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Research Article

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The genetic implications of translocations on Fisher (*Pekania pennanti*) populations in Montana and Idaho

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Abstract

Translocations are the intentional movement of animals across landscapes for conservation purposes and are used as a common method for restoring populations. Fisher (*Pekania pennanti*) populations have been extensively reintroduced and augmented in the Western United States, often using multiple source populations. To date, little is known about the success of past translocation efforts for Fisher recovery in the West, nor what the effects of using distinct populations for translocations were on contemporary population composition and genetic diversity. To understand the effects of historic translocations on contemporary Fisher population recovery, we analyzed >34 years of genetic data from fishers in Idaho and Montana ($n = 315$) that received multiple translocations from divergent source populations. We observed high genetic differentiation between fishers descendant from translocations using source populations in the Midwestern United States and translocated to the Cabinet Mountain range (MID) and fishers sampled throughout the rest of Idaho and Montana. Fishers outside of the Cabinet Mountains exhibited little genetic structure and had endemic US Northern Rocky Mountain or British Columbia mitochondrial haplotypes (BC-CLR), consistent with remnant populations that persisted in Montana and Idaho, intermixed with mid-20th century translocations of British Columbia populations. Five fishers had a low probability of nuclear genetic assignment to either the MID or the BC-CLR genetic clusters but showed evidence of recently derived British Columbia genetic ancestry. MID and BC-CLR genetic clusters in the US Northern Rocky Mountains had similar levels of genetic diversity across time and space but exhibited no evidence of gene flow between them. This pattern suggests that while translocation efforts succeeded in creating Fisher populations that persisted on the landscape, they have not created enough propagule pressure to produce movement between populations.

Key words: fishers, genetic structure, microsatellites, mitochondrial haplotypes, population assignment, translocation

Wildlife translocations—the capture and movement of an animal from one location to another—have served a variety of conservation purposes, including population augmentation, assisted colonization, and reintroduction (Gaywood and Stanley-Price 2022). Until the past 2 decades, genetic factors were given little, if any, prioritization in these processes (Schwartz 2005; Stepkovitch et al. 2022), although more recently genetics have been used for the selection of source populations for translocations (Tallmon et al. 2004; Bertola et al. 2022). Several recent reviews have advocated for an even greater inclusion of genetics in both translocation decision-making processes as well as for subsequent monitoring, management, and research (Frankham 2015; Whiteley et al. 2015; Frankham et al. 2017; Ralls et al. 2017; Happe et al. 2020). These reviews underscore the importance of incorporating genetics in the selection of the source population and in the assessment of the success of translocations to recover and increase the genetic diversity of target populations (Laikre et al. 2010; Lewis et al. 2012). Pairing ecological monitoring methods with genetic tools, for example, has allowed us to estimate relative reproductive success of individuals and estimate population viability following translocations (Facka et al. 2016; Golding et al. 2022). Genetic tools also provide a way to monitor populations for future conservation challenges such as increased inbreeding or dramatic reductions in genetic diversity over time (Bell et al. 2019; Fitzpatrick et al. 2023). The inclusion of genetics in these efforts has provided key insights into how translocated individuals interact with endemic individuals, providing information on how successful translocations were to recovery goals (Van Rossum et al. 2020; Seaborn et al. 2021a).

There have been many translocations to assist recovery of the Fisher (*Pekania pennanti*), a mid-sized forest carnivore, throughout their range. By the mid-1800s, fishers had experienced significant range contractions (~43%) due to overexploitation for their high value

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fur pelts and to habitat loss (Powell 1993; Powell et al. 2017). To alleviate population declines, Fisher translocations began in 1896 with fishers being moved into Quebec from an unknown location (Lewis et al. 2012). Since then, there have been at least 37 documented Fisher translocations across North America, with varying rates of success (Powell et al. 2017; Stewart et al. 2018; Green et al. 2022). Fisher translocations occurring in the 1950s and 1960s in the Northeast were thought to result in greater Fisher recovery than analogous efforts in the West (Williams et al. 2000; Aubry and Lewis 2003; Hapeman et al. 2011; Lapoint et al. 2015). The higher recovery of fishers in the Northeastern United States has been attributed to the higher forest productivity, lower predation risk, strict harvest regulations, and recovered habitat of Fisher in these regions (Powell and Zielinski 1994; Lewis and Stinson 1998; Lapoint et al. 2015; Green et al. 2018).

In the Western United States, historical distribution of fishers included the Cascade and Sierra Nevada Mountains of Washington, Oregon, and California as well as the Rocky Mountains of Northern Idaho and Western Montana (Powell 1993; Schwartz et al. 2012). Translocations in the West were initially conducted by foresters because fishers were natural predators of porcupines (*Erethizon dorsatum*), which were girdling trees valuable for timber production. Translocations included Boreal fishers (*P. p. columbiana*) and Columbian fishers (*P. p. pacifica*) from British Columbia to Idaho and Montana from 1959 to 1963 ($n=78$) and into Oregon in 1961 (Weckwerth and Wright 1968; Drew et al. 2003; Vinkey 2003; Vinkey et al. 2006; Knaus et al. 2011; Lewis et al. 2012). In the late 1980s and early 1990s, fishers from Wisconsin and Minnesota in the Midwestern United States (*P. p. pennanti*) were translocated into Montana (1989 to 1991, $n=110$; Heinimeyer 1993; Heinimeyer and Jones 1994). These translocations did not consider the source population(s) nor the implication of genetic mixture with any relict Fisher populations (Williams et al. 2000; Aubry and Lewis 2003; Drew et al. 2003; Vinkey et al. 2006; Schwartz 2007). Broadly, these historic translocations were believed to have had mixed success due to competition and predation by other carnivores, changes in the ecosystem including the loss of white pine, and lack of protection during the recovery phase in some areas (Schwartz et al. 2013; Green et al. 2022). The use of distinct source populations and subspecies of Fisher likely also contributed to the outcomes of these early translocation efforts. However, these factors have not been well characterized due to limited record keeping and challenges of post-translocation monitoring (Knaus et al. 2011; Lewis et al. 2012; Stewart et al. 2018).

