Conservation Genetics **5:** 631–645, 2004.

Assessing losses of genetic diversity due to translocation: long-term case histories in Merriam's turkey (*Meleagris gallopavo merriami*)

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Received 9 October 2003; accepted 8 February 2004

Key words: bottleneck, microsatellite, translocation, wild turkey

Abstract

Translocation is a widely used tool in wildlife management, but populations established as a result of translocations may be subject to a range of genetic problems, including loss of genetic diversity and founder effects. The genetic impact of single translocation events can be difficult to assess because of complex management histories in translocated or source populations. Here we use molecular markers to assess the genetic impact of three well-documented translocation events, each occurring between 42 and 53 years ago and each originating from a native, extant source population that we also included in our study. Comparing translocated populations to their sources, we found genetic evidence of a recent bottleneck in all three translocated populations, including one which is now a very large, productive population. Based on our results, we recommend caution in (1) using short term census data to assess the long term success of a translocation and (2) conducting serial translocations (i.e., using translocated populations as the source for other translocations), which could exacerbate a genetic bottleneck. We also used the data on translocated populations to investigate the relative utility of three bottleneck detection methods. With this dataset, only assessment of the modal allele frequency distribution, described by Luikart et al. [Journal of Heredity, 89, 238–247 (1998)], provided evidence of a bottleneck in the absence of source population data.

Introduction

The restoration of the wild turkey (*Meleagris gallopavo*) in the U. S. is generally considered to be one of the most dramatic successes in the history of wildlife management. The wild turkey was extirpated from large portions of its historical range following European settlement, apparently due to a combination of habitat alterations and unregulated overhunting (Mosby and Handley 1943; Walker 1949; Mosby 1949; Mosby 1959; Bent 1963; Williams 1981). These declines impacted all subspecies, although they were particularly dramatic in the Eastern subspecies (*M. g. silvestris*), which was extirpated from approximately eighty percent of its pre-settlement range. Intensive management efforts, including hunting restrictions, habitat improvement, and widespread translocation programs, led to the restoration of the wild turkey throughout most of its historical range (Kennamer et al. 1992). Since that time, translocation has continued to be a common and popular tool in the management of wild turkey and many other wildlife species, both for restoration and for the establishment of populations well beyond the animals' historical range (Mock et al. 2001; Tapley et al. 2001). In wild turkey and other game species, it has become a common practice to conduct "serial translocations," whereby a population of birds is

established via translocation and then itself becomes the source for further translocation.

There are several risks to recipient populations associated with supplementation of wildlife species, including ecological disruption, the spread of epizoonotic diseases to both wild and domestic populations, the facilitation of hybridization between different species or subspecies, and the genetic "swamping" of locally adapted populations with genotypes adapted to different conditions. There also are genetic risks associated with the establishment of new populations via translocations, primarily due to a reduction in genetic diversity and potentially leading to inbreeding depression, divergence due to founder effects, or limitations on the ability of a population to adapt to changing environments (Lande 1988; Leberg 1991; Frankham 1995, 1999; Singer et al. 2000). The success of a translocation is dependent on the sex ratio of the individuals translocated, the number and genetic diversity of the individuals contributing to subsequent generations, and the effective size of the population over time (Lacy 1987; Griffith et al. 1989; Haig et al. 1990; Leberg 1990; Newman and Pilson 1997). A number of studies have investigated the genetic consequences of wildlife translocations using neutral markers as indicators of diversity (e.g., Maruyama and Fuerst 1985; Haig et al. 1990; Leberg 1992; Leberg et al. 1994; Luikart et al. 1998; Leberg and Ellsworth 1999; LePage et al. 2000; Spencer et al. 2000; Garza and Williamson 2001; Williams et al. 2002). Unfortunately, many of these studies are complicated by multiple translocations into the same area, the preexistence of a native population of the same species, migration into the translocated population from other populations, short time frames, or uncertain translocation histories. These factors make it difficult to empirically assess the loss of genetic diversity due to a single translocation.

In Colorado and Arizona, three well-documented translocations of the Merriam's wild turkey (*M. g. merriami*) were made from two proximal native source populations into isolated areas between 42 and 53 years ago. The source populations had not received prior or subsequent translocations, and the translocated populations were not supplemented following their initial establishment. The source populations are thought to represent two of the remaining original populations of the Merriam's subspecies, and are comparable to native populations of other turkey subspecies with respect to genetic diversity measures (Mock et al. 2002). These three translocated populations, and their respective source populations, provide an excellent opportunity to investigate the loss of genetic diversity due to single translocation events. Additionally, two of the translocated populations were derived from the same source population, but were introduced into two very differently sized habitat patches, allowing us to assess the importance of habitat patch size and population expansion potential in translocations.

The three translocations used in this study also provided an opportunity to investigate the relative utility of bottleneck detection methods. Each translocation is well documented, and the bottleneck age, size and duration are known. The translocated populations are isolated, and thus the genetic signatures associated with the bottleneck have not been obscured by gene flow. Finally, the source populations have remained relatively unchanged since the translocation event, and therefore represent a non-bottlenecked population that can be used as a baseline for comparison. In recent years, several methods have been developed to detect genetic bottlenecks, each of which relies on a basic theoretical prediction about the behavior of a population during and after a bottleneck. However, these methods have not been evaluated empirically in a clear-cut system. Three methods will be considered here: the test for heterozygosity excess (Cornuet and Luikart 1996), the *M* ratio test (Garza and Williamson 2001), and the mode shift test (Luikart et al. 1998).

