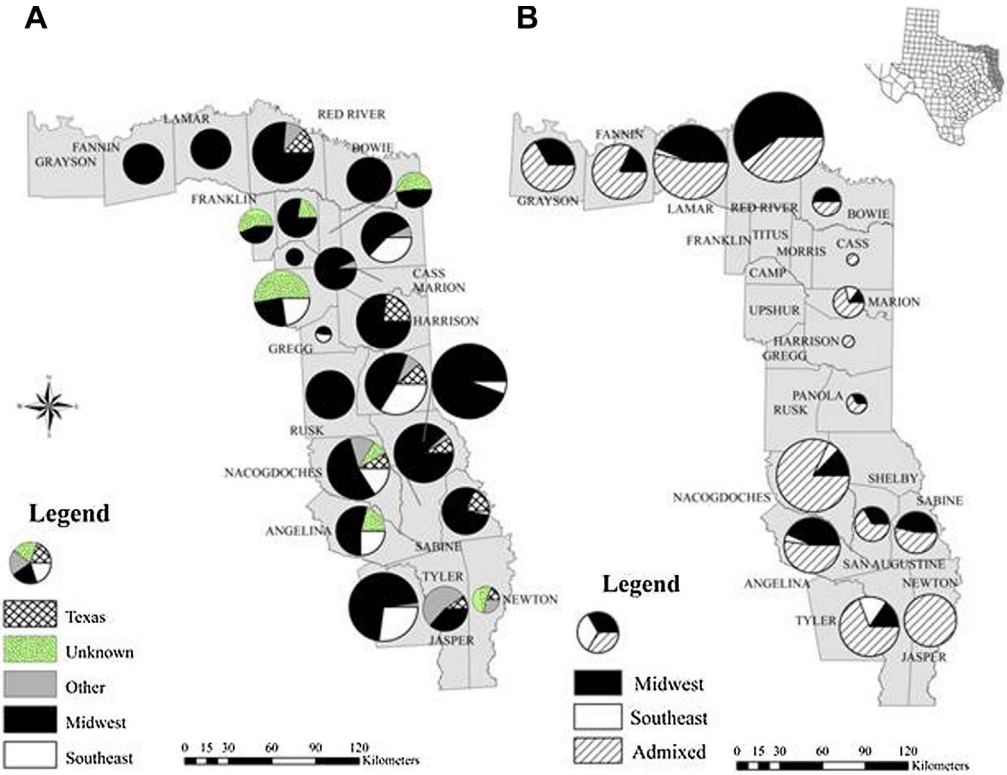

Figure 2. (A): Regions of origin by county for eastern wild turkeys translocated between 1979 and 2006 into east Texas, and (B) the regional origin of east Texas wild turkeys as identified by the program STRUCTURE (version 2.3.2; Pritchard et al. 2000) based on 8 microsatellite loci amplified from hunter-harvested and wild-captured wild turkey samples from east Texas (2007–2009). The size of the pie chart is proportional to the number of samples or translocations in that county.

1 and 3 ($F_{ST} = 0.067$) and cluster 1 and 2 were the most genetically similar clusters ($F_{ST} = 0.057$).

The genetic clusters appeared to correspond to 3 geographic regions within east Texas. We refer to these geographic regions as north (Bowie, Red River, Lamar, Fannin, and Grayson counties), southeast (Newton, Jasper, Sabine, and San Augustine counties), and southwest (Nacogdoches and Angelina counties; Fig. 3). We assigned individuals to a geographic region based on the county of harvest or capture and evaluated genetic differentiation among the regions with F_{ST} in the program ARLEQUIN. The pairwise F_{ST} values for the geographic regions of east Texas were significant ($P < 0.05$) and ranged from 0.029 to 0.041. The north and the southeast were the most similar ($F_{ST} = 0.029$), followed by the southeast and southwest ($F_{ST} = 0.039$), and the southwest and north ($F_{ST} = 0.041$). In the southern part of the region, Jasper and San Augustine counties appeared to be an admixture zone with influence from both southwest and southeast regions. To better understand the dynamics in this area, we removed the intermediate counties (San Augustine and Jasper) and recalculated F_{ST}. We found that the F_{ST} value between the southwest region (Angelina and Nacogdoches) and the eastern counties (Sabine and Newton) rose from 0.039 to 0.063.

