NRC Research Press

ARTICLE

Genetic population structure of fishers (*Pekania pennanti*) in the Great Lakes region: remnants and reintroductions

Paul Hapeman, Emily K. Latch, Olin E. Rhodes, Brad Swanson, and C. William Kilpatrick

Abstract: Reintroduction programs have been pivotal in augmenting populations of fishers (*Pekania pennanti* (Erxleben, 1777)) and re-establishing them to their former range in North America. The majority of reintroduction efforts in fishers have been considered demographically successful, but reintroductions can alter genetic population structure and success has rarely been evaluated in fishers from a genetic standpoint. We used microsatellite data ($n = 169$) to examine genetic population structure of fishers in the Great Lakes region and comment on the success of past reintroductions at two different spatial scales. We found significant genetic population structure among source and reintroduced populations within the Great Lakes region and large-scale genetic structure between fisher populations located in two geographically distant regions (Great Lakes and Northeast) in the eastern United States. Reintroductions associated with the Great Lakes produced results that were largely consistent with other studies of fisher reintroductions in the Northeast. However, our data are the first to support a measurable impact on genetic population structure in *Pekania pennanti pennanti* (Erxleben, 1777) from a reintroduction using geographically distant source and reintroduced populations. When feasible, we strongly recommend that reintroduction programs include an investigation of the underlying genetic structure to better define intended goals and supplement measures of demographic success.

Key words: Great Lakes, fishers, *Pekania pennanti*, structure, reintroductions.

Résumé : Les programmes de réintroduction ont joué un rôle clé dans l'accroissement des populations de pékans (*Pekania pennanti* (Erxleben, 1777)) et leur rétablissement dans leur ancienne aire de répartition en Amérique du Nord. S'il est estimé que la majorité des efforts de réintroduction ont été des réussites sur le plan démographique, la réintroduction peut modifier la structure génétique des populations, et le succès de ces efforts a rarement été évalué chez les pékans d'un point de vue génétique. Nous avons utilisé des données de microsatellites ($n = 169$) pour examiner la structure génétique de populations de pékans dans la région des Grands Lacs et émettons des commentaires sur le succès de réintroductions passées à deux échelles spatiales différentes. Nous avons décelé des structures génétiques significatives parmi les populations sources et réintroduites à l'intérieur de la région des Grands Lacs et une structure génétique à grande échelle entre des populations de pékans situées dans deux régions éloignées l'une de l'autre sur le plan géographique (les Grands Lacs et le Nord-Est) de l'est des États-Unis. Les réintroductions associées aux Grands Lacs ont produit des résultats qui concordent généralement avec ceux d'autres études sur des réintroductions de pékans dans le Nord-Est. Nos données sont toutefois les premières à indiquer une influence mesurable sur la structure génétique des populations de *Pekania pennanti pennanti* (Erxleben, 1777) d'une réintroduction dans laquelle les populations source et réintroduite sont géographiquement éloignées. Nous recommandons fortement que, dans la mesure du possible, les programmes de réintroduction comprennent une étude de la structure génétique sous-jacente pour mieux en définir les objectifs et compléter les mesures du succès démographique. [Traduit par la Rédaction]

Mots-clés : Grands Lacs, pékans, *Pekania pennanti*, structure, réintroductions.

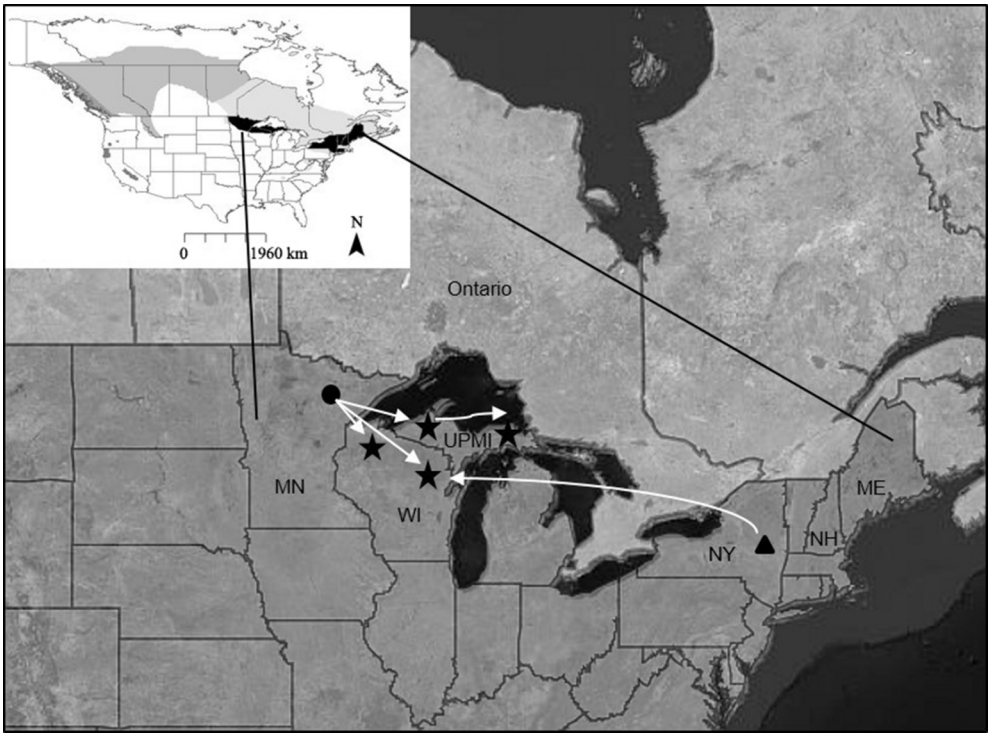
Introduction

Wildlife reintroductions have been pivotal in conservation efforts to rescue declining populations and re-establish species in their former range (Sarrazin and Legendre 2000). Early reintroduction programs seldom used multiple source populations and the source populations chosen were often based on availability or convenience, and success was likely defined based on the sustained presence of the focal species in the area of the reintroduction (Griffith et al. 1989; Seddon 1999; Le Gouar et al. 2008). The development of variable genetic markers along with advances in analytical techniques have now made it possible to consider genetic factors in both the planning and monitoring stages of reintroduction programs (Olech and Perzanowski 2002; Joyce and Pullin 2004; Ralls and Ballou 2004; Latch and Rhodes 2005; Drauch and Rhodes 2007; Swanson and Kyle 2007; Hedrick and Fredrickson 2008). Reintroductions have the potential to alter genetic population structure, thus it has become increasingly common to examine reintroduction success from a genetic perspective (Mock et al. 2004; Latch and Rhodes 2005; Wisely et al. 2005; Swanson et al. 2006; Mowry et al. 2015). Contemporary reintroductions now have the potential to consider not only the persistence of the reintroduced population, but also whether the genetic composition of the reintroduced population reflects the desired outcome (e.g., high levels of genetic variation, minimal divergence from source

Received 7 January 2017. Accepted 22 June 2017.