Study locations and population histories

The Merriam's subspecies of wild turkey, native to the southwestern U.S. (Figure 1), was less affected by the dramatic declines of the early 20th century than the more eastern subspecies, but has nonetheless been the subject of many translocation efforts in the past to restore or expand its range (Tapley et al. 2001). Three of these translocations are the focus of our study. The first of these was a translocation from Stoneman Lake, AZ (MSL) to the Kaibab Plateau (MNK) on the north rim of the Grand Canyon in 1950 (Figure 1). The MSL population is thought to be a native population of

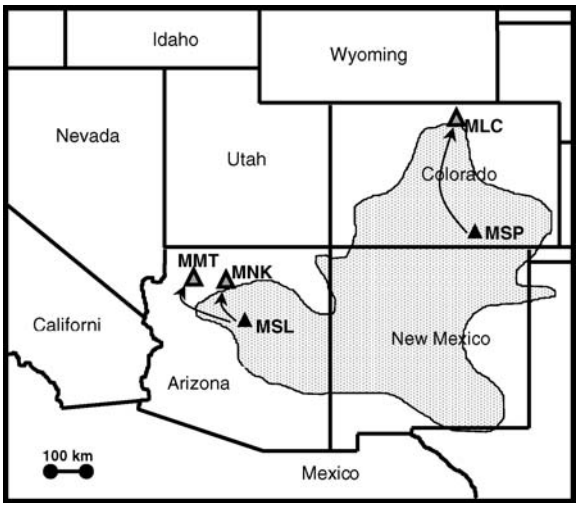

Figure 1. Location of Merriam's wild turkey sample populations: Larimer County, Colorado (MLC), Spanish Peaks, Colorado (MSP), Mt. Trumbull, Arizona (MMT), North Kaibab Ranger District, Kaibab National Forest, Arizona (MNK), Stoneman Lake, Arizona (MSL). Shaded area represents approximate boundaries of pre-European distribution of the Merriam's turkey (Schorger 1966). Black triangles represent translocation source populations, and populations resulting from these translocations are represented by shaded triangles.

Merriam's turkey, and wild turkeys have not been translocated into this region from other locations. The habitat occupied by this population is predominated by ponderosa pine (*Pinus ponderosae*), other mixed conifers and oaks (*Quercus* spp.). The Stoneman Lake area is somewhat contiguous with large areas of suitable habitat in eastern Arizona and western New Mexico, and there is evidence of long term gene flow across this range (Mock et al. 2002). The translocated birds consisted of 14 males and 28 females, captured during a series of three trapping efforts in different areas near Stoneman Lake. The Kaibab Plateau is a large area (about 1,065,000 acres) of contiguous habitat that is isolated from other areas of suitable turkey habitat by large expanses of desert. This population, now one of the largest and most robust in the state of Arizona, is thought to be larger than the Stoneman Lake population (Brian Wakeling, Arizona Game and Fish Department, personal communication) and has become a common source for further translocations into habitats within and outside of Arizona.

MSL also was the source of the second translocation in our study, which established a population of wild turkeys at Mount Trumbull, Arizona (MMT) 11 years later. Mount Trumbull is a volcanic peak with surrounding suitable turkey habitat that encompasses approximately 30,000 acres. The area consists of a small ''island'' of turkey habitat dominated by ponderosa pine and mixed conifers. It also is isolated from other potential turkey habitat by large tracts of intervening deserts. This translocation consisted of 16 males and 21 females, collected during three trapping efforts near Stoneman Lake. The MMT population is small but has a high density relative to other populations in Arizona.

The third translocation in our study was from the Spanish Peaks area (MSP) in southern Colorado to Larimer County, Colorado (MLC). Both of these areas are dominated by ponderosa pine and mixed conifer stands, although Larimer County is just beyond the historical boundaries of both oak brush and wild turkeys. This translocation included only 8 males and 7 females, collected in a single trapping effort in 1957. The habitat occupied by the MLC population is not completely isolated from other occupied wild turkey habitat in northern Colorado, but the amount of migration between the MLC population and other populations is thought to be very low (Richard Hoffman, Colorado Division of Wildlife, personal communication). The MLC population ranges over an area of approximately 410,000 acres.

Methodology

Sample collection

Tissue samples (MSL = 16, MNK = 19, MMT = 9) were obtained from the Arizona populations at hunter check stations or through the submission of samples via the mail from individual hunters in 1998 and 1999. These tissues were collected using clean razor blades, pulverized in a petri dish, and immediately placed in 5 ml of a lysis buffer (0.1 M Tris-HCl pH 8.0, 0.1 M EDTA, 0.01 M NaCl, 0.5% [w/v] SDS) (Longmire et al. 1988). Blood samples from the Colorado populations were obtained as a part of a trapping effort conducted during the winter of 1995 and 1996. Samples from these populations, MSP (n = 21) and MLC (n = 14), were collected by jugular venipuncture and preserved by collecting directly into

serological tubes containing EDTA. In the laboratory, 0.5 ml of each blood sample was mixed with 4.5 ml lysis buffer.

DNA extraction and microsatellite amplification

A 1.5 ml aliquot of each sample/buffer mixture was digested using 500 μg proteinase K and 100 μl 0.1 M dithiothreitol and overnight incubation in a 55 °C water bath. DNA was extracted from all samples using a salt-chloroform protocol and precipitated with isopropanol (Mullenbach et al. 1989). The quantity and quality (fragment size range) of DNA from all samples was assessed using electrophoresis on 0.7% agarose gels stained with ethidium bromide. Nine microsatellite loci, including loci previously described in Huang et al. (1999) and Latch et al. (2002), were amplified from each of the samples using the primers and reaction conditions described in Table 1. PCR-amplified microsatellite loci were then combined in groups of two or three, mixed with ROX400HD internal lane standard (Applied Biosystems) and electrophoresed through a 5% polyacrylamide gel (Long Ranger Singel Packs; Cambrex) on an ABI 377–96 DNA sequencer. Allele sizes were determined using GeneScan 3.1 and Genotyper 2.5. Ambiguous genotypes and individuals whose genotypes were at low intensity (< 100) were rescored to confirm their genotype.