Table 1. The log probability (L[*K*]), standard deviation (SD) and the change in mean likelihood value (ΔK) for each assumed number of genetic clusters (*K*) in east Texas. Results were generated by STRUCTURE (version 2.3.2; Pritchard et al. 2000) and were based on 10 microsatellite loci amplified from 294 wild turkey samples collected from east Texas (2007–2009).

K	L[*K*]	SD	ΔK
1	−11049.8	0.32	
2	−10758.8	8.56	7.78
3	−10534.3	1.99	29.78
4	−10368.9	3.89	14.04
5	−10258.1	55.33	0.21
6	−10135.5	5.55	10.26
7	−10069.8	9.44	

The spatial autocorrelation analyses in GENALEX were difficult to interpret, primarily because of a lack of precision in many locations provided by hunters. Frequently, they only provided the county or some other broad location for harvest, resulting in several samples having the same location. Nonetheless, we did not observe any evidence of spatial autocorrelation in the dataset. The clustered samples from captured turkeys only represented 17% of total samples, and the hunter-harvested birds appeared to be distributed evenly across the occupied counties; therefore, we did not consider biases due to spatial autocorrelation likely.

Genetic Diversity

Genetic diversity varied considerably among east Texas counties as measured by allelic richness (5.9–10.1), observed heterozygosity (0.60–0.76), and F_{IS} (0.0005–0.197; Table 2). In general, we observed the highest levels of genetic diversity