P. Hapeman. Department of Biology, Central Connecticut State University, New Britain, CT 06050, USA.
E.K. Latch. Department of Biological Sciences, University of Wisconsin–Milwaukee, 3209 North Maryland Avenue, Milwaukee, WI 53211-3102, USA.
O.E. Rhodes. Savannah River Ecology Laboratory P.O. Drawer E, Aiken, SC 29802, USA.
B. Swanson. Department of Biology, Central Michigan University, Mount Pleasant, MI 05405-0086, USA.
C.W. Kilpatrick. Department of Biology, University of Vermont, Burlington, VT 05405-0086, USA.
Corresponding author: Paul Hapeman (email: hapeman@ccsu.edu).

Fig. 1. Map of the study area showing reintroductions of the fisher subspecies *Pekania pennanti pennanti*. Arrows indicate the direction of transfer of animals from source populations in Minnesota (MN; circle) and Adirondacks, New York (NY; triangle), USA, to reintroduced populations in Wisconsin (WI; stars) and the Upper Peninsula of Michigan (UPMI; stars), USA. Inset map shows approximate geographical extents (shaded regions) of three subspecies of fishers (*P. p. pennanti*, *Pekania pennanti columbiana* Goldman, 1935, and *Pekania pennanti pacifica* Rhoads, 1898) adapted from Hall (1981) and Drew et al. (2003). Areas in black in the inset correspond to the sampled regions.



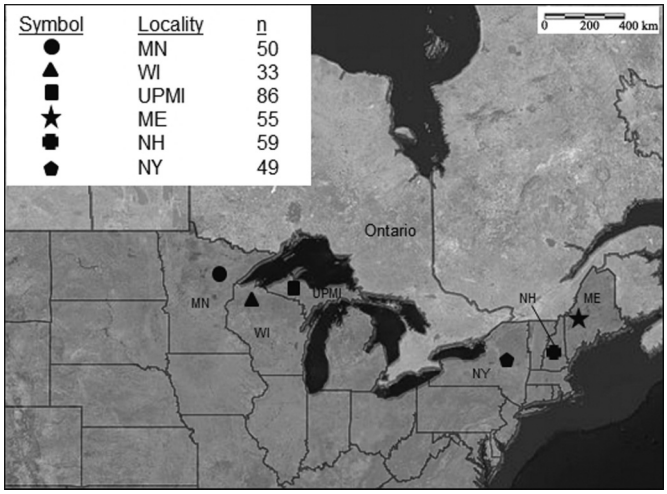
populations, and maximum retention of native alleles). Despite a general understanding of the importance of genetics to the long-term success of a population, follow-up studies to assess the genetic success of reintroductions remain uncommon in many species because they are expensive, labor intensive, and may be perceived as unnecessary after the focal species has been established at the site of the reintroduction.

Fishers in eastern North America (*Pekania pennanti pennanti* (Erxleben, 1777)), ranging from Manitoba to New Brunswick, Canada, and south in the Appalachians to Tennessee, USA (inset of Fig. 1), are one of three currently recognized subspecies (Hall 1981; Wozencraft 2005) supported by morphological and molecular data (Goldman 1935; Drew et al. 2003; Knaus et al. 2011). Like many carnivores, fishers in eastern North America have experienced a long history of human persecution resulting in the local extirpation of the species, and thus, have been a focal group for reintroduction efforts (e.g., Servheen et al. 1987; Russell et al. 1994; Raesly 2001; Swanson et al. 2006). Prior to European settlement, fishers were widely distributed and abundant, but by the early 1900s, fishers in the range of *P. p. pennanti* likely occurred as remnant populations in habitat fragments in the Adirondacks of New York (NY; USA), the White Mountains of New Hampshire (NH; USA), the Moosehead Plateau of Maine (ME; USA), Cumberland Plateau of New Brunswick (Canada), the Big Bog area of Minnesota (MN; USA), and Algonquin Provincial Park and Quebec (Canada) (deVos 1952; Brander and Books 1973; Carr et al. 2007).

In an effort to restore fishers to their previous abundance and distribution and to reduce the level of damage to timber by porcupines (*Erethizon dorsatus* (L., 1758)) (Williams et al. 2006), trapping seasons were closed and a series of well-documented reintroductions ($n = 25$) were implemented across eastern North America (see Lewis et al. 2012 and Fig. 1) between 1896 and 2004 (Berg 1982; Lewis et al. 2012). Fishers have since recovered demographically throughout a large portion of their range in eastern North America, and even though regional genetic structure has been largely retained (Hapeman et al. 2011), reintroductions have resulted in distinct genetic signatures (Williams et al. 2000; Hapeman et al. 2011, 2014) with lower genetic diversity in reintroduced populations compared with their sources (Hapeman et al. 2011, 2014) and with adjacent indigenous populations (Kyle et al. 2001). Results from these studies included genetic data from reintroduced populations that were geographically close to their sources within the same region. How reintroductions have impacted the underlying genetic population structure locally within some regions (eastern Canada, Great Lakes) of eastern North America and more broadly across the range of *P. p. pennanti* remains unclear.

In this study, we examine the genetic population structure of fishers from three populations in the Great Lakes region at two spatial scales to comment on the success of past reintroductions and place genetic population structure of fishers in the Great Lakes region in a broader geographical framework within the southern portion of *P. p. pennanti*. Fisher populations in the Great Lakes region have been particularly pivotal in the reintroduction history of the species in North America, having been involved in 26% of all documented fisher reintroductions and used as sources for reintroductions that occurred in all three subspecies. Our specific objectives were (*i*) to examine genetic population structure among source and reintroduced populations of fishers in the Great Lakes region, (*ii*) place fishers in the Great Lakes region in a broader context of genetic population structure within the southern portion of *P. p. pennanti*, and (*iii*) comment on the success of fisher reintroductions that took place in the Great Lakes region. Our study will contribute to the limited data available on the genetic success of reintroductions and improve our understanding of how reintroductions impact genetic population structure at multiple spatial scales in fishers.

Fig. 2. Map of the study area showing sampling localities for the fisher subspecies *Pekania pennanti pennanti* designated by different shapes along with sample sizes (*n*) from each locality (inset). MN, Minnesota; WI, Wisconsin; UPMI, Upper Peninsula of Michigan; ME, Maine; NH, New Hampshire; NY, Adirondacks, New York.



Materials and methods

Great Lakes region only

We obtained muscle tissue samples of fishers from cooperating state agencies during their trapping seasons between 1997 and 2006 in the Great Lakes region (Minnesota (MN; $n = 50$), Wisconsin (WI; $n = 33$), and the Upper Peninsula of Michigan (UPMI; $n = 86$)) (Fig. 2). Locations for samples were reported by county when collected, which was sufficient resolution for our analyses and were located near documented sites where reintroductions occurred (WI, and multiple counties in the UPMI) and west and south of the source of the original founders in MN. We genotyped all samples ($n = 169$) at 11 microsatellite loci following published protocols and quality control measures (Hapeman et al. 2011).

We used the program STRUCTURE version 2.34 (Falush et al. 2003) to characterize patterns of genetic population structure in the Great Lakes region without using prior population information. We ran models in STRUCTURE with a burn-in of 200 000 iterations and run length of 500 000 iterations assuming admixture and correlated allele frequencies among clusters. Models were set to K = 2–6 genetic clusters with 10 independent runs at each value of K and all other parameters set to default. The method of Evanno et al. (2005) in the program STRUCTURE HARVESTER version 0.6.94 (Earl and vonHoldt 2012) allows the identification of fine substructure using the log-likelihood scores and provides the best estimate of the number of genetic clusters (K) in the data set using the ad hoc statistic ΔK. Genetic clusters inferred from STRUCTURE within the total data set were further examined for substructuring using additional runs.