Data analysis: assessing effects on wild turkey populations

We evaluated deviations from Hardy-Weinberg equilibrium (HWE) using exact testing with a Monte Carlo approach in GENEPOP software (Raymond and Rousset 1995). Combined probabilities over all loci for HWE deviations were calculated for each population.

The genetic effect of primary concern with translocation is the loss of genetic diversity due to neutral processes (i.e., population bottlenecks followed by drift). We used observed multilocus unbiased heterozygosity (Nei 1978) and allelic richness to compare neutral genetic diversity in the

Table 1. Locus-specific primers and reaction conditions for microsatellite loci used in this study

Quantities are in μl, and are appropriate for a 10 μl reaction volume. All reactions included 0.15 μl (5 U/μl) Taq polymerase, 1 μl dNTPs (0.2 mM), and 1 μl PCR buffer with MgCl2 (10X). GenBank accession numbers are provided in parens following the locus name. Forward primers were fluorescently labeled on the 5′ end with either JOE (green), TAMRA (yellow), or 6-FAM (blue)

Locus	Primers (5′ → 3′)	DNA (10 ng/μl)	Primer (10 μM)	MgCl2 (25 mM)	°C
TUM6*	F:AAATCAGTGTCATTGTGCAA	0.2	0.3	0.2	59
(U79372)	R:TTCTGCTACCTGACCATGTA				
TUM23*	F:CGGCATCTCCAGCTCCAT	0.5	0.4	0	60
(U79332)	R: CCACGGAGAGTCCTGGAT				
TUM50*	F:CTGATGTCTTAAAGGCT	0.5	0.2	0.2	46
(U79306)	R: ACAAAAACGAACTGATCA				
WT10§	F:TTGGAACAGGAGAAATTTCAGT	1	0.4	0	55
(AF111453)	R: TATTTGTTGCAAGGCAGCAG				
WT32*	F:TGTTGGAGCTGACTGGAACA	0.2	0.3	0	59
(U79387)	R:TGTCTAGATGAGCAGCTGAATG				
WT54§	F:AAAGAGCAGCGTGTTCCAGT	0.2	0.2	0	60
(U79330)	R: TTCAAAACAGTGTCACGATTCC				
WT30-2*	F:GAAGGAGGAACCAAAAACTACG	0.5	0.2	0	58
(U79391)	R: CAACCATGGTGTGAGGAGG				
WT38-2§	F:GGTTTGAGCAGAGTGAATCTCA	0.2	0.3	0	60
(U79365)	R: ATTGGTTGGGGGAGGAAC				
WT90-2§	F:AATCAACCCATTTGTTCCCA	0.5	0.2	0	58
(AF111645)	R: GTGCTTTGATTTAAAAGCCCC				

Loci originally described in Huang et al. (1999)* and Latch et al. (2002)§ are so denoted.

source and translocated populations of wild turkey. The significance of gene diversity differences between source/translocated population pairs was assessed using the Wilcoxon paired sign rank test (Zar 1984), pairing locus-specific data. Because there was a large variation in sample sizes among populations, and because measures of allelic richness can be quite sensitive to sample size, we used rarefaction (Hurlbert 1971; Krebs 1989; Petit et al. 1998) to adjust for sample size discrepancies in pairwise population comparisons with PAST (PAleontological STatistics) software (Hammer et al. 2001).

Translocated populations may show considerable genetic divergence from source populations (e.g., Leberg et al. 1994; Rowe et al. 1998; Williams et al. 2000; Williams et al. 2002) due to founder effects and genetic drift acting on selectively neutral loci. We assessed genetic divergence among populations using four approaches. First, we performed exact tests of population differentiation among pairs of source and translocated populations using a Markov Chain Monte Carlo approach (Raymond and Rousset 1995) on a locus-by-locus basis with Tools for Population Genetics Analysis (TFPGA) software version 1.3 (Miller 1997). To assess the probability of differentiation between pairs of populations, we used Fisher's combined probability test with a Bonferroni correction as a global test over all loci (Sokal and Rohlf 1995). Second, we constructed a UPGMA dendrogram using a matrix of Nei's (1972) unbiased distances to illustrate the relationships among populations, using TFPGA 1.3. The relative strength of each node in this dendrogram was assessed by bootstrapping 1000 times over loci. Third, we performed assignment tests using GeneClass software (Cornuet et al. 1999) to determine whether individuals sampled from the translocated populations could be associated with their source populations based on genotypic information. For this analysis, a likelihood approach was used to assign individuals from translocated populations (MLC, MMT, and MNK) to one of the source populations (MSL or MSP). We performed separate analyses using alternate threshold rejection criteria of $P < 0.01$ and $P < 0.05$. Probabilities of assignment to each of the source populations were estimated on a per-individual basis by simulation (10,000 individuals per population), using Bayesian estimates of population allele frequencies. Fourth, we used factorial correspondence analysis (FCA) to assess patterns of variation among individuals in our study. Because missing data can distort variance patterns in FCA, we excluded three samples (one from MNK, two from MSL) from our dataset prior to this analysis. We used Genetix Software, Version 4.03 (Belkhir et al. 2000) to produce a FCA plot along the three axes capturing the majority of variation in the dataset.