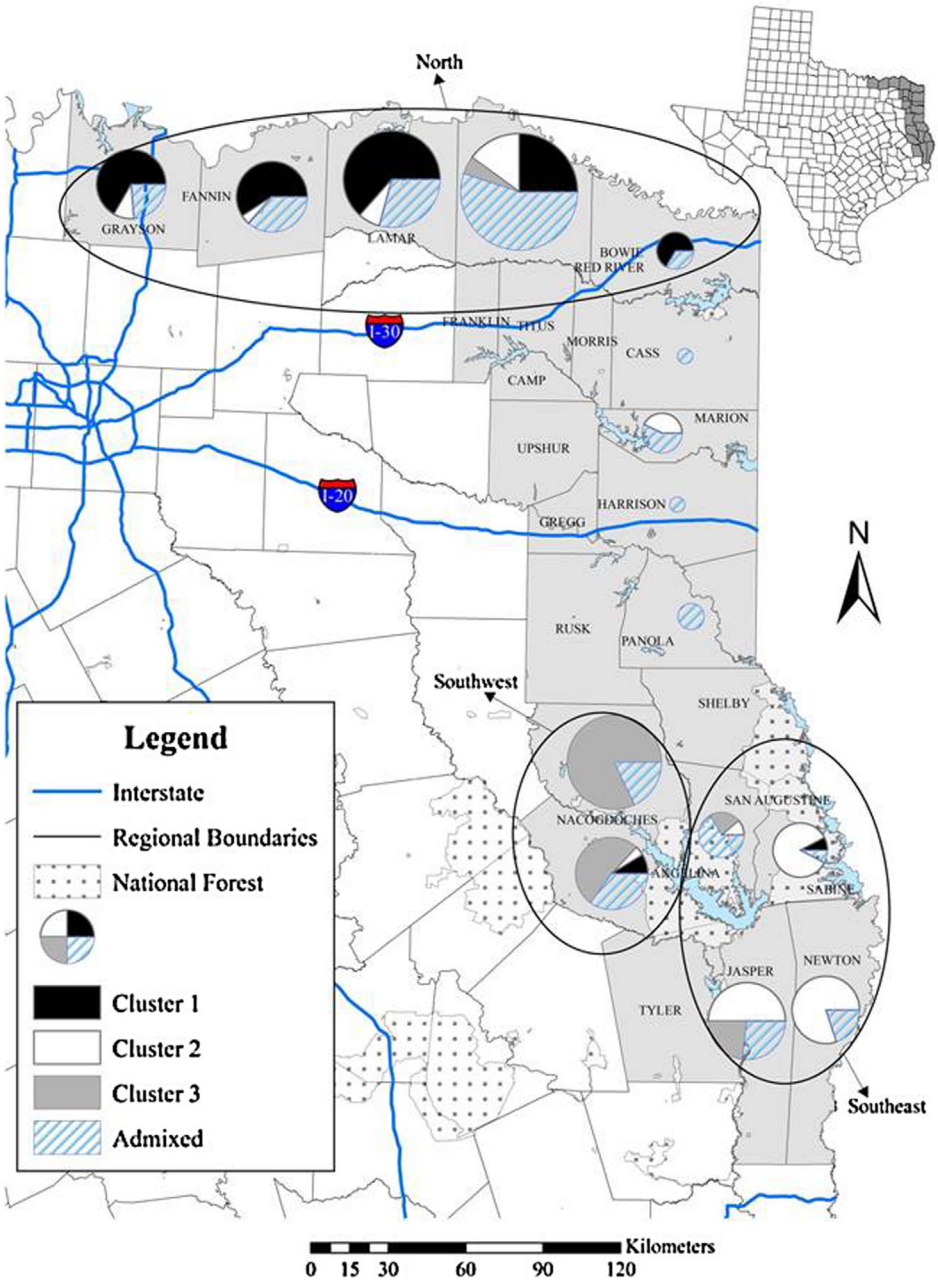

Figure 3. Genetic cluster assignment for east Texas wild turkeys as identified by the program STRUCTURE (version 2.3.2; Pritchard et al. 2000). Results were based on 10 microsatellite loci amplified in 294 hunter-harvested and wild-captured wild turkey tissue samples from east Texas (2007–2009). The size of the pie chart is proportional to the number of samples or translocations in that county.

Table 2. Summary statistics, including number of samples (n), average number of alleles (a), allelic richness (A), expected heterozygosity (H_{exp}), observed heterozygosity (H_{obs}), probability value for deviation from Hardy–Weinberg expectations (P), and F_{IS}, for genetic diversity of eastern wild turkeys from 9 counties in eastern Texas, 2007–2009.

County[a]	n	a	A	H_{exp}	H_{obs}	P	F_{IS}
Angelina	23	7.6	7.4	0.73	0.64	0.47	0.114
Fannin	22	8.6	7.2	0.75	0.72	0.48	0.020
Grayson	21	6.8	6.0	0.74	0.60	0.33	0.197
Jasper	26	7.4	7.4	0.71	0.60	0.24	0.163
Lamar	41	9.9	9.1	0.74	0.66	0.27	0.094
Nacogdoches	39	6.6	5.9	0.62	0.61	0.34	0.005
Newton	20	7.1	7.1	0.72	0.67	0.33	0.077
Red River	60	10.5	10.1	0.77	0.70	0.26	0.080
Sabine	13	6.9	6.5	0.72	0.66	0.41	0.096

[a] We did not include counties with <10 samples (Bowie, Cass, Harrison, Marion, Panola, San Augustine, and Wharton).

in counties along the Red River in the northeast portion of the region (e.g., Lamar and Red River) and in those counties with the greatest number of turkeys harvested. Between 1 and 4 individual loci deviated from Hardy–Weinberg equilibrium in most counties, primarily because of an excess of homozygotes compared to expectations (Table 2). We also found evidence for linkage disequilibrium for several loci between various counties. Although technical problems with microsatellite analyses (e.g., null alleles and binning issues) can cause deviations from Hardy–Weinberg equilibrium, null alleles and binning problems have not been noted with these loci in previous studies (e.g., Latch et al. 2006*c*). Similarly, no evidence for linked loci has occurred in previous studies (Latch et al. 2006*c*). As outlined further below, we suspect that factors of the population such as translocation of individuals from multiple source populations and past periods of small effective population size have resulted in these deviations from equilibrium at multiple loci.