We examined genetic differentiation between three pre-defined populations (based on sampling locality) in the Great Lakes region (MN, WI, and UPMI) using pairwise measures of F_{ST} (Weir and Cockerham 1984; Hedrick 2005) calculated in FSTAT version 2.9.3 (Goudet 2001). We also examined the relative probability that an individual belonged to one of the three pre-defined populations in which it was sampled using assignment tests in GENECLASS2 (Piry et al. 2004). We used a majority rule to assign samples to a population using the Bayesian method of Rannala and Mountain (1997) and the frequency-based method of Paetkau et al. (1995) in GENECLASS2 (Piry et al. 2004). For the frequency-based method, missing alleles are not permitted, thus we coded missing alleles as low-frequency alleles ($P = 0.01$; Paetkau et al. 2004). We derived a single mean assignment value for each population pair using two runs (each population served as the reference for the other population) and by averaging twice; once across samples within a run, and second, by averaging the mean values obtained from the two runs. Finally, we used the simulation algorithm of Paetkau et al. (2004) in GENECLASS2 to exclude individuals as members of a population using a threshold value of 0.05.

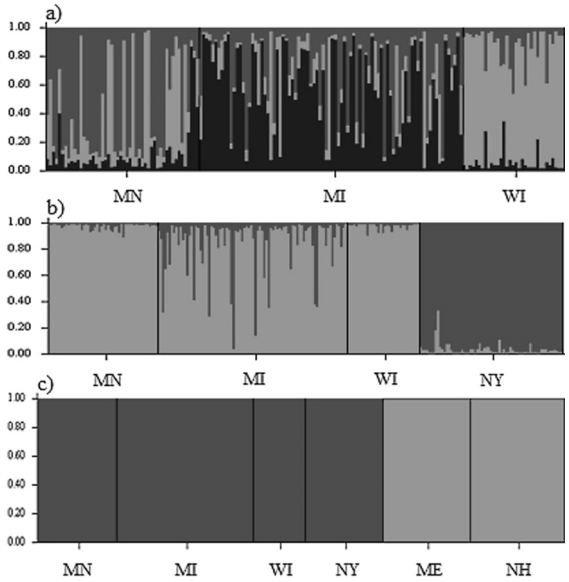
We calculated observed and expected heterozygosities, and mean numbers of alleles in each of the three pre-defined populations using GDA version 1.1 (Lewis and Zaykin 2001). We used exact tests in the program GENEPOP version 3.4 (Raymond and Rousset 1995) to test for deviations from Hardy–Weinberg and linkage equilibrium and adjusted the results to account for multiple comparisons using a sequential Bonferroni correction (Rice 1989). We also examined each population for its deviation from Hardy–Weinberg expectations by calculating F_{IS} in GDA.

Fishers were severely reduced in numbers in the Great Lakes region due to overtrapping and this may have resulted in a bottleneck that impacted genetic population structure. We used multiple methods to examine the three pre-defined populations in the Great Lakes for evidence of historical bottlenecks using both the mode shift and heterozygosity excess methods (Cornuet and Luikart 1996) in the program BOTTLENECK version 1.2 (Piry et al. 1999). We also calculated the *M*-ratio (Garza and Williamson 2001) using the programs Critical *M* and MP Val (Garza and Williamson 2001). Allelic diversity is sensitive to changes in population size and can be a good indicator of recent historical bottlenecks (Spencer et al. 2000). Thus, we also compared allelic richness (calculated using HP-RARE version 1.02 (Kalinowski 2005) between source and reintroduced populations using two-tailed t tests. Finally, we used a relatively recent coalescent-based method to detect past changes in the effective population sizes (N_e) of each of the six populations in this study using the package VAREFF version 1.2 (Nikolic and Chevalet 2014) in the software R version 3.4. VAREFF simulates demographic histories using microsatellite data with a coalescent approach to estimate changes in recent and ancestral effective population sizes. We modeled demographic changes using a two-phase mutation model with a mutation rate of 0.001 and 10% of the mutations greater than a single step. The generation time for fishers was set to 5 years following Tucker et al. 2012 and the number of generations since the origin of each population was varied from 10 for reintroduced populations to 100 for source populations. Source populations have likely been present much longer than this, but we were interested only in the recent history that included European settlement. For each population, we ran models with three separate prior effective population sizes (minimum, intermediate, and maximum values) based on the global theta (θ) estimates produced in the first step of the modeling process. Models were run for 10 000 000 steps with a burn-in of 10 000 and all other variables in the models were set to what was suggested in the VAREFF user manual. We assessed whether effective population sizes had changed during three different time periods (0–10, 0–20, and 0–100 generations in the past) and made inferences about past expansions and declines based on posterior distributions and their attributes (mean, median, mode, etc.). The reintroductions of fishers to WI and MI were relatively recent, thus we only examined WI and UPMI at the 0–10 period. For each population, we compared median estimates of N_e from the posterior distributions at different time intervals and calculated the RN criterion from Nikolic and Chevalet (2014). The RN criterion represents the ratio of the range of N_e estimates to the mean of the N_e estimates for a particular time period. An RN value >0.10 supports a past change in effective population size during the period examined (Nikolic and Chevalet 2014).

Larger geographical framework and reintroduction success

We examined genetic structure at a larger geographical scale (Great Lakes vs. Northeast) by incorporating into the present data set previously collected data from fishers in the Northeast (Hapeman

Fig. 3. Plots of individual membership proportions from STRUCTURE analyses for (*a*) Great Lakes populations only, (*b*) Great Lakes populations with New York, and (*c*) all six populations of the fisher subspecies *Pekania pennanti pennanti* from the Great Lakes and the Northeast.



et al. 2011). First, we ran analyses in STRUCTURE (same parameters described above and up to $K = 8$) where the three populations in the Great Lakes were combined with three populations from the Northeast including NY ($n = 49$), NH ($n = 59$), and ME ($n = 55$). The three populations from the Northeast were selected because NY served as a source population for the WI reintroduction (Petersen et al. 1977) and all three were considered the only remnant fisher populations in the northeastern United States by the early 1900s (Brander and Books 1973). We then used additional runs to check for substructure in clusters that resulted from the initial analysis. We repeated previous analyses of genetic differentiation and assignment tests in pairwise fashion between populations in the Great Lakes and the Northeast. Finally, we conducted a hierarchical analysis (AMOVA) using two groups of three populations from the Great Lakes (MN, WI, and UPMI) and the Northeast (NY, ME, and NH). We used F_{ST} as our distance metric for the squared distance matrices calculated in the AMOVAs and determined the significance of the observed Phi statistics (Φ_{RT}, Φ_{PT}, Φ_{PR}) by randomization of the data using 9999 iterations in the program GenAlEx version 6.5 (Peakall and Smouse 2012).

Results

Great Lakes region only

The microsatellite data collected for the Great Lakes populations contained a small number of samples with missing data (3%) and greater than 98% of the data was available for all 11 loci.