The impact of historic translocations on contemporary Fisher populations found in the inland Northwest remains ambiguous to date (Powell and Zielinski 1994). US Northern Rocky Mountain fishers are currently classified as a Distinct Population Segment (DPS) by the US Fish and Wildlife Service (USFWS) and have been petitioned for listing under the Endangered Species Act multiple times (USFWS 2017). Fishers were initially thought to have been extirpated from this region, leaving the closest known Fisher population ~400 km to the North in British Columbia (Vinkey et al. 2006; Lofroth et al. 2010; Weir et al. 2024). However, previous genetic work identified a unique mitochondrial haplotype (haplotype 12) found only in fishers in Northern Idaho (Vinkey et al. 2006). A subsequent ancient DNA study using a Fisher sampled prior to any translocations (in 1896) confirmed this conclusion, which suggested that US Northern Rocky Mountain fishers (*P. p. columbiana*) were never truly extirpated (Schwartz 2007). Additional genetic analyses have found that remnant fishers in Idaho primarily consisted of individuals with endemic and British Columbia genetic ancestries (Vinkey 2003; Vinkey et al. 2006; Lucid et al. 2016, 2019). The origin of this British Columbia ancestry, whether derived from translocated animals or the result of historic gene flow, remains unclear. Furthermore, a significant gap exists to determine the genetic ancestry of fishers found in Northern Idaho and Montana, which received translocations from both British Columbia and Midwestern Fisher populations (Heinemeyer 1993; Heinemeyer and Jones 1994; Vinkey 2006).

While these previous studies have provided critical snapshots of Fisher status over time, a comprehensive analysis of Fisher recovery since and across all translocated regions in the US Northern Rocky Mountains is necessary to understand the status of the population today. We used 397 genetic samples to explore the impacts of mixed translocation history on the population genetics and recovery of US Northern Rocky Mountains Fisher. We addressed 4 major questions for fishers in the US Northern Rocky Mountains population: (i) what is the current population genetic structure; (ii) is there any evidence of gene flow with contemporary British Columbia fishers; (iii) how have microsatellite allele frequencies or mitochondrial haplotype frequencies changed over time and space; and (iv) given the mixed population sources used for translocations, which genetic ancestries do we primarily detect now? The inferences gained will contribute to our broader understanding of how translocation efforts can affect the genetic and demographic recovery of extirpated or threatened populations of Fisher in the Western United States. Additionally, it provides key information necessary for the management of a species of federal conservation concern that is cryptic, elusive, and challenging to monitor.

Methods

Study area.

Our focal study area included Northern Idaho, North of the Salmon River, and Northwestern Montana, West of the Beaverhead Mountains and North of Lost Trail Pass (Fig. 1A). In both Idaho and Montana, fishers are primarily distributed in the Rocky Mountain chain, including the Cabinet, Clearwater, Bitterroot, and Selkirk Mountains (Olson et al. 2024). High densities of Fisher samples were collected West of the Bitterroot Mountains, in the Clearwater Mountains near Lolo Pass. Our sampling area overlaps with the locations of the historic translocation sites from central British Columbia into 3 sites in Idaho and 3 sites in Montana and from the Midwest into 1 site in Montana (Fig. 1; Vinkey 2003). We also included samples from British Columbia as reference populations. While precise sampling locations were unknown in British Columbia, relative geographic landmarks were ascribed as shown in the sampling map (Fig. 1B). Fisher samples throughout the "central interior" region, which is sub-boreal, as well as the Western edge of the boreal "interior" region Northeast of the Rocky Mountains were included (Weir et al. 2024). All research on live animals followed American Society of Mammalogy guidelines (Sikes et al. 2016).

Sample collection.

Overall, we genotyped 397 samples from British Columbia and the United States. We genotyped 309 samples from Montana and Idaho and 6 from the Midwest (Fig. 1; Supplementary Data SD1) collected between 1989 and 2022. The samples included tissues from the hides of legally harvested fishers, tissues from animals handled during radiotelemetry studies (Schwartz et al. 2013; Sauder and Rachlow 2014; Olson et al. 2024), and hair from non-invasive monitoring surveys targeting fishers and other forest carnivores from 2004 to 2022. To examine the influence of mixed translocation histories on contemporary populations of Fisher, we also included samples from the putative source populations of each of the translocations including samples from 6 of the originally translocated animals from Minnesota ($n=2$) and Wisconsin ($n=4$), hereafter referred to as the Midwestern Fisher (Vinkey 2003; Vinkey et al. 2006). Our data set included 119