Pairwise F_{ST} values among east Texas counties varied from −0.096 to 0.330. All pairwise values were significant ($P \leq 0.05$) except for those involving counties with small numbers of samples ($n \leq 3$), suggesting that sufficient differentiation exists for the clustering algorithm.

DISCUSSION

The 30 or more years of widespread eastern wild turkey translocations into east Texas remain the dominant influence on genetic structure across the landscape. We found that 33% of the samples were genetically similar to the Midwest region, <5% were similar to the Southeast, and approximately 63% were admixed or derived from some other source (e.g., other states, native Texas birds). The current influence of each region is similar to the relative contributions of these regions in historical translocation records (67% were Midwestern and 10% were Southeastern). Even at the county level, the proportions of Midwestern and Southeastern birds in translocations were comparable to the genetic contribution of Midwestern and Southeastern turkeys in many counties. For example, in Nacogdoches County approximately 60% of birds were translocated from the Midwest, 17% from the Southeast, and 23% from other sources (e.g., other states or within Texas). The relative contributions from each region compare favorably to 12% Midwestern origin and 5% Southeastern origin among turkeys sampled from Nacogdoches County. Our use of a relatively low fixed α value in the STRUCTURE calculations, although based on the inferred α from the source and reference populations independently, increased the proportion of individuals assigned to a source population and may have influenced our observations. The low α inferred in the unknown, east Texas turkeys may further suggest that the turkeys currently on the landscape retain a strong genetic signature of the reintroductions.

All studies of the genetic influence of translocations have potential biases because the source population is incompletely sampled. This is particularly true if the number of reference samples is small or they are spatially clustered and if the origin of translocated animals is not known precisely. For at least 1 of our source states (Iowa) our sample number was low ($n = 6$) and most translocation records indicated only the state of origin. However, the 6 reference samples from Iowa were from 6 different counties so they were not spatially clustered. Furthermore, we combined reference samples into larger regions (e.g., we had 42 reference samples from the Midwest region) that should have reduced the effect of small sample numbers in any 1 state.

Differences in translocation history were reflected in the presence of distinct genetic clusters in east Texas. In fact, the F_{ST} between these clusters (0.056–0.078) was similar to or greater than that between the Southeast and Midwest source regions. The high number of samples defined as admixed suggests that genetic mixing has occurred at the local and county scale, and that the block stocking strategy may have functioned as planned in some areas. Furthermore, the presence of turkeys of Southeastern origin in Red River, Lamar, and Jasper counties despite no recorded translocations to those counties from the Southeast indicates that some larger scale movements have occurred (although both Red River and Jasper counties received a large number of within-state translocations). However, low gene flow at the regional scale appears to be contributing to the continuing presence of larger scale genetic clusters despite the lack of clear geographic boundaries in the region. In Indiana, contiguous forested cover increased gene flow among reintroduced wild turkey populations, although the genetic signature of source populations remained detectable even in areas of heavy forest cover (Latch and Rhodes 2005). East Texas is a heavily forested region; however, in accordance with TPWD harvest records, large areas of the region remain sparsely populated or unoccupied by wild turkeys. These areas of low density may be preventing exchange of genetic material among populations. Although wild turkeys in Texas and elsewhere are mobile and may use large annual home ranges (Isabelle 2010), turkeys are not generally long-distance dispersers or colonizers. Brown (1980) found that dispersal distance could be as far as 20.1 km, but the maximum distance traveled by eastern wild turkeys in Alabama and Kentucky was 11.1 km (Speake et al. 1975). Translocated turkeys in east Texas moved a mean maximum dispersal distance of 4.4 km and only 1 bird dispersed >8 km (Hopkins 1981). Such distances may not be sufficient for significant gene flow among the regions in this study.