Based on our results from the method of Evanno et al. (2005), ΔK was maximized at $K = 3$ (Supplementary Fig. S1*a*).[1] The three genetic clusters corresponded to the three sampled populations in MN, WI, and UPMI (Fig. 3*a*). Mean assignment values for each of the three populations were high and ranged from 89% to 95%, and were consistent between assignment methods in GENECLASS2. Two samples from MI were excluded as members of any of the three sampled populations based on the algorithm of Paetkau et al. (2004) with 10 000 simulated individuals and alpha set equal to 0.05.

Table 1. Genetic differentiation between population pairs of fishers (*Pekania pennanti*) within the range of the subspecies *Pekania pennanti pennanti*.

	MN	NY	NH	ME	*WI*	*UPMI*
MN	—	0.29*	0.40*	0.28*	0.06*	0.06*
NY	1	—	0.17*	0.14*	0.33*	0.18*
NH	1	0.924	—	0.05*	0.50*	0.32*
ME	1	0.915	0.878	—	0.35*	0.20*
WI	0.898	1	1	1	—	0.12*
UPMI	0.949	1	1	1	0.95	—

Note: Pairwise values are given for Hedrick's standardized F_{ST} (Hedrick 2005) above the diagonal and were calculated in FSTAT (Goudet 2001) using 10 000 iterations. All pairwise values were significantly different ($P < 0.05$) from zero (*). Assignment values (lower diagonal) here were calculated (for description see the Materials and methods) as a relative measure of genetic distinctiveness between population pairs. Values were obtained using the Bayesian method of Rannala and Mountain (1997) and were calculated using the program GENECLASS2 (Piry et al. 2004). MN, Minnesota; NY, Adirondacks, New York; NH, New Hampshire; ME, Maine; WI, Wisconsin; UPMI, Upper Peninsula of Michigan. Labels set in italic type are reintroduced populations.

All source–reintroduced population pairs exhibited significant genetic differentiation; however, the values were generally low (Table 1). MI and WI were in Hardy–Weinberg and linkage equilibrium after a sequential Bonferroni correction for multiple comparisons (Rice 1989). A significantly positive F_{IS} value was found in UPMI (Table 2) that could indicate a departure from Hardy–Weinberg equilibrium or the presence of cryptic population substructure too weak to be detected in our analyses.

Recent bottlenecks were not detected (refer to Supplementary Table S1)[1] in any of the three Great Lakes populations using the BOTTLENECK and *M*-Ratio programs. Results of the two-tailed tests comparing allelic richness between source and reintroduced populations were not significant for any pairwise comparison. Heterozygosity and allelic richness in WI were reduced compared with MN, but were similar between MN and UPMI populations (Table 2). Recent declines in effective population size were detected in reintroduced and source populations from models developed in the VAREff version 1.2 package. RN values greater than 0.1 were found in MI for the period 0–10 generations in the past and for ME, NY, NH, and MN during the period from 0 to 100 generations ago. The NH population had the lowest estimate of N_e for the six populations in the study (Supplementary Table S3).[1]

Larger geographical framework and reintroduction success

The uppermost level of genetic structure when all six populations were included in STRUCTURE resulted in genetic clusters ($K = 2$; Supplementary Fig. S1*b*[1]) that corresponded to populations in the Great Lakes region and NY separate from ME and NH (Fig. 3*c*). Membership of the NY population (mean $\hat{Q}$ from STRUCTURE runs) to the Great Lakes – NY cluster was greater than 0.99. Additional substructure ($K = 2$; Supplementary Fig. S1*c*[1]) was found in the Great Lakes – NY cluster and corresponded to NY separate from the three Great Lakes populations (Fig. 3*b*). For this analysis, population membership for NY was lower (0.954), but more notable was the high membership of the UPMI population ($\hat{Q} = 0.253$) to NY. Significant genetic differentiation was found between fisher populations in the Northeast and the Great Lakes based on pairwise estimates of F_{ST} (0.18–0.50), and genetic differentiation was higher between NY and WI ($F_{ST} = 0.33$) than between NY and UPMI ($F_{ST} = 0.18$; Table 1). In pairwise comparisons, individuals in all Great Lakes populations were assigned to their own populations or those within the region and not with populations in the Northeast. A hierarchical analysis of genetic population structure (AMOVA) from fishers found throughout the southern extent of

[1]Supplementary figure and tables are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2016-0325.

Table 2. Measures of genetic diversity in the fisher subspecies *Pekania pennanti pennanti* from source and reintroduced populations in the USA.

Population	n	H_e	H_o	$\bar{A}$	A_r	F_{IS}
Source						
NY	49	0.56 (0.05)	0.52 (0.05)	4.27 (0.43)	3.95 (0.33)	0.07 (0.05)
MN	50	0.56 (0.07)	0.55 (0.07)	4.82 (0.50)	4.52 (0.47)	0.01 (0.04)
NH	59	0.51 (0.05)	0.48 (0.05)	4.09 (0.45)	3.75 (0.36)	0.06 (0.03)
ME	55	0.60 (0.06)	0.61 (0.02)	4.55 (0.43)	4.23 (0.38)	−0.01 (0.03)
Reintroduced						
WI (MN and NY)	33	0.49 (0.07)	0.48 (0.07)	4.09 (0.42)	3.79 (0.40)	0.02 (0.04)
UPMI (MN)	86	0.58 (0.07)	0.55 (0.07)	4.82 (0.46)	4.72 (0.45)	**0.05** (0.02)

Note: Sources for reintroduced populations are in parentheses. Genetic variation was quantified using expected heterozygosity (H_e), observed heterozygosity (H_o), and mean number of alleles across 11 loci ($\bar{A}$) in GDA version 1.1 (Lewis and Zaykin 2001). Allelic richness (A_r) was calculated using HP-Rare version 1.0 (Kalinowski 2005) and corrected using the smallest population size (WI; n = 33). F_{IS} for each population (Weir and Cockerham 1984) were calculated in GDA version 1.1 (Lewis and Zaykin 2001) with values significantly different from zero (P < 0.05) set in boldface type and standard errors in parentheses. NY, Adirondacks, New York; MN, Minnesota; NH, New Hampshire; ME, Maine; WI, Wisconsin; UPMI, Upper Peninsula of Michigan.

P. p. pennanti revealed significant differentiation (Φ_{RT} = 0.150, P < 0.001) among regions (Great Lakes vs. Northeast; Supplementary Table S2[1]).