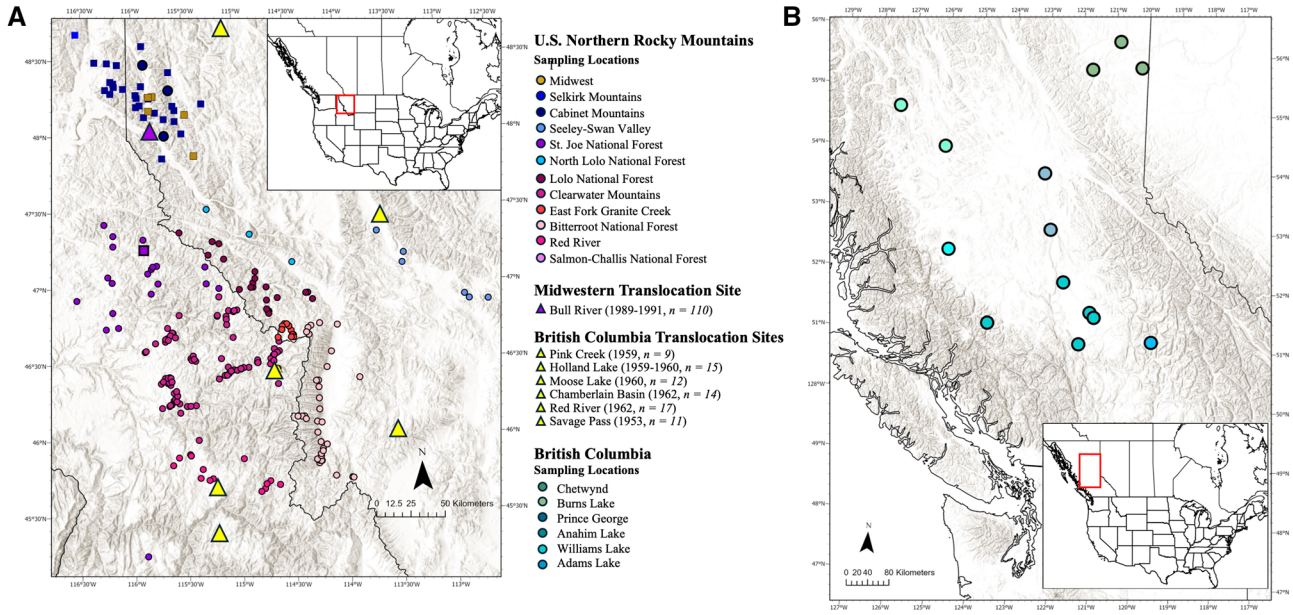

Fig. 1. Locations of the 397 trapped and non-invasively sampled fishers in (A) Idaho and Montana, United States and in (B) British Columbia, Canada included in this study. All circles represent Fisher sampling locations with colors corresponding to sampling location site name. Yellow triangles represent British Columbia translocation sites and the purple triangle represents the Midwest translocation site. Exact coordinates for Fisher samples in British Columbia were unknown and thus points represent approximate locations given for cohorts of samples from different sampling locations. Squares and circles (A) were indicative of the final genetic cluster assignments of fishers in the US Northern Rocky Mountain population.

Fisher samples that had been previously haplotyped at the mitochondrial control region (Vinkey et al. 2006), 5 individuals that had their entire mitochondrial genome sequenced (Knaus et al. 2011), and 26 samples that were microsatellite genotyped but only at a subset of the loci genotyped in our study (Lucid et al. 2019).

Additionally, we genotyped 82 samples previously collected across British Columbia by the British Columbia Ministry between 2003 and 2004 from locations that were potential source populations for Fisher in the translocations throughout Idaho and Montana (Fig. 1; Roy 1991; Heinemeyer 1993; Vinkey 2003). These samples were hide tissue collected from legally harvested carcasses (Vinkey et al. 2006). We used the approximate geographic location referenced in Table 1 when exact geographic sample locations were not recorded.

DNA extraction, amplification, and sequencing.

Laboratory work was performed at the US Forest Service Rocky Mountain Research Station, National Genomics Center for Wildlife and Fish Conservation. Genomic DNA was extracted from tissue and hair samples using the QIAGEN DNeasy Blood and Tissue kit (Qiagen, Valencia, California, United States) according to the manufacturer instructions but using modifications for hair samples that followed Mills et al. (2000). Prior to microsatellite genotyping, species identification was conducted by amplifying and sequencing 360 base pairs of mitochondrial 16 S rRNA using universal primers (Hoelzel and Green 1992; Golding et al. 2022). After species confirmation, we genotyped a total of 397 individual Fisher samples at 15 microsatellite loci that have been described in previous mustelid studies: Ggu101, Ggu216; Lut604, Lut733 (Dallas and Piertney 1998); Ma1, Tt1 (Davis and Strobeck 1998); Mer022 (Fleming et al. 1999); Mf1.18 (Basto et al. 2010); Mp0059, Mp0144, Mp0175, Mp0197, Mp0200, Mp0247 (Jordan et al. 2007); and Mvi1321 (Vincent et al. 2003). The reaction volume (10 mL) contained 1.0 mL DNA, 1× reaction buffer (Applied Biosystems), 2.0 mM $MgCl_2$, 200 mM of each dNTP, 1 mM reverse primer, 1 mM dye-labeled forward primer, 1.5 mg/mL BSA, and 1U Taq polymerase (Applied Biosystems). The PCR profile was 94 °C for 5 min for an initial denaturing step followed by 45 cycles of 94 °C for 1 min, 55 °C for 1 min, and 72 °C for 30 s. We performed replicate genotyping from all hair and scat DNA samples, with each sample PCR-amplified initially twice across the 15 variable microsatellite loci to screen for allele dropout, stutter artifacts, and false alleles (DeWoody et al. 2006). PCR products were visualized on a LI-COR DNA analyzer (LI-COR Biotechnology). We used the programs Dropout (McKelvey and Schwartz 2005; Schwartz et al. 2006) and GenAlEx v6.5 (Peakall and Smouse 2006, 2012) to check for genotyping errors.