Data analysis: assessing effectiveness of bottleneck detection methods

We used three different approaches to determine whether a population bottleneck was detectable in the translocated populations. First, we performed the heterozygosity excess test described by Cornuet and Luikart (1996). This test relies on the fact that during a bottleneck, allelic diversity is reduced faster than heterozygosity (H_e, expected under Hardy-Weinberg equilibrium), due to a loss of rare alleles that do not contribute significantly to overall H_e. The deficiency of alleles is a complex function of four parameters: time since the beginning of the bottleneck (t), the ratio of effective population sizes before and after the bottleneck (α), the mutation rate of the locus (μ), and the sample size of genes (n) (Cornuet and Luikart 1996). The magnitude of an allele deficiency will initially increase with t, but upon reaching a maximum (as determined by α, μ, and n) will decrease asymptotically toward zero, corresponding to a new mutation-drift equilibrium (Maruyama and Fuerst 1985). To test for a heterozygote excess in each of the translocated populations, we compared H_e (based on observed allele frequencies) to the heterozygosity expected from the observed number of alleles at mutation-drift equilibrium (H_{eq}) using BOTTLENECK software (Cornuet and Luikart 1996) under the two-phased model of mutation (TPM with 70% SMM; Di Rienzo et al. 1994). The significance of the deficiency was calculated using both a Wilcoxon sign-rank test and sign test (Cornuet and Luikart 1996; Luikart and Cornuet 1998).

Second, we calculated the mean ratio (M) of the total number of alleles to the allelic size range, following Garza and Williamson (2001). The M ratio test also is based on the tendency for rare

alleles to be lost during a bottleneck. Because the allelic losses are correlated with frequency, and not size, the number of alleles (k) will decrease more rapidly than the range in allele sizes (r) during a bottleneck. The ratio $M = k/r$ will therefore be smaller in bottlenecked populations than in equilibrium populations. Because only a subset of mutations (those that increase k by a greater proportion than they increase r) contribute to an increase in M, this method may be able to detect older bottlenecks than other methods. We calculated M for both source and translocated populations, averaging over polymorphic loci.

Finally, we employed the mode shift test, which uses the distribution of allele frequencies to detect bottlenecks (Luikart et al. 1998). Non-bottlenecked populations are expected to be near mutation-drift equilibrium and thus they should have more alleles at low frequency (< 0.1) than at intermediate or higher frequencies. While the expected proportion of these low frequency alleles will vary with the mutation rate and the model of mutation at a particular locus, they are always expected to be more abundant than alleles at intermediate frequency (Nei et al. 1975). The mode shift test detects the distortion in the distribution of allele frequencies in recently bottlenecked populations from many rare alleles to fewer, more common alleles (Luikart et al. 1998). For this approach, we excluded the data from the two loci (TUM6 and WT10) that had only two alleles.

Results

Genotypic proportions did not vary significantly from Hardy-Weinberg expectations in any of the populations tested (MSL: $P = 0.880$, MNK: $P = 0.251$, MMT: $P = 0.075$, MSP: $P = 0.575$, MLC: $P = 0.096$). Average heterozygosity over all loci was lower in two of the translocated populations (MNK and MMT) than in their respective source populations (Table 2). The difference in gene diversity was significant ($P < 0.05$) only in the MSL versus MMT comparison. The total number of alleles over all loci in the translocated populations was consistently reduced relative to their source populations (Table 2). This pattern persisted when expected allele numbers were adjusted for differing sample sizes through rarefaction. This trend also was evident in locus-specific data (Table 3). A reduction in the total number of unique alleles in samples from the translocated populations was particularly dramatic: MSL(7) versus MNK(3), MSL(13) versus MMT(1), and MSP(11) versus MLC(1)(Appendix 1). There was a clear tendency for the rarer alleles to be lost in the translocated populations (Appendix 1). Allelic deficiency relative to the source population was most pronounced in the MMT and MLC populations.

Table 2. Genetic diversity indices for source and translocated (italics) population pairs of Merriam's wild turkey H = Nei's (1978) average unbiased heterozygosity over all loci. Population designated with an asterisk had significantly ($P < 0.05$) lower gene diversity using the Wilcoxon paired sign rank test

Population	H	Total # alleles (w/rarefaction)
MSL	0.5666	39
MNK	0.4830	35 (32.7)
MSL	0.5666	39 (34.7)
MMT	0.4604*	27
MSP	0.4881	38 (35.4)
MLC	0.4950	27

Exact tests of population differentiation indicated that all pairs of populations were distinct from each other ($P < 0.005$). However, the UPGMA dendrogram (Figure 2) indicated strong bootstrap support for the close association between translocated populations and their source populations. This association also was evident in the FCA plot of interindividual variation in the dataset, which illustrated the extent of covariance between the source and translocated populations (Figure 3).

Assignment testing, using the two source populations as references, linked translocated individuals to the correct source population or both source populations (with a threshold rejection criterion of $P < 0.01$) for 11/14 (78.6%) of the individuals from the MLC population, 8/9 (88.9%) of the individuals from the MMT population, and 17/19 (89.5%) of the individuals from the MNK population (Table 4). In the 10 cases where individuals were assigned to both source populations, the probability of belonging to the correct source population exceeded the probability of belonging to the other source population in all but three individuals from the MNK population. For these three MNK individuals, P[MSP] versus

Table 3. Locus-specific allelic richness contrasts between source and translocated (italics) populations of Merriam's wild turkey. Observed numbers of alleles and number of alleles expected following rarefaction (*r*), including the standard deviation and lower or upper 95% confidence limit (italics) are provided. An asterisk indicates that the 95% confidence interval for the rarefied population did not include the number of alleles observed in the comparative population