Discussion

We found significant genetic structure among fisher populations in the Great Lakes region. The reintroductions of fishers in the Great Lakes region have been considered largely successful (6 out of 7 documented reintroductions) from a demographic perspective, but have led to genetically distinct populations. Genetic structure following reintroductions has been found in other species (Mucci et al. 2010; Williams and Scribner 2010), but it is unclear how frequently this occurs since the number of studies that have collected genetic data on reintroduced populations and their sources is somewhat limited. The creation of genetic structure following a reintroduction may be an undesirable outcome if the goal is to create reintroduced populations that are genetically diverse or that are similar in genetic diversity to the source populations used (IUCN 2013). Both WI and UPMI were derived from the same source population in MI and exhibit genetic differentiation from their source and even greater differentiation from each other (Table 1). Genetic variation in the Great Lakes populations was lowest in WI, but there was no evidence of a recent bottleneck or a substantial change in N_e since the time of the reintroductions that occurred between 1956 and 1967. It is possible that the number of animals used in the reintroduction along with trapping restrictions that began in 1922 in WI (Williams et al. 2006) allowed fishers to recover rapidly, eliminating any evidence of past decline. This same rapid recovery following a bottleneck has also been reported in other species such as bobcat (*Lynx rufus* (Schreber, 1777)) (Anderson et al. 2015) and elk (*Cervus elaphus* L., 1758) (Hundertmark and Van Daele 2010). Alternatively, we may have lacked power to detect recent bottlenecks based on our sample size and the presence of a number of factors (e.g., population subdivision, recent gene flow) that have previously been attributed to the low power of detecting recent bottlenecks (Peery et al. 2012; Tucker et al. 2012). We did find evidence that effective population sizes declined during the time intervals examined in all other populations in our study and the decline ranged from 25% (NY, MI) to 62% (NH). The decline that we detected in the MI population may explain the level of differentiation with WI despite having the same source population (MN). Source populations had their lowest estimates of N_e at a period of time that corresponded to the early to mid-1800s when trapping and habitat loss reduced fisher populations across their range. The declines that we observed in our models were gradual and did not appear to be sudden and severe, and this may have affected the ability of other methods to detect genetic bottlenecks in the sampled populations.

The reintroduction of fishers from NY to WI (1955–1957) was considered a demographic success (Bradle 1957), but based on our genetic data, we did not find evidence of that success in WI. We may not have detected any signs of the NY reintroduction because our fisher samples from WI were taken from an area 90 miles (144.84 km) west of the original reintroduction site in the Nicolet National Forest (Williams et al. 2006). Our sample area was close to the Chequamegon National Forest where fishers from MN (n = 60) were reintroduced between 1966 and 1967 (Petersen et al. 1977). Thus, it is evident from our genetic data that the reintroduction of fishers from MN was the origin of the fishers within our sample area in WI. Fishers like other mustelids are capable of long-distance dispersal (Kyle and Strobeck 2001; Mowry et al. 2015; de Groot et al. 2016), and despite the distance of our sample site to the Nicolet National Forest, we expected to find evidence of the NY reintroduction in our WI samples had it been successful. This was not the case in our study and it appears that the original founders did not spread west in WI despite a strong recovery by fishers in the state. It is possible that the NY reintroduction was simply not successful because it did not meet the criteria described by Lewis et al. (2012) in that they used too few animals (n = 18; 12 females) in the founding population. Reintroduction success in other carnivores including Canada lynx (*Lynx canadensis* Kerr, 1792), American marten (*Martes americana* (Turton, 1806)), and sable (*Martes zibellina* (L., 1758)) has also been associated with small release numbers (Slough 1994; Steury and Murray 2004; Powell et al. 2012). However, we propose that at least some reintroduced fishers from NY moved north from the Nicolet National Forest into the adjacent Ottawa National Forest in MI and contributed to the founding population along with fishers reintroduced from MN between 1961 and 1963 (Williams et al. 2006). A similar kind of movement between MI and WI was suggested for marten (Williams and Scribner 2007).

The UPMI population was reportedly founded from a single source (MN; Williams et al. 2006), yet it appears to be composed of samples that have ancestry from more than one population based on a positive and significant F_{IS} value and a level of genetic variation that is more consistent with a multisource reintroduction. Additionally, two alleles were found in both NY and UPMI, but not in MN and WI. The UPMI population also had a lower level of genetic differentiation and greater ancestry with NY compared with the other populations from the Northeast (NH and ME). Collectively, our results support that fishers from NY contributed to the founding population of fishers in MI (Irvine et al. 1964). The Nicolet National Forest is close enough to the Ottawa National

Forest for dispersal to occur, but our results are somewhat unexpected considering that only a limited number of fishers were reintroduced from NY (n =18) into the Nicolet National Forest (Petersen et al. 1977) and a much greater number of fishers were reintroduced from MN to Nicolet National Forest (n = 42) and Ottawa National Forest (n = 61) during the same period. One alternative explanation for the UPMI data are that fishers are connected throughout eastern Canada and into the Northeast. Fishers were reported in several areas of southern Ontario during the 1950s when fishers were either declining or just beginning to recover and could have acted as stepping stones for dispersal to connect fishers in the UPMI with those farther east (Carr 2005). At least some connectivity between fishers in southeastern Ontario, Canada, and the Adirondacks of NY has been previously established (Carr et al. 2007), but that connectivity appears to be recent. Therefore, it seems unlikely that the UPMI data are the result of ongoing gene flow from NY. The two samples from the UPMI that were not assigned to a population that we sampled could indicate some level of gene flow into the UPMI population from fishers farther north in Ontario, Canada. Thus, the current genetic composition of fishers in the UPMI appears to be derived from MN and NY through reintroduction efforts and from recent gene flow from Ontario, Canada, to the north.

In a larger geographical context, fisher populations in the Great Lakes region (MN, WI, and UPMI) are genetically distinct (Figs. 3*b*, 3*c*) from fishers in NY and the remainder of the Northeast. Based on the distribution of mtDNA haplotypes from previous studies (Drew et al. 2003; Vinkey et al. 2006; Hapeman et al. 2014), it is evident that fishers throughout the range of *P. p. pennanti* were connected in the past. However, following European settlement, fishers declined and were found in only a limited number of remnant populations in eastern North America by the early 1930s (Coulter 1966; Brander and Books 1973). Those remnant populations served as sources for natural expansions and reintroductions during recovery efforts in the mid-twentieth century. Fishers have recovered well in the last 50 years and are now thought to be continuously distributed throughout their range in eastern North America.

The magnitude of genetic differentiation between the Great Lakes and the Northeast region in our study is much greater (mean pairwise F_{ST} among populations between regions = 0.32; P. Hapeman, unpublished data) than has been found previously for fisher populations separated by similar geographic distances (Kyle et al. 2001). Although gaps in our sample coverage limit our ability to fully characterize genetic structure across the entire range of *P. p. pennanti*, we attribute part of the between-region difference that we observed to isolation by distance (IBD) due to restricted dispersal. IBD has previously been suggested in other genetic studies of fishers in *P. p. pennanti* at similar scales (Kyle et al. 2001; Drew et al. 2003; Carr et al. 2007) and was evident in samples of fishers from the northeast region (Mantel R = 0.687, $P < 0.05$; P. Hapeman, unpublished data). Additional sampling in areas contiguous with our study area, such as portions of southern Ontario, would be required to confirm the extent of IBD across the subspecies. Our data supports the role of reintroductions in shaping genetic population structure at multiple scales and is consistent with what has been found in other studies of fishers (Kyle et al. 2001; Vinkey et al. 2006). Reintroductions alongside the severe reduction in fisher abundance by the early 1900s (Brander and Books 1973; Hapeman et al. 2011), IBD, dispersal barriers, and deeper historical mechanisms (i.e., range expansion, fragmentation) (Drew et al. 2003; Hapeman 2006; Carr et al. 2007; Hapeman et al. 2011) explain the complex genetic population structure of fishers in eastern North America.