We amplified the left domain of the control region of mtDNA (385 base pairs) using primers L15926 and H16498 (Kocher and Wilson 1991) to identify the mitochondrial haplotype of each sample. Reaction volumes of 30 µL contained 50 to 100 ng DNA, 1× reaction buffer (Life Technologies, New York, United States), 2.5 mM $MgCl_2$, 200 µM of each dNTP, 1 µM of each primer, 1 U Amplitaq Gold polymerase (Life Technologies, New York, United States). The PCR program was 94 °C for 5 min, [94 °C for 1 min, 55 °C for 1 min, 72 °C for 1 min and 30 s] × 34 cycles, 72 °C for 5 min. We determined the quality and quantity of template DNA using 1.6% agarose gel electrophoresis. PCR products were purified using ExoSap-IT (Affymetrix-USB Corporation, Ohio, United States) according to manufacturer's instructions, and amplicons were sequenced using the PCR primers at Eurofins Genomics (Louisville, Kentucky, United States) using standard Sanger sequencing protocols. We viewed and aligned the resulting DNA sequence data with the software Sequencher (Gene Codes Corp., Michigan, United States).

Population genetic structure analyses.

Evaluating genetic structure in British Columbia and US Northern Rocky Mountain fisher populations

We used 2 individual-based methods to investigate population genetic structure of fishers sampled in the US Northern Rocky Mountains and British Columbia: Discriminant Analysis of Principal Components (DAPC: Jombart 2008; Jombart et al. 2010) and STRUCTURE (Pritchard et al. 2000). DAPC employs principal components analysis to generate uncorrelated axes of genetic variation that discriminant analyses then use to summarize between group differentiation. To do this, we first

Table 1. All Fisher samples and their mitochondrial haplotypes are organized by their genetic cluster assignment results (bolded values) and sampling locations across the United States and British Columbia, Canada.

		Mitochondrial haplotypes									
Genetic cluster assignment		**1C**	**4**	**5**	**6**	**7**	**9**	**10**	**11**	**12**	**1D**
Boreal (BOR)	**25**	**0**	**1**	**0**	**4**	**7**	**1**	**0**	**12**	**0**	**0**
Burns Lake (British Columbia, Canada)	1	0	0	0	0	1	0	0	0	0	0
Chetwynd (British Columbia, Canada)	21	0	1	0	3	6	0	0	11	0	0
Prince George (British Columbia, Canada)	3	0	0	0	1	0	1	0	1	0	0
Columbian (COL)	**31**	**0**	**9**	**0**	**3**	**6**	**13**	**0**	**0**	**0**	**0**
Adams Lake (British Columbia, Canada)	1	0	0	0	0	0	1	0	0	0	0
Chetwynd (British Columbia, Canada)	2	0	1	0	0	0	0	0	0	0	0
Prince George (British Columbia, Canada)	4	0	2	0	2	0	0	0	0	0	0
Williams Lake (British Columbia, Canada)	15	0	6	0	1	6	12	0	0	0	0
British Columbia/Clearwater (BC-CLR)	**260**	**0**	**65**	**0**	**70**	**11**	**0**	**0**	**0**	**114**	**0**
Bitterroot National Forest (Montana, USA)	48	0	9	0	17	0	0	0	0	22	0
Cabinet Mountains (Montana and Idaho, USA)	1	0	1	0	0	0	0	0	0	0	0
Clearwater Mountains (Idaho, USA)	126	0	33	0	34	3	0	0	0	56	0
East Fork Granite Creek (Idaho, USA)	16	0	3	0	7	0	0	0	0	6	0
Lolo National Forest (Montana, USA)	23	0	7	0	4	1	0	0	0	11	0
North Lolo National Forest (Montana, USA)	3	0	2	0	1	0	0	0	0	0	0
Red River (Idaho, USA)	18	0	3	0	2	3	0	0	0	10	0
Seeley-Swan Valley (Montana, USA)	6	0	1	0	3	1	0	0	0	1	0
St. Joe National Forest (Idaho, USA)	19	0	6	0	2	3	0	0	0	8	0
Midwest (MID)	**48**	**12**	**4**	**23**	**0**	**0**	**0**	**9**	**0**	**0**	**0**
Cabinet Mountains (Montana and Idaho, USA)	39	10	4	18	0	0	0	7	0	0	0
Midwest (Wisconsin and Minnesota, USA)	6	2	0	2	0	0	0	2	0	0	0
Selkirk Mountains (Idaho, USA)	2	0	0	2	0	0	0	0	0	0	0
St. Joe National Forest (Idaho, USA)	1	0	0	1	0	0	0	0	0	0	0
Unassigned	**33**	**1**	**4**		**12**	**9**	**3**		**2**		**2**
Anahim Lake (British Columbia, Canada)	**2**				**2**						
Burns Lake (British Columbia, Canada)	**3**					**2**	**1**				
Cabinet Mountains (Montana and Idaho, USA)	**4**	**1**			**2**	**1**					
Chetwynd (British Columbia, Canada)	**6**					**3**			**2**		**1**
Clearwater Mountains (Idaho, USA)	**1**				**1**						
East Fork Granite Creek (Idaho, USA)	**1**		**1**								
Prince George (British Columbia, Canada)	**3**				**1**		**1**				**1**
Salmon-Challis National Forest (Idaho, USA)	**1**				**1**						
Williams Lake (British Columbia, Canada)	**12**		**3**		**5**	**3**	**1**				
Total	**364**	**12**	**79**	**23**	**77**	**24**	**14**	**9**	**12**	**114**	**2**