We observed a clear geographic and genetic separation between the northern region (mostly cluster 1) and southern counties (mostly clusters 2 and 3). These regions are separated by Cass, Marion, Harrison, Panola, and Shelby counties (see Fig. 3), which had low turkey density (<5 birds per 2.6 km^2; National Wild Turkey Federation 2000) and included the I-20 and I-30 interstate corridors and associated urban development. Three major river basins (Sabine, Cypress, and Sulfur) also run east to west separating the northern tier of counties from the more southern counties. All of these factors (few wild turkeys, natural barriers, and anthropogenic barriers) have likely limited gene flow. Sample

numbers from these intermediate counties were generally low (<7) and most were not assigned to any of the defined genetic clusters, suggesting that this is an admixture zone with low gene flow from the northern and the southern regions. If ongoing, regular dispersal occurred from the northern or southern regions, then we expected to see more evidence of first generation migrants (pure individuals), especially in counties (e.g., Cass and Shelby) adjacent to the defined regional clusters. Except for Marion County, all of the turkeys that we sampled were admixed in origin. Marion County exhibited a strong influence of cluster 2 (3/7 turkeys). This could be a result of natural migration from the south; however, turkeys historically were translocated into Marion County from Jasper and Newton counties (Texas Parks and Wildlife Department, unpublished data), both of which contain a strong influence from genetic cluster 2.

Despite the geographic proximity of the southeastern and southwestern regions, the genetic signatures of translocations remained evident in these regions. Nacogdoches and Angelina counties had among the greatest historical contributions from the Southeast United States (Georgia and South Carolina). The southeastern counties, particularly Jasper and Newton, had translocations from many source populations, including from other parts of east Texas, from Louisiana, and from Mississippi (see Table S1, available online at www.onlinelibrary.wiley.com). Furthermore, turkeys were translocated from Jasper County into Harrison County (near the northern region) and both these counties reportedly received turkeys from Trinity County in east Texas (Texas Parks and Wildlife Department, unpublished data). These within-state translocations of birds may help explain the closer genetic link between the north and southeast regions.

The reason that genetic separation has been maintained between the southeast and southwest regions is not clear from habitat differences or geographic boundaries. Sam Rayburn reservoir has separated parts of Angelina and Nacogdoches counties from the southeastern counties for 45 years (Fig. 3; Texas Parks and Wildlife Department 2010); however, the reservoir is not a complete barrier to movements. Turkeys appear to be distributed across this part of the state, albeit at low density. In addition to geographic and habitat separation, the genetic influence of translocations was similarly evident in white-tailed deer in Mississippi despite a continuous distribution across the landscape (DeYoung et al. 2003). Wild turkeys may have very little incentive to disperse from their natal area if densities are well below carrying capacity and habitats are relatively homogenous in the region. Jasper and San Augustine counties consisted of individuals that were affiliated with clusters 2 and 3, suggesting a second admixture zone in these counties. County-level F_{ST} test results suggest that Sabine and Newton counties are more differentiated from the southwest region than San Augustine and Jasper counties. The STRUCTURE results indicate that the southeast region forms a discrete genetic cluster. Thus, San Augustine and Jasper counties appear to represent an admixture zone with more influence from the east and minor genetic contributions from the west and from original translocations to those 2 counties. These 2 counties are among the most rural, heavily forested counties in east Texas, and the presence of contiguous forest cover in the counties may have facilitated admixture from adjacent clusters.