Management implications

We have provided data demonstrating that human-mediated reintroductions have contributed greatly to observed patterns of genetic population structure in fishers in the Great Lakes and these results complement the findings from previous studies (Kyle et al. 2001; Wisely et al. 2004; Carr et al. 2007; Hapeman et al. 2011; Lewis et al. 2012). Numerous studies have demonstrated the importance of demographic variables to the success of reintroductions in fishers and genetic characteristics of reintroductions have begun to draw considerable attention with successful reintroductions being associated with regions of North America (east vs. west) and distance of source population to release site (Lewis et al. 2012). Similar in spirit to the framework developed by Gusset 2009, we believe that a more comprehensive approach should be taken when planning and evaluating the success of a reintroduction. Reintroduction success in fishers should not only consider demographic factors in the planning process, but also consider the underlying genetic structure and implications of gene flow to the underlying genetic structure at multiple spatial scales when choosing source populations. This would require a shift in the paradigm that simply choosing the closest source population is the best choice even though many successful reintroductions have used source populations from neighboring states or provinces (Lewis et al. 2012). Emphasis on the underlying genetic structure may be particularly important in areas with unique genetic variation (Schwartz 2007) or where fishers appear to exhibit local adaptations (Knaus et al. 2011; Lewis et al. 2012). The presence of population structure in fishers at multiple scales may be particularly important when the geographic distance of source population to release site is being used as a proxy for genetic relatedness (Lewis et al. 2012). In recognition of the complex historical biogeography and the large number of translocations already carried out in fishers, we agree with the guidelines by the IUCN (1998) that reintroduced animals should be as genetically similar to former resident genotypes as possible. Therefore, in fishers, we suggest that adequate consideration of the underlying genetic structure should begin with differences at the subspecies level and extend to regional and local genetic population structure.

Each of the three subspecies of fishers is characterized by unique reintroduction histories, genetic structure, and conservation concerns (Drew et al. 2003; Knaus et al. 2011). We recommend that future translocations within *P. p. pennanti* select sources from within the subspecies because all past reintroductions within *P. p. pennanti* have used source populations only from within the subspecies. Further, we encourage managers to use pre-existing studies that have elaborated on regional and population-level genetic structure within the subspecies (Williams et al. 2000; Kyle et al. 2001; Drew et al. 2003; Carr et al. 2007; Hapeman et al. 2011; this study) to help guide their decisions prior to simply choosing the closest source for a reintroduction.

Acknowledgements

This research was funded by the University of Vermont and the Rhodes laboratory at Purdue University. Many people deserve thanks for contributing time, effort, samples, and resources to this project including J. Fike, M. Brown, S. Smith, and New York Department of Environmental Conservation; C. Brown and Rhode Island Division of Fish and Wildlife; E. Orff, W. Staats, and New Hampshire Fish and Game Department; K. Royar and Vermont Fish and Wildlife; P. Rego and employees at Connecticut Department of Environmental Protection; C. Henner, T. Gola, and Massachusetts Division of Fish and Wildlife; W. Jakubas and Maine Department of Inland Fisheries and Wildlife; as well as G. Gallant, R. Crowe, T. Stevens, E. Worster, H. Seekins, and D. Pennell.

References

Anderson, C.S., Prange, S., and Gibbs, H.L. 2015. Origin and genetic structure of a recovering bobcat (*Lynx rufus*) population. Can. J. Zool. **93**(11): 889–899. doi:10.1139/cjz-2015-0038.

Berg, W.E. 1982. Reintroduction of fisher, pine marten, and river otter. *In* Midwest Furbearer Management. Proceedings of Symposia 43rd Midwest Fish and Wildlife Conference, Wichita, Kans., 7–8 December 1981. *Edited by*