Columns indicate the number of samples collected per genetic cluster, sampling location, and the number of different mitochondrial haplotypes detected. Individuals translocated from Wisconsin and Minnesota (Midwest) into the Cabinet Mountains in Northern Idaho and Montana were included as part of the Midwestern genetic cluster (MID) based on their genetic cluster assignment. Individuals that were "unassigned" included those with discordant genetic assignment results between STRUCTURE and DAPC, low probability of assignment to a genetic cluster based on either method (<90%), and/or exhibited genetic admixture. These unassigned individuals were not included in downstream population genetic analyses.

determined the optimal number of principal components (PCs) to retain from the DAPC, selecting the number that explained ≥ 90% of the variance in our data. Second, we performed K-means clustering analysis to identify the optimal number of distinct genetic clusters using these PCs (K). We tested K-values between 1 and 10 and selected the visual "elbow" or the lowest Bayesian Information Criterion score (BIC) using the least genotypic data. STRUCTURE is a Bayesian model-based method that we used to probabilistically assign global ancestry proportions from each of the tested genetic clusters (K) to each individual. We ran this model, allowing for admixture for 10,000 iterations after a burn-in of 5,000. We tested K 1-10 and used the Evanno method to identify the optimal K value; this method looks for the greatest change in the marginal likelihood values computed for each tested K value (ΔK; Evanno et al. 2005). We removed Fisher samples that had discordant DAPC and STRUCTURE genetic cluster assignments or those that had low probability of genetic cluster assignment (≤ 90% of their ancestry from a single genetic cluster and/or had ≤ 85% posterior probability of assignment of a genetic ancestry proportion) from downstream analyses unless otherwise specified. We ran both population genetic structure analyses on the British Columbia reference populations independently from the US Northern Rocky Mountain Fisher population because we did not predict admixture between these populations.

Evaluating genetic structure across the Rocky Mountains

We conducted additional genetic structure analyses to estimate the impacts of the mixed translocation history on contemporary population genetic structure of US Northern Rocky Mountain fishers. Fishers from both British Columbia and the United States were included in this analysis and relationships among individuals were visualized using sampling location. We conducted a principal coordinates analysis (PCOA) to first visualize the genetic similarity amongst all individuals using the R package "Adegenet" (Jombart 2008). Genetic distances were calculated using the eigenvector output from principal component analysis (PCA) using the "graph4lg" R package (Savary et al. 2021). We investigated similarity among genetic clusters (as defined by the genetic structure results) using the proportion of shared alleles (DPS) genetic distance metric from the R package "graph4lg." We also conducted an individual-based PCOA again using the eigenvectors from the PCA to calculate genetic distance but only retained individuals confidently assigned to genetic clusters (see Methods section "Population genetic structure analysis"). Finally, we

ran STRUCTURE, using the parameters described above, including all individuals and allowing for "admixture."

Evaluating gene flow between local and translocated fisher populations in the United States

We tested the role of geographic (isolation by distance; IBD) and translocation (isolation by distance to a translocation release site; IBT) distances on genetic distances for each pair of fishers to evaluate the impact of translocations on the genetic structure of US Northern Rocky Mountain fishers. We generated geographic distance matrices using Euclidean pairwise distance (IBD: $n=1$ matrix) and geographic distance matrices between all pairs of individuals and any/each translocation site (IBT: $n=10$ matrices). Pairwise genetic distances among individuals were derived using the proportion of shared microsatellite alleles (DPS) in the R package "graph4lg" (Bowcock et al. 1994; Savary et al. 2021). We used generalized linear models to determine if translocation history (IBT) better explained genetic distance than Euclidean distance (IBD) among fishers. More details regarding model construction, selection, and parameterization can be found in the Supplementary Data SD2.