Some of the genetic structure evident in the population may result from the influence of remnant native turkeys. Remnant populations in the mid-1900s were believed to persist in Tyler, Polk, Newton, and Hardin counties (Texas Game, Fish, and Oyster Commission 1945) and the fate of these populations is unknown. We would expect to observe the greatest genetic influence of native birds in Jasper and Newton counties. Natural immigration of eastern wild turkeys from adjacent Oklahoma and Louisiana into the northern and southeastern clusters, respectively, may also have contributed to the observed clustering. Both states have areas of relatively high wild turkey density (6–15 birds per 2.6 km^2) near the Texas border (National Wild Turkey Federation 2000).

Perhaps as a result of limited gene flow and residual founder effects, the genetic diversity of some Texas counties was low compared to other studied wild turkey populations (Latch and Rhodes 2005; Latch et al. 2006*a*, *c*). The average allelic richness (A) for east Texas counties ranged from 5.9 to 10.1 (see Table 2), and several counties had values less than those reported for Indiana (7.3–9.8, Latch and Rhodes 2005), west Texas ($\bar{x} = 8.9$, Latch et al. 2006*c*), and Kansas ($\bar{x} = 17.8$; Latch et al. 2006*a*). The average observed heterozygosity (H_o) for the east Texas counties ranged from 0.61 to 0.72, which is similar to other studies where the average observed heterozygosities ranged from 0.61 to 0.74 (Latch and Rhodes 2005; Latch et al. 2006*a*, *c*). The allelic richness and F_{IS} values suggest that some counties in east Texas have suffered diversity loss. This was particularly true for counties in the putative admixture zones, where harvest was limited to small numbers of turkeys; however, some counties with relatively large numbers of turkeys (e.g., Nacogdoches, Grayson, Sabine) also showed evidence of reduced diversity. Diversity at the larger scales (e.g., the genetic clusters) was high and similar to other studies (A 7.2–11.3, H_o 0.61–0.66), perhaps reflecting the diversity in the source populations for translocated birds (16 states represented in the last 20 years). The subsequent mixing of these multiple source translocations could have produced a population with greater overall genetic diversity than what would result from a single-source translocation (Bodkin et al. 1999). Furthermore, the high level of human-induced immigration present in east Texas may have resulted in a restoration of genetic variation even after a founder event or bottleneck (Keller et al. 2001).

MANAGEMENT IMPLICATIONS

Limited gene flow appears to be occurring at regional scales in east Texas. Forming 2 or 3 distinct turkey management units reflecting the regions identified in this study may be appropriate so that restoration or harvest practices can be customized to meet the goals for that area. Movement of wild turkeys into low-density areas (e.g., Cass, Marion, Shelby

counties) is apparently occurring only slowly. Additional management actions such as harvest limitations or further translocations to enhance these low-density turkey populations may be necessary to achieve abundance goals in these counties. Furthermore, the limited gene flow and maintenance of source population genetics in wild turkeys suggests that the population connectivity that the traditional block stocking approach relies upon has not occurred in many parts of the region. Alternative strategies such as super-stocking turkeys may be a more effective method (Lopez et al. 2000, Isabelle 2010).

Some studies in east Texas found that male turkeys from Midwestern states had considerably lower survival rates than turkeys translocated from Southeastern states (George et al. 2000, Feuerbacher et al. 2005), possibly because of habitat differences between source states and east Texas. These results have led to some concern about the long-term survival and effectiveness of translocating Midwestern birds to east Texas. However, we found that the genetic contribution of turkeys from Iowa, Missouri, and Wisconsin was consistent with their representation in translocation records and we saw little evidence to support the assertion that turkeys from the Midwest performed poorly compared to those from the Southeast.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Table S1. Regional affiliation of eastern wild turkeys in 9 eastern Texas counties based on translocation records (1979–2006) and on genetic assignments from 8 microsatellite loci amplified from 294 wild turkey samples (2007–2009).

Table S2. Cluster affiliation of wild turkeys sampled in east Texas counties. Results were generated by STRUCTURE (version 2.3.2; Pritchard et al. 2000) and were based on 10 microsatellite loci amplified from 294 wild turkey samples collected from east Texas (2007–2009).