G.C. Sanderson. Office of Printing Services, University of Illinois at Urbana–Champaign, Urbana–Champaign. pp. 159–173.
Bradle, B.J. 1957. The fisher returns to Wisconsin. Wisconsin Conserv. Bull. **22**: 9–11.
Brander, R.B., and Books, D.J. 1973. Return of the fisher. Nat. Hist. **82**: 52–57.
Carr, D. 2005. Genetic structure of a recolonizing population of fishers (*Martes pennanti*). M.S. thesis, Trent University, Peterborough, Ont.
Carr, D., Bowman, J., Kyle, C.J., Tully, S.M., Koen, E.L., Robitaille, J.-F., and Wilson, P.J. 2007. Rapid homogenization of multiple sources: genetic structure of a recolonizing population of fishers. J. Wildl. Manage. **71**: 1853–1861. doi:10.2193/2006-274.
Cornuet, J.-M., and Luikart, G. 1996. Description and power analysis of two tests for detecting recent demographic bottlenecks from allele frequency data. Genetics, **144**: 2001–2014. PMID:8978083.
Coulter, M.W. 1966. Ecology and management of fishers in Maine. Xerox University Microfilms, Ann Arbor, Mich.
de Groot, G.A., Hofmeester, T.R., La Haye, M., Jansman, H.A.H., Perez-Haro, M., and Koelewijn, H.P. 2016. Hidden dispersal in an urban world: genetic analysis reveals occasional long-distance dispersal and limited spatial substructure among Dutch pine martens. Conserv. Genet. **17**: 111–123. doi:10.1007/s10592-015-0765-6.
deVos, A. 1952. Ecology and management of fisher and marten in Ontario. Technical Bulletin, Ontario Department of Lands and Forests, Peterborough.
Drauch, A.M., and Rhodes, O.E., Jr. 2007. Genetic evaluation of the lake sturgeon reintroduction program in the Mississippi and Missouri Rivers. J. Fish. Manage. **27**: 434–442. doi:10.1577/M06-024.1.
Drew, R.E., Hallett, J.G., Aubry, K.B., Cullings, K.W., Koepf, S.M., and Zielinski, W.J. 2003. Conservation genetics of the fisher (*Martes pennanti*) based on mitochondrial DNA sequencing. Mol. Ecol. **12**: 51–62. PMID:12492877.
Earl, D.A., and vonHoldt, B.M. 2012. STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conserv. Genet. Res. **4**: 359–361. doi:10.1007/s12686-011-9548-7.
Evanno, G., Regnaut, S., and Goudet, J. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Mol. Ecol. **14**: 2611–2620. doi:10.1111/j.1365-294X.2005.02553.x. PMID:15969739.
Falush, D., Stephens, M., and Pritchard, J.K. 2003. Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. Genetics, **164**: 1567–1587. PMID:12930761.
Garza, J.C., and Williamson, E.G. 2001. Detection of reduction in population size using data from microsatellite loci. Mol. Ecol. **10**: 305–318. PMID:11298947.
Goldman, F.A. 1935. New American mustelids of the genera *Martes*, *Gulo*, *Lutra*. Proc. Biol. Soc. Wash. **48**: 175–186.
Goudet, J. 2001. FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3). Lausanne University, Lausanne, Switzerland. Updated from Goudet (1995). Available from https://www2.unil.ch/popgen/softwares/fstat.htm [accessed December 2010].
Griffith, B., Scott, J.M., Carpenter, J.W., and Reed, C. 1989. Translocation as a species conservation tool: status and strategy. Science, **245**: 477–480. doi:10.1126/science.245.4917.477. PMID:17750257.
Gusset, M. 2009. A framework for evaluating reintroduction success in carnivores: lessons from African wild dogs. *In* Reintroduction of top-order predators. *Edited by* M.W. Hayward and M.J. Somers. Blackwell Publishing, Ltd., Oxford, UK. pp. 307–320.
Hall, E.R. 1981. The mammals of North America. Vol. 2. John Wiley and Sons, New York.
Hapeman, P. 2006. Population genetics of fishers (*Martes pennanti*) across northeastern North America. Ph.D. thesis, University of Vermont, Burlington.
Hapeman, P., Latch, E.K., Fike, J.A., Rhodes, O.E., Jr., and Kilpatrick, C.W. 2011. Landscape genetics of fishers (*Martes pennanti*) in the Northeast: dispersal barriers and historical influences. J. Hered. **102**: 251–259. doi:10.1093/jhered/esr001. PMID:21389071.
Hapeman, P., Latch, E.K., Rhodes, O.E., and Kilpatrick, C.W. 2014. When recent and evolutionary histories meet: deciphering temporal events from contemporary patterns of mtDNA from fishers (*Martes pennanti*) in north-eastern North America. J. Zool. Syst. Res. **52**: 331–337. doi:10.1111/jzs.12060.
Hedrick, P.W. 2005. A standardized genetic differentiation measure. Evolution, **59**: 1633–1638. doi:10.1554/05-076.1. PMID:16329237.
Hedrick, P.W., and Fredrickson, R.J. 2008. Captive breeding and the reintroduction of Mexican and red wolves. Mol. Ecol. **17**: 344–350. doi:10.1111/j.1365-294X.2007.03400.x. PMID:18173506.
Hundertmark, K.J., and Van Daele, L.J. 2010. Founder effect and bottleneck signatures in an introduced, insular population of elk. Conserv. Genet. **11**: 139–147. doi:10.1007/s10592-009-0013-z.
Irvine, G.W., Magnus, L.T., and Bradle, B.J. 1964. The restocking of fishers in lake state forests. Trans. N. Am. Wildl. Nat. Resour. Conf. **29**: 307–315.
IUCN. 1998. Guidelines for re-introductions. IUCN, Gland, Switzerland.
IUCN. 2013. Guidelines for re-introductions. IUCN, Gland, Switzerland.
Joyce, D.A., and Pullin, A.S. 2004. Using genetics to inform re-introduction strategies for the chequered skipper butterfly (*Carterocephalus palaemon*, Pallas) in England. J. Insect Conserv. **8**: 69–74. doi:10.1023/B:JICO.0000027510.59074.16.
Kalinowski, S.T. 2005. HP-RARE 1.0: a computer program for performing rarefaction on measures of allelic richness. Mol. Ecol. Notes, **5**: 187–189. doi:10.1111/j.1471-8286.2004.00845.x.
Knaus, B.J., Cronn, R., Liston, A., Pilgrim, K., and Schwartz, M.K. 2011. Mitochondrial genome sequences illuminate maternal lineages of conservation concern in a rare carnivore. BMC Ecol. **11**: 10. doi:10.1186/1472-6785-11-10. PMID:21507265.
Kyle, C.J., and Strobeck, C. 2001. Genetic structure of North American wolverine (*Gulo gulo*) populations. Mol. Ecol. **10**: 337–347. doi:10.1046/j.1365-294x.2001.01222.x. PMID:11298949.
Kyle, C.J., Robitaille, J.F., and Strobeck, C. 2001. Genetic variation and structure of fisher (*Martes pennanti*) populations across North America. Mol. Ecol. **10**: 2341–2347. doi:10.1046/j.1365-294X.2001.01351.x. PMID:11555275.
Latch, E.K., and Rhodes, O.E. 2005. The effects of gene flow and population isolation on the genetic structure of reintroduced wild turkey populations: Are genetic signatures of source populations retained? Conserv. Genet. **6**: 981–997. doi:10.1007/s10592-005-9089-2.
Le Gouar, P., Robert, A., Choisy, J.P., Henriquet, S., Lecuyer, P., Tessier, C., and Sarrazin, F. 2008. Roles of survival and dispersal in reintroduction success of griffon vulture (*Gyps fulvus*). Ecol. Appl. **18**: 859–872. doi:10.1890/07-0854.1. PMID:18536248.
Lewis, J.C., Powell, R.A., and Zielinski, W.J. 2012. Carnivore translocations and conservation: insights from population models and field data for fishers (*Martes pennanti*). PLoS ONE, **7**: e32726. doi:10.1371/journal.pone.0032726. PMID:22479336.
Lewis, P.O., and Zaykin, D. 2001. Genetic Data Analysis (GDA) version 1.1: computer program for the analysis of allelic data. Free program distributed by the authors available from http://phylogeny.uconn.edu/software/ [accessed September 2010]
Mock, K.E., Brim-Box, J.C., Miller, M.P., Downing, M.E., and Hoeh, W.R. 2004. Genetic diversity and divergence among freshwater mussel (Anodonta) populations in the Bonneville Basin of Utah. Mol. Ecol. **13**: 1085–1098. doi:10.1111/j.1365-294X.2004.02143.x. PMID:15078447.
Mowry, R.A., Schneider, T.M., Latch, E.K., Gompper, M.E., Beringer, J., and Eggert, L.S. 2015. Genetics and the successful reintroduction of the Missouri river otter: restored otter genetic structure. Anim. Conserv. **18**: 196–206. doi:10.1111/acv.12159.
Mucci, N., Arrendal, J., Ansorge, H., Bailey, M., Bodner, M., Delibes, M., et al. 2010. Genetic diversity and landscape genetic structure of otter (*Lutra lutra*) populations in Europe. Conserv. Genet. **11**: 583–599. doi:10.1007/s10592-010-0054-3.
Nikolic, N., and Chevalet, C. 2014. Detecting past changes of effective population size. Evol. Appl. **7**: 663–681. doi:10.1111/eva.12170. PMID:25067949.
Olech, W., and Perzanowski, K. 2002. A genetic background for reintroduction program of the European bison (*Bison bonasus*) in the Carpathians. Biol. Conserv. **108**: 221–228. doi:10.1016/S0006-3207(02)00108-8.
Paetkau, D., Calvert, W., Stirling, I., and Strobeck, C. 1995. Microsatellite analysis of population structure in Canadian polar bears. Mol. Ecol. **4**: 347–354. doi:10.1111/j.1365-294X.1995.tb00227.x. PMID:7663752.
Paetkau, D., Slade, R., Burden, M., and Estoup, A. 2004. Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. Mol. Ecol. **13**: 55–65. doi:10.1046/j.1365-294X.2004.02008.x. PMID:14653788.
Peakall, R., and Smouse, P.E. 2012. GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research — an update. Bioinformatics, **28**: 2537–2539. PMID:22820204.
Peery, M.Z., Kirby, R., Reid, B.N., Stoelting, R., Doucet-Bëer, E., Robinson, S., Vásquez-Carrillo, C., Pauli, J.N., and Palsbøll, P.J. 2012. Reliability of genetic bottleneck tests for detecting recent population declines. Mol. Ecol. **21**: 3403–3418. doi:10.1111/j.1365-294X.2012.05635.x. PMID:22646281.
Petersen, L.R., Martin, M.A., and Pils, C.M. 1977. Status of fishers in Wisconsin. Wisc. Dep. Nat. Resour. Rep. **92**: 1–14.
Piry, S., Luikart, G., and Cornuet, J.-M. 1999. Bottleneck: a computer program for detecting recent reductions in the effective population size using allele frequency data. J. Hered. **90**: 502–503. doi:10.1093/jhered/90.4.502.
Piry, S., Alapetite, A., Cornuet, J.-M., Paetkau, D., Baudouin, L., and Estoup, A. 2004. GENECLASS2: a software for genetic assignment and first-generation migrant detection. J. Hered. **95**: 536–539. doi:10.1093/jhered/esh074. PMID:15475402.
Powell, R.A., Lewis, J.C., Slough, B.G., and Murakami, T. 2012. Evaluating translocations of martens, sables, and fishers: testing model predictions with field data. *In* Biology and conservation of martens, sables, and fishers: a new synthesis. Chapter 6. *Edited by* K.B. Aubry, W.J. Zielinski, M.G. Raphael, G. Proulx, and S.W. Buskirk. Cornell University Press, Ithaca, N.Y. pp. 93–137.
Raesly, E.J. 2001. Progress and status of river otter reintroduction projects in the United States. Wildl. Soc. Bull. **29**: 856–862.
Ralls, K., and Ballou, J.D. 2004. Genetic status and management of California condors. Condor, **106**: 215–228. doi:10.1650/7348.
Rannala, B., and Mountain, J. 1997. Detecting immigration by using multilocus genotypes. Proc. Natl. Acad. Sci. U.S.A. **94**: 9197–9201. doi:10.1073/pnas.94.17.9197. PMID:9256459.
Raymond, M., and Rousset, F. 1995. GENEPOP (version 3.4): population genetics software for exact tests and ecumenicism. J. Hered. **86**: 248–249.
Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution, **43**: 223–225. doi:10.1111/j.1558-5646.1989.tb04220.x. PMID:28568501.