Characterizing the spatio-temporal distribution of microsatellite and mitochondrial alleles

To determine how Fisher translocations impacted genetic diversity, we characterized how genetic diversity changed spatially and temporally. We calculated observed heterozygosity (H_o), expected heterozygosity (H_e), the mean allelic richness (A_r), the number of alleles private to each genetic cluster (private alleles), and Wright's F statistic (F_{IS}) for each genetic cluster using the R package "Hierfstat" (Goudet 2005). We also calculated pairwise Weir and Cockerham's F_{ST} using "Hierfstat" and the composition of mitochondrial haplotypes to characterize genetic differentiation among genetic clusters. We determined the effective population sizes of each genetic cluster (N_e) using the linkage disequilibrium based (LDN_e) and temporal Ne (TpN_e) estimators in NeEstimator v2 (Do et al. 2014; Waples 2025). The LDN_e method, based on the assumption that drift impacts both linked and unlinked loci, calculates the N_e based on the amount of linkage disequilibrium (Hill 1981; Waples and Do 2010). The TpN_e method in NeEstimator v2 uses the standard variance in the changes in allele frequencies between individuals from the same genetic cluster sampled between 2 time points to estimate N_e (Nei and Tajima 1981; Waples 1989; Schwartz et al. 1998). Given that sampling was not done in a standardized manner across space and time, we used samples collected from the earliest and latest time periods (5-yr periods; Supplementary Data SD1) for each putative genetic cluster to estimate TpN_e (Supplementary Data SD1). Since reference fishers from British Columbia were sampled during the same time period, TpN_e was not estimated for these genetic clusters. Statistical significance was determined if credible intervals did not bound zero or infinity. We evaluated how F_{ST} and allelic richness changed over time to determine if there were any temporal shifts in genetic variation within the genetic clusters identified in the US Northern Rocky Mountain Fisher population. We use the "hs.test" in the R package "Adegenet" to determine if there were differences in expected heterozygosity over time within genetic clusters. We simulated 500 replications and considered results statistically significant if P-values < 0.01.

Genetic assignment test to infer genetic ancestry and translocation success

We conducted genetic mixture analysis using the R package "RUBIAS" to determine the relative contribution and origin of admixed individuals with ambiguous genetic ancestry (Anderson et al. 2008; Moran and Anderson 2019). This program used Bayesian models to infer the genetic composition of individuals from different genetic clusters. Individuals that were successfully assigned to genetic clusters were used as "reference." Given that multiple source populations contributed individuals for translocations in the US Northern Rocky Mountains, we tested whether genetic mixture might have occurred between local and translocated fishers. While we did not have samples from the fishers originally translocated from British Columbia as we do from the Midwest, we included data from numerous potential British Columbia source populations (Table 1). We used these reference individuals to identify the genetic composition of unassigned or mixed ancestry fishers from the population genetic structure analyses. Small collections of Fisher samples ($n<3$ per sampling location) were excluded from the reference set but retained in the "mixture" set.

We ran simulations in "RUBIAS" to test the impacts of variance in the sampling design (uneven total sample sizes and variance in temporal sampling period) across our "reference." We used the "self-assign" function in "RUBIAS" to test the probability of accurately reassigning reference individuals back to their "true" (1) genetic cluster and (2) sampling location. We then tested the probability of reassignment of simulated, admixed individuals to their "true" genetic cluster and sampling location to determine the relative power of assignment of our reference set to delineate ancestry at each hierarchical level. Ultimately, we retained individuals in the "reference" set that had ≥ 90% probability of reassigning simulated ancestry to the "true" genetic cluster. Individuals that were removed from the reference collection were retained in the "mixed" sample set and tested in the genetic mixture analyses. We tested the probability of assigning genetic ancestry in the "mixture" set to a reference genetic cluster (≥85% posterior probability of assignment).

Results

We detected 10 unique mitochondrial haplotypes among the 397 Fisher samples from both the United States and British Columbia that we included in this study (Table 1). We detected 7 unique haplotypes in the 315 US Northern Rocky Mountain Fisher samples and 6 unique haplotypes in the 82 British Columbia Fisher samples. The endemic haplotype 12 and Midwestern haplotypes 1C, 5, and 10 were unique to fishers sampled in Idaho and Montana (Drew et al. 2003; Vinkey et al. 2006; Schwartz 2007; Knaus et al. 2011; Table 1). Our average microsatellite genotype rate was 98.5% across all 397 individuals, with the individual with the most missing genotype data missing 4 microsatellite genotypes (73% genotyping rate).

Genetic structure analyses of US Northern Rocky Mountain and British Columbia populations.

We detected 2 major genetic clusters (K) in the US Northern Rocky Mountain Fisher population (Fig. 2A and B). The genetic clusters split the fishers translocated from the Midwestern United States into the Cabinet Mountains in Northern Idaho and Montana and their direct descendants from the remainder of the samples collected throughout Idaho and Montana (Fig. 2). We named our genetic clusters to reflect the derived genetic ancestry present in both clusters. The genetic cluster that contained the ancestors of the Midwest translocation are hereafter the "Midwestern" (MID) genetic cluster. The genetic cluster that contained the rest of the Idaho and Montana fishers were hereafter referred to as the "British Columbia/Clearwater" (BC-CLR) genetic cluster because they were either putatively endemic or the ancestors of translocated individuals from British Columbia. We used "Clearwater" because this is analogous to the Idaho Department of Fish and Game designation for the management unit in the Nez Perce-Clearwater National Forest from which the majority of our