Population contrast	Locus								
	TUM 23	TUM 50	TUM 6	WT 10	WT 30-2	WT 32	WT 38-2	WT 54	WT 90-2
MSL (n = 12)	5	8	2	2	3	3	8	4	4
MNK (n = 19)	4	6	2	2	3	3	6	4	5
MNK (*r* = 12)	3.50	5.85	1.96	2	2.26	2.59	5.94	3.83	4.79
SD	(0.58)	(0.35)	(0.40)	(<0.01)	(0.67)	(0.52)	(0.48)	(0.76)	(0.43)
Upper 95% c.l.	*(4.64)**	*(6.55)**	*(2.36)*	*(2.00)*	*(3.58)*	*(3.61)*	*(6.42)**	*(4.59)*	*(5.63)*
MSL (n = 12)	5	8	2	2	3	3	8	4	4
MSL (*r* = 9)	4.37	6.17	1.85	2.00	2.79	2.95	6.88	3.83	3.84
SD	(0.62)	(0.96)	(0.36)	(<0.01)	(0.42)	(0.21)	(0.81)	(0.38)	(0.36)
Lower 95% c.l.	(3.15)*	*(4.29)*	*(1.15)*	*(2.00)*	*(1.97)*	*(2.54)**	*(5.29)**	*(3.09)**	*(3.14)**
MMT (n = 9)	3	6	2	2	2	2	4	3	3
MSP (n = 21)	5	8	1	2	4	5	5	5	3
MSP (*r* = 14)	4.63	7.26	n/a	1.99	3.33	4.00	4.55	4.94	3.00
SD	(0.50)	(0.50)		(0.09)	(0.66)	(080)	(0.56)	(0.25)	(0.62)
Lower 95% c.l.	(3.65)	*(6.28)**		*(1.80)*	*(2.04)**	*(2.44)*	*(3.45)**	*(4.45)**	*(2.86)*
MLC (n = 14)	4	6	1	2	2	3	3	3	3

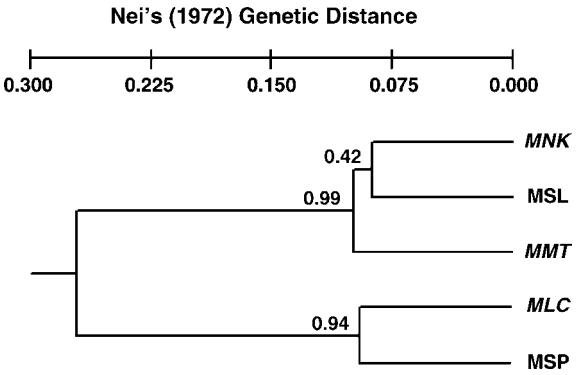

Figure 2. UPGMA dendrogram of source and translocated (italics) Merriam's wild turkey populations. Bootstrap support over loci (1000 replicates) is indicated at interior nodes.

P[MSL] were not strikingly different: 0.045 versus 0.023, 0.038 versus 0.015, and 0.224 versus 0.167, respectively. Using the threshold rejection criterion of $P < 0.01$, only one individual from the MMT population was classified to the wrong source population ($P = 0.0195$). Using the threshold rejection criterion of $P < 0.05$ in the assignment tests, fewer individuals were assigned to the correct or both source populations, more were assigned to neither source population, and fewer were assigned to the wrong population (Table 4).

A significant heterozygosity excess (consistent with a population bottleneck) was detectable in the MLC population with the Wilcoxon test ($P = 0.0039$) under the TPM model of mutation. None of the other populations (source or translocated) showed significant evidence of a population bottleneck using this approach (Table 5). The *M* ratios for all the translocated populations were reduced compared to their respective source populations, although the 95% confidence intervals for these means did overlap between all source-translocation population pairs (Table 5). The MMT population showed the most dramatic decrease in the *M* ratio.

The mode shift method for assessing changes in allele frequency distributions (Luikart et al. 1998) (Figure 4) showed that all three translocated populations had undergone a modal shift characteristic of a population bottleneck, a pattern that was absent in the source populations. The mode-shift test did not compensate for variation in sample sizes, and it is possible that the small sample sizes in MMT and MLC reduced the number of alleles in the lowest frequency class to the extent that a mode shift was observed. In the source populations, however, the number of alleles required to be lost from the lowest frequency classes to induce a mode shift (15 for MSP and 5 for MSL) (Figure 4) would have exceeded the total number of alleles lost through rarefaction in both MSP (reduction by three al-

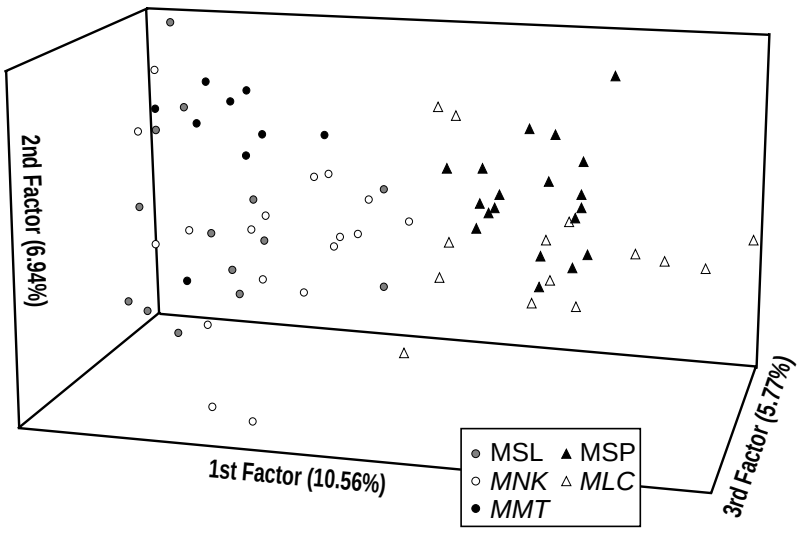

Figure 3. Factorial correspondence analysis (FCA) plot of individual Merriam's wild turkeys from five populations. Italicized populations were the result of translocation from source population MSL or MSP. Percentage of variance captured by each of the three axes is designated.