Russell, W.C., Thorne, E.T., Oakleaf, R., and Ballou, J.D. 1994. The genetic basis of black-footed ferret reintroduction. Conserv. Biol. **8**: 263–266. doi:10.1046/j.1523-1739.1994.08010263.x.

Sarrazin, F., and Legendre, S. 2000. Demographic approach to releasing adults versus young in reintroductions. Conserv. Biol. **14**: 488–500. doi:10.1046/j.1523-1739.2000.97305.x.

Schwartz, M.K. 2007. Ancient DNA confirms native Rocky Mountain fisher (*Martes pennanti*) avoided early 20th century extinction. J. Mammal. **88**: 921–925. doi:10.1644/06-MAMM-A-217R1.1.

Seddon, P. 1999. Persistence without intervention: assessing success in wildlife reintroductions. Trends Ecol. Evol. **14**: 503. doi:10.1016/S0169-5347(99)01720-6. PMID:10542463.

Servheen, C., Kasworm, W., and Christensen, A. 1987. Approaches to augmenting grizzly bear populations in the Cabinet Mountains of Montana. Intl. Conf. Bear Res. Manage. **7**: 363–367. doi:10.2307/3872645.

Slough, B.G. 1994. Translocations of American martens: an evaluation of factors in success. *In* Martens, sables, and fishers: biology and conservation. Cornell University Press, Ithaca, N.Y. pp. 165–178.

Spencer, C.C., Neigel, J.E., and Leberg, P.L. 2000. Experimental evaluation of the usefulness of microsatellite DNA for detecting demographic bottlenecks. Mol. Ecol. **9**: 1517–1528. doi:10.1046/j.1365-294x.2000.01031.x. PMID:11050547.

Steury, T.D., and Murray, D.L. 2004. Modeling the reintroduction of lynx to the southern portion of its range. Biol. Conserv. **117**: 127–141. doi:10.1016/S0006-3207(03)00287-8.

Swanson, B.J., and Kyle, C.J. 2007. Relative influence of temporal and geographic separation of source populations in a successful marten reintroduction. J. Mammal. **88**: 1346–1348. doi:10.1644/07-MAMM-A-003R.1.

Swanson, B.J., Peters, L.R., and Kyle, C.J. 2006. Demographic and genetic evaluation of an American marten reintroduction. J. Mammal. **87**: 272–280. doi:10.1644/05-MAMM-A-243R1.1.

Tucker, J.M., Schwartz, M.K., Truex, R.L., Pilgrim, K.L., and Allendorf, F.W. 2012. Historical and contemporary DNA indicate fisher decline and isolation occurred prior to the European settlement of California. PLOS ONE, **7**: e52803. doi:10.1371/journal.pone.0052803. PMID:23300783.

Vinkey, R.S., Schwartz, M.K., McKelvey, K.S., Foresman, K.R., Pilgrim, K.L., Giddings, B.J., and LoFroth, E.C. 2006. When reintroductions are augmentations: The genetic legacy of fishers (*Martes pennanti*) in Montana. J. Mammal. **87**: 265–271. doi:10.1644/05-MAMM-A-151R1.1.

Weir, B.S., and Cockerham, C.C. 1984. Estimating F-statistics for the analysis of population structure. Evolution, **38**: 1358–1370. doi:10.1111/j.1558-5646.1984.tb05657.x. PMID:28563791.

Williams, B., and Scribner, K.T. 2007. Demographic and genetic evaluation of an American marten reintroduction: a comment on Swanson et al. J. Mammal. **88**: 1342–1345. doi:10.1644/06-MAMM-A-291R1.1.

Williams, B.W., and Scribner, K.T. 2010. Effects of multiple founder populations on spatial genetic structure of reintroduced American martens. Mol. Ecol. **19**: 227–240. doi:10.1111/j.1365-294X.2009.04455.x. PMID:20041991.

Williams, B.W., Gilbert, J.H., and Zollner, P.A. 2006. Historical perspective on the reintroduction of the fisher and American marten in Wisconsin and Michigan. USDA For. Serv. Gen. Tech. Rep. NRS-5, USDA, Rhinelander, Wisc.

Williams, R.N., Rhodes, O.E., Jr., and Serfass, T.L. 2000. Assessment of genetic variance among source and reintroduced fisher populations. J. Mammal. **81**: 895–907. doi:10.1644/1545-1542(2000)081<0895:AOGVAS>2.3.CO;2.

Wisely, S.M., Buskirk, S.W., Russell, G.A., Aubry, K.B., and Zielinski, W.J. 2004. Genetic diversity and structure of the fisher (*Martes pennanti*) in a peninsular and peripheral metapopulation. J. Mammal. **85**: 640–648. doi:10.1644/BEL-011.

Wisely, S.M., Santymire, R.M., Marinari, P., Kreeger, J., Livieri, T., Marinari, P.E., Kreeger, J.S., Wildt, D.E., and Howard, J. 2005. Environment influences morphology and development for *in situ* and *ex situ* populations of the black-footed ferret (*Mustela nigripes*). Anim. Conserv. **8**: 321–328. doi:10.1017/S1367943005002283.

Wozencraft, W.C. 2005. Family Mustelidae. *In* Mammal species of the world. *Edited by* D.E. Wilson and D.M. Reeder. The Johns Hopkins University Press, Baltimore, Md. pp. 601–610.