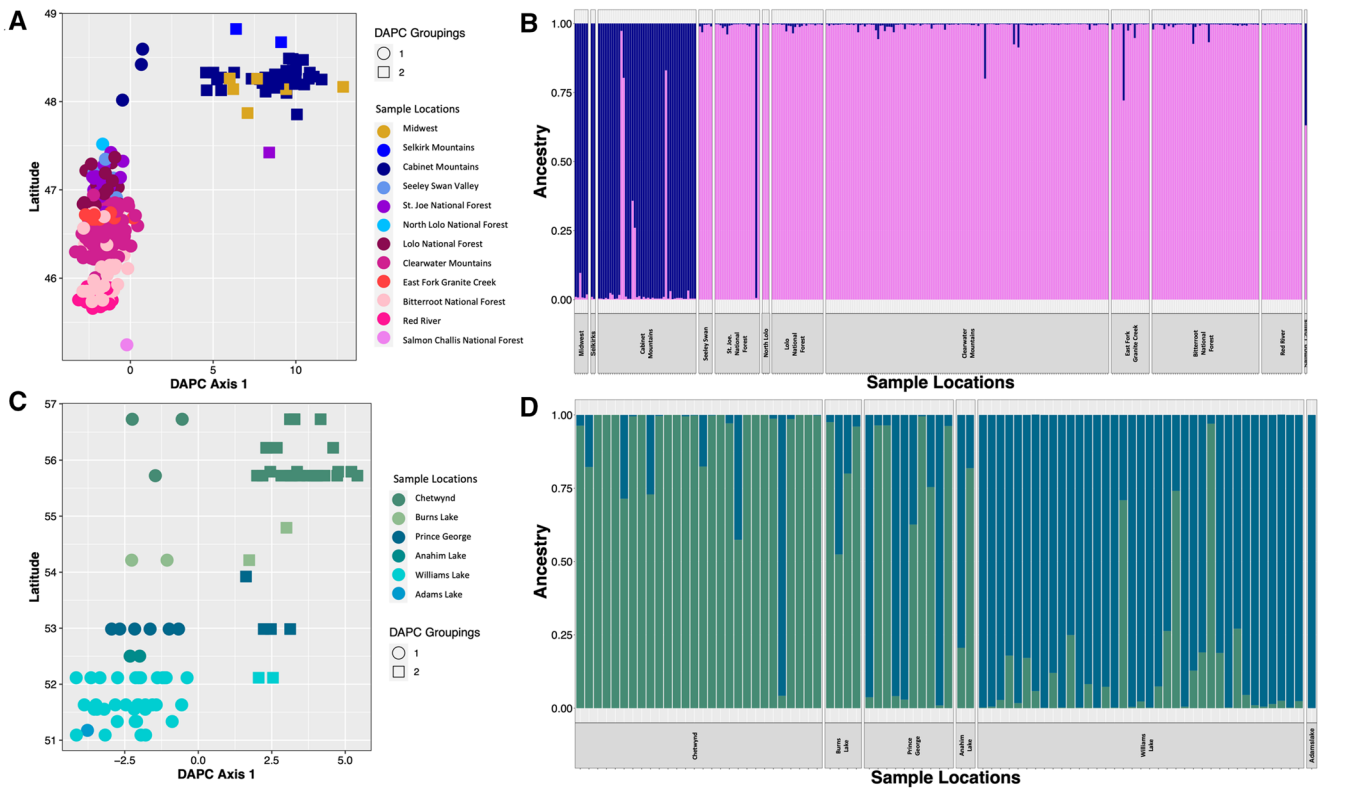

Fig. 2. A) Discriminant analyses of principal components (DAPC) and B) STRUCTURE results for the optimal number of genetic clusters (K = 2) for all fishers sampled across the US Northern Rocky Mountains. These analyses also included the 6 translocated individuals from Wisconsin and Minnesota labeled as (Midwest) on the x-axis. C) DAPC and D) STRUCTURE results for the optimal *K* (K = 2) for all fishers sampled in British Columbia. For DAPC plots (A, C), the x-axis was the first and only discriminant axis of significance, and the y-axis split points by latitude. Shapes were indicative of assigned genetic cluster, and color was based on sampling location. For STRUCTURE plots (B, D) each vertical bar represents an individual. Sampling locations were organized latitudinally from left to right along the x-axis. Colors represent a distinct genetic cluster. Proportions of colors represent the global ancestry proportions for each genetic cluster assigned to each individual.

samples were collected. Testing additional K values from 2 to 5 did not explain any additional, genetic substructure in either analysis (Supplementary Data SD3 and SD4). Both DAPC and STRUCTURE showed that 260 out of the 263 individuals sampled in central Idaho and Western Montana, outside of the Cabinet Mountains, assigned to the BC-CLR genetic cluster (Table 1; Fig. 1). All but 3 of the fishers sampled in the Cabinet Mountain range assigned to the MID genetic cluster (Table 1).

We similarly detected 2 genetic clusters in our reference samples collected from British Columbia (Fig. 2C and D). These clusters delineated individuals collected to the West (Columbian; COL) and to the East (Boreal; BOR) of the Rocky Mountains, reflecting genetic structure results in previous work (Weir et al. 2024; Figs 1B and 2C). Increasing K-values did not explain additional genetic substructure using either STRUCTURE or DAPC (Supplementary Data SD5 and SD6). We consistently assigned 25 individuals to the BOR and 31 individuals to the COL genetic clusters, respectively across both genetic structure analyses (≥85% posterior probability of assignment). There were 33 individuals that we could not assign to a single genetic cluster that we left out of downstream analyses (Table 1).

Limited evidence of gene flow between local and translocated fisher populations in the US.