Table 4. Results of assignment tests on individuals from translocated (MNK, MMT, or MLC) versus source (MSL or MSP) populations of wild turkey, using two rejection threshold criteria: $P < 0.01$ and $P < 0.05$)

Assignment testing results	Rejection threshold criterion	Population tested		
		MNK (n = 19)%	MMT (n = 9)%	MLC (n = 14)%
# (%) assigned only to	$P < 0.01$	10 (52.6)	7 (77.8)	9 (64.3)
Correct source population	$P < 0.05$	9 (47.4)	7 (77.8)	10 (71.4)
# (%) assigned to both	$P < 0.01$	7 (36.8)	1 (11.1)	2 (14.3)
Source populations	$P < 0.05$	3 (15.8)	0	1 (7.1)
# (%) assigned to neither	$P < 0.01$	2 (10.5)	0	3 (21.4)
Source population	$P < 0.05$	7 (36.8)	2 (22.2)	3 (21.4)
# (%) assigned to wrong	$P < 0.01$	0	1 (11.1)	0
Source population	$P < 0.05$	0	0	0

leles with rarefaction to n = 14) and MSL (reduction by four alleles with rarefaction to n = 9). These results suggest that the mode shifts observed in MMT and MLC were unlikely to have been due to small sample size alone. Furthermore, a modal shift was also observed in the MNK population, which was represented by a larger sample size than MSP.

Discussion

Genetic effects of translocations

All three of the long-term translocations in our study showed reduced genetic diversity relative to their founder populations, although these reductions were not always significant and may have been confounded by small sample sizes. Our analyses also assume that the source populations have not changed with respect to genetic diversity since the time of these translocations.

The reduction in translocated population diversity was more evident in the MMT and MLC populations than in the MNK population. This is interesting because the MMT translocation was essentially a replicate of the MNK translocation: the number of translocated individuals, the sex ratios, and the number of trapping efforts was similar. A notable difference between these two translocations is the size of the habitat into which the introductions were made. The habitat occupied by the MNK population is about 35 times larger than that occupied by the MMT population. Presuming that the number and diversity of founders contributing to the generations following these translocations is comparable, our results suggest that habitat patch size can be an important component in the retention of genetic diversity. This is

Table 5. *M* ratios (# alleles:allelic size range) and results of testing for heterozygosity excess in source and translocated (italics) populations of Merriam's wild turkey. Significance in heterozygosity excess testing was assessed using the sign test and the Wilcoxon one-tailed test. *P*-values less than 0.05 are designated with an asterisk

Result	Population				
	MSL	*MNK*	*MMT*	MSP	*MLC*
M ratio	0.726	0.666	0.611	0.566	0.502
(95% c.i.)	(0.598–0.855)	(0.504–0.827)	(0.453–0.769)	(0.467–0.664)	(0.388–0.615)
Sign test $P[H_{obs}]$	0.6036	0.6129	0.5826	0.2018	0.0684
Wilcoxon test $P[H_{obs}]$	0.2852	0.5898	0.5449	0.8086	0.0039*

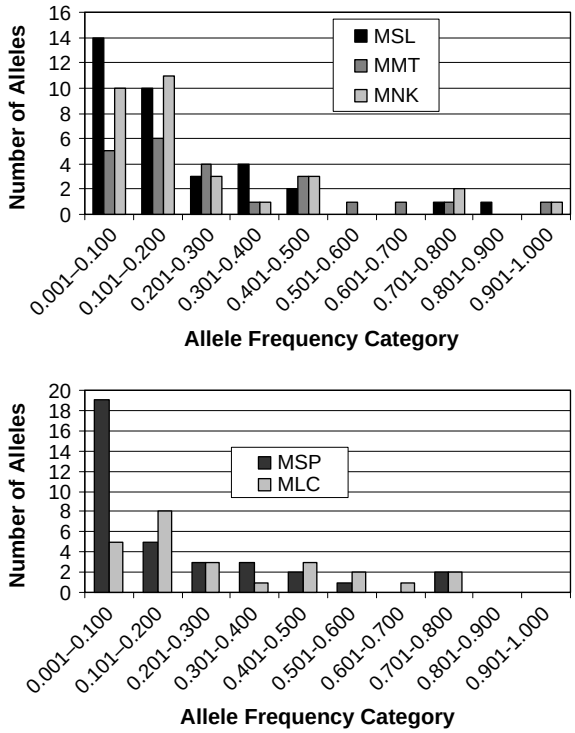

Figure 4. Allele frequency distributions (7 microsatellite loci with >2 alleles) for all pairs of source (black bars) versus translocated (grey bars) populations of Merriam's wild turkey.

consistent with theoretical and modeled predictions about the effect of population size on population heterozygosity (Lacy 1987; Hedrick 2000).

We found it surprising that a decrease in genetic diversity was detectable in the MNK population, with its extensive high quality habitat, large number of founders and trapping efforts, and large current population size. This translocation would seem to represent ideal conditions. It is possible, however, that the number of founders actually contributing to subsequent generations of turkeys in this population was reduced by mortality or other factors related to social structure such as strong polygyny or introduction of related individuals.

The MLC population was established with fewer than half the individuals used in the Arizona translocations (MMT and MNK), using only a single trapping effort. Either or both of these factors may have contributed to a loss of genetic diversity in the MLC population comparable to that found in the MMT population. Multiple trapping efforts at different sites may be an important way to avoid using closely related individuals for translocations and to better represent the source population diversity.

In all three cases, the translocated populations have diverged significantly from their source populations, primarily as a result of the loss of allelic diversity and concomitant shift in allele frequencies. These results should not be taken as evidence of adaptive divergence among these populations, since our markers are selectively neutral and adaptation requires selection. Despite the loss of genetic diversity and molecular divergence, the translocated populations still resembled their source populations enough to yield high probabilities of correct identity in individual assignment testing and strong associations at both the population (UPGMA clustering) (Figure 2) and individual (FCA plot) (Figure 3) levels. These results suggest that a translocated population does indeed retain the genetic signatures of its source population for quite some time, corroborating the findings of Leberg et al. (1994) in deer (*Odocoileus virginianus*) and eastern wild turkey (*M. g. silvestris*) and Rhodes et al. (2001) in pronghorn (*Antilocapra americana*). Furthermore, our results illustrate that assignment testing is an appropriate and potentially powerful tool to use in identifying the source of individuals that have migrated or been translocated out of a particular population.

Overall, our results suggest that detectable, long-term reductions in genetic diversity are a common consequence of translocations, even under the best of circumstances (e.g., the robust MNK translocation). This finding may be particularly important given the common practice of conducting translocations in a serial fashion, using source populations for translocations that themselves have only recently been established via translocation. In such cases, the loss of genetic diversity would be compounded with each successive translocation. The MNK population, for example, is currently being used as a source population for the establishment of new Merriam's turkey populations in Arizona because it is such a large population. Our results suggest that translocations from the MSL population would be a better choice for a translocation source in terms of maximizing genetic diversity. Our results also suggest that factors such as numbers of founders, numbers of trapping efforts, habitat quality, and habitat size may contribute significantly to the retention of genetic diversity in translocations, and

we recommend that these factors be carefully considered in translocation programs.

The biological significance of reductions in genetic diversity resulting from wildlife translocations has not been well studied. There is a well-established correlation between fitness and heterozygosity in natural populations (Jiménez et al. 1994; Keller et al. 1994; Frankham 1995, 1999; Westemeier et al. 1998; Saccheri et al. 1998; Singer et al. 2000; Hoelzel et al. 2002), although there is no agreement about its mechanism or direct implications (Hansson and Westerberg 2002). The particular levels of inbreeding that result in fitness reductions are likely to vary with the species, population history, and underlying genetic reasons for the correlation. Unfortunately, detailed studies of reproductive success and population trends are necessary to demonstrate fitness reduction in a translocated population, and are often prohibitively expensive in wildlife species. As a result, molecular data is frequently used as a conservative tool to detect losses of adaptive diversity through neutral processes such as genetic drift. Further study, including close monitoring of translocated populations in a variety of taxa, is certainly necessary to determine whether this measure is biologically appropriate and broadly applicable in wildlife species.

Assessment of bottlenecks

The existence of three translocated populations and their original source populations provided us with the opportunity to compare a variety of different methodologies designed to detect past bottlenecks based on current population-level genetic data. In our study, the reduction in the diversity of translocated populations was most apparent when the numbers of unique alleles were directly compared between source and translocated populations (Appendix 1). However, this method is not typically an option when assessing population bottlenecks resulting from translocation because the source population is unknown, extinct, or has been manipulated in a way that makes the comparison invalid.

One common approach to detecting population bottlenecks is to compare the expected mutation-drift equilibrium heterozygosity of a population, based on allelic composition, to the expected heterozygosity of the sample (Cornuet and Luikart 1996). Using this approach, a bottleneck was detectable in the MLC translocation, but not in either of the translocations from the MSL population (MNK or MMT). Although this approach does take sample sizes into account when estimating H_{eq}, small sample sizes will reduce the power of the analysis. Furthermore, the sign test has been shown to identify only 50–75% of recent bottlenecks (Luikart and Cornuet 1998).

All of our translocated populations showed a numerical reduction in the value of M, compared to their source populations, but with overlapping 95% confidence intervals. Garza and Williamson (2001) provide M ratios for a variety of wildlife populations with known histories as a comparative reference, but the M ratios for our source populations were lower than any of the "stable" populations reviewed by these authors. The source populations in this study (MSL and MSP) are not thought to have undergone a severe recent bottleneck, even with the mid-century range reductions, and are not notably less diverse than other native populations of wild turkey (Mock et al. 2002). The comparatively low M ratios observed in the present study may be due to inadequate sample sizes, leading to incomplete sampling of alleles and an artificially reduced equilibrium M ratio. Alternatively, they may suggest that equilibrium M ratios are lineage-specific, and that the detection of bottlenecks in wildlife populations may require comparison to known stable populations of the same or closely related species.

In our study populations, the most effective approach for bottleneck detection was via the modal allele frequency distribution shifts described by Luikart et al. (1998). In all three translocated populations, there was a modal shift away from the lowest frequency category, a pattern not found in either of the source populations. Even if we had lacked information about the source populations, this approach would have detected a population bottleneck in all three translocated populations, and neither of the source populations, despite the low sample sizes. Because we did have information about source populations, we were able to determine that the modal shifts detected were consistent with a loss of rare alleles present in source populations (Appendix 1). Luikart et al. (1998) suggest that

the mode shift method is most appropriate for small, recent bottlenecks, certainly characteristic of those resulting from wildlife translocation programs. However, there must be some caution in using this method, as there are a number of reasons why a bottlenecked population may not exhibit a mode shift in its allele frequency distribution. First, the population bottleneck may not have been recent enough to be detectable. A mode shift will no longer be detectable once mutation-drift equilibrium has been restored, which will occur if the effective population size (N_e) remains stationary for $4N_e$ to $10N_e$ generations (Nei and Li 1976). Second, too few polymorphic loci and/or too few individuals may be sampled to have sufficient power for detecting a bottleneck. Small sample sizes also may be responsible for misidentifying mode shifts in stable populations, because rare alleles may be missed in the sample. Third, the individuals sampled may not be representative of the bottlenecked population. Fourth, a demographic bottleneck may have occurred without a genetic bottleneck (i.e., $N_e >> N_{census}$). Fifth, the population bottlenecked may not be completely isolated, and thus the sample may contain genes from immigrants that have obscured the genetic effects of the bottleneck. Despite these caveats, the mode shift test of Luikart et al. (1998) appears to be a potentially useful and exceptionally simple test for detecting losses of allelic diversity due to translocation events in wildlife populations.

Acknowledgments

We gratefully acknowledge the financial assistance from the National Wild Turkey Federation that made this work possible, and the sampling and information assistance provided by Ron Engel-Wilson and Brian Wakeling of the Arizona Game and Fish Department, Rick Hoffman of the Colorado Division of Wildlife, and Rick Dujay of Colorado State University. We also thank Purdue University for support provided to Emily Latch, and Courtney Shattuck for her assistance in the laboratory.

Appendix I. Comparative allele frequencies for pairs of source/translocated populations of Merriam's wild turkey: Spanish Peaks, Colorado (MSP), Larimer County, Colorado (MLC), Stoneman Lake, Arizona (MSL), Mt. Trumbull, Arizona (MMT), Kaibab Plateau, Arizona (MNK). Data for translocated populations are italicized. Unique alleles within pairs of source/translocated populations are denoted with an asterisk. Missing data in columns indicated that the allele was not detected in either of the source/translocation populations

Locus/Allele	MSL (n = 16)	*MNK* (n = 19)	MSL (n = 16)	*MMT* (n = 9)	MSP (n = 21)	*MLC* (n = 14)
TUM23						
150	–	–	–	–	0.024*	*0.000*
152	–	–	–	–	0.143	*0.250*
156	0.375	*0.447*	0.375	*0.389*	0.476	*0.179*
158	0.062	*0.053*	0.062*	*0.000*	-	-
160	0.156	*0.026*	0.156	*0.111*	0.071	*0.036*
162	0.375	*0.474*	0.375	*0.500*	0.286	*0.536*
164	0.031*	*0.000*	0.031*	*0.000*	-	-
TUM50						
121	–	–	–	–	0.071	*0.143*
125	0.031	*0.053*	0.031	*0.222*	0.190	*0.107*
137	0.031	*0.342*	0.031	*0.056*	0.000	*0.107**
139	0.031*	*0.000*	0.031*	*0.000*	0.024	*0.036*
141	0.188*	*0.000*	0.188	*0.167*	0.024*	*0.000*
143	0.094	*0.105*	0.094*	*0.000*	0.095	*0.464*
145	0.406	*0.132*	0.406	*0.444*	0.071*	*0.000*
147	0.188	*0.184*	0.188	*0.056*	0.167*	*0.000*
149	0.031	*0.184*	0.031	*0.056*	0.357	*0.143*

Appendix I. (Continued)

Locus/Allele	MSL (n = 16)	*MNK* (n = 19)	MSL (n = 16)	*MMT* (n = 9)	MSP (n = 21)	*MLC* (n = 14)
TUM6						
146	0.067	*0.079*	0.067	*0.056*	–	–
148	0.933	*0.921*	0.933	*0.944*	1.000	*1.000*
WT10	–	–	–	–	–	–
151	0.467	*0.605*	0.467	*0.722*	0.905	*0.500*
156	0.533	*0.395*	0.533	*0.278*	0.095	*0.500*
WT30-2						
173	0.833	*0.947*	0.833	*0.944*	0.762	*0.750*
175	–	–	–	–	0.024*	*0.000*
177	0.100	*0.026*	0.100*	*0.000*	–	–
179	0.067*	*0.000*	0.067*	*0.000*	0.024*	*0.000*
188	0.000	*0.026**	0.000	*0.056**	0.190	*0.250*
WT32						
232	0.750	*0.895*	0.750	*0.833*	0.524	*0.500*
242	0.107	*0.026*	0.107	*0.167*	–	–
244	0.143	*0.079*	0.143*	*0.000*	0.405	*0.429*
252	–	–	–	–	0.024	*0.071*
254	–	–	–	–	0.024*	*0.000*
256	–	–	–	–	0.024*	*0.000*
WT38-2						
109	0.033	*0.079*	0.033	*0.167*	0.500	*0.643*
111	0.067	*0.237*	0.067	*0.278*	0.048*	*0.000*
113	0.167	*0.263*	0.167	*0.056*	0.333	*0.321*
115	0.167	*0.132*	0.167*	*0.000*	–	–
117	0.267	*0.184*	0.267	*0.500*	0.024	*0.036*
119	0.067*	*0.000*	0.067*	*0.000*	–	–
127	0.200*	*0.000*	0.200*	*0.000*	–	–
129	0.000	*0.105**	–	–	–	–
131	–	–	–	–	0.095*	*0.000*
135	0.033*	*0.000*	0.033*	*0.000*	–	–
WT54						
166	0.467	*0.711*	0.467	*0.667*	0.286	*0.214*
168	0.133	*0.158*	0.133	*0.111*	0.071	*0.036*
172	0.333	*0.053*	0.333	*0.222*	0.238	*0.571*
174	0.067	*0.079*	0.067*	*0.000*	0.071*	*0.000*
176	–	–	–	–	0.333	*0.179*
WT90-2						
235	0.067	*0.056*	0.067	*0.278*	–	–
237	0.267	*0.278*	0.267	*0.556*	0.167	*0.179*
241	0.300	*0.056*	0.300*	*0.000*	–	–
243	0.367	*0.444*	0.367	*0.167*	0.786	*0.714*
245	0.000	*0.167**	–	–	0.048	*0.107*
Unique Alleles	7	*3*	13	*1*	11	*1*

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