The first axis of our PCOA primarily described genetic differences between the MID and BC-CLR genetic clusters, with COL and BOR falling intermediate to these clusters and not clearly distinguishable from one another along the first or second axis (Supplementary Data SD7). We found no evidence of ongoing gene flow between contemporary British Columbia and US Fisher populations (Supplementary Data SD8).

We observed strong evidence of IBD, which explained the US Northern Rocky Mountain genetic structure (Supplementary Data SD9). Mantel tests of permutations of Euclidean and genetic distance matrices further supported IBD, with a stronger signal being observed broadly across all US Northern Rocky Mountain Fisher pairs (Mantel statistic, $R = 0.56$, $P < 0.01$) compared with the subset of fishers in the BC-CLR genetic cluster (Mantel statistic, $R = 0.18$, $P < 0.01$; Supplementary Data SD9). While generalized linear model results similarly reflected support for IBD, the Euclidean Distance model ranked fourth among the 11 tested models (Supplementary Data SD10). The Full Model, which contained all geographic distance metrics was the top model ranked by AIC, followed by the distance to the Chamberlain Basin translocation site, which was the most geographically centralized translocation site (ΔAICc = 3077.23; Supplementary Data SD10). While the predictor variables for the Chamberlain Basin model did not bound 0, neither did any of the proceeding ranked models. Counter to our expectations, minimum distance to a translocation site had low predictive power.

Changes in spatio-temporal allelic diversity.

We observed the greatest genetic differentiation (F_{ST}) between MID and BC-CLR genetic clusters ($F_{ST} = 0.22$). Genetic differentiation was higher between the MID and Canadian genetic clusters (BOR or COL) than either was with BC-CLR fishers (Fig. 3A). MID had the highest number of private alleles, but the smallest, albeit statistically insignificant, coefficient of inbreeding (F_{IS}; Table 2). We observed greater heterozygosity and allelic richness in BOR and COL compared to BC-CLR (Fig. 3B; Table 2). BC-CLR also had significantly different estimates of expected heterozygosity compared to the other 3 genetic clusters ($P < 0.01$; Table 2). Observed heterozygosity was lower and not

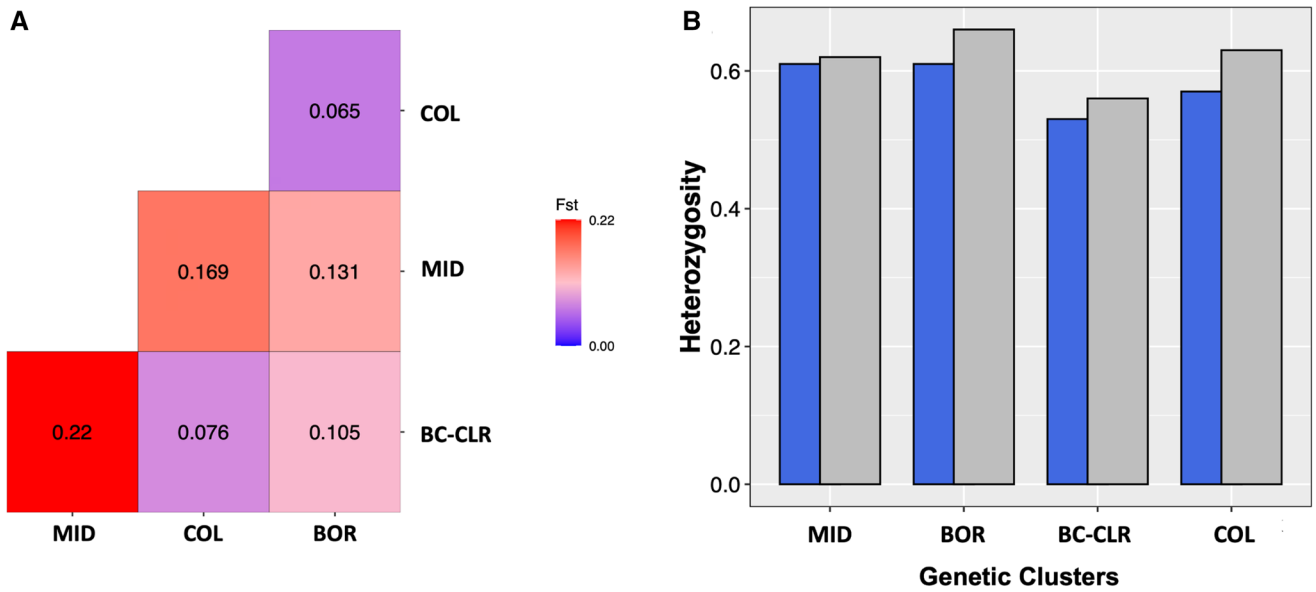

Fig. 3. (A) We consistently observed the greatest level of genetic differentiation between the MID and the other 3 genetic clusters (COL, BOR, and BC-CLR) as measured by Weir and Cockerham's F_{ST} (B). Bootstrapped confidence intervals of all pairwise F_{ST} values did not overlap 0 and thus were all considered to be statistically significant. (B) BOR appeared to have the highest observed (blue bars) and expected heterozygosity (grey bars). COL had higher expected heterozygosity than MID but lower observed.

Table 2. Population genetic summary statistics for the 4 genetic clusters identified from British Columbia, Canada, and the US Northern Rocky Mountain population.

	Population genetic statistics						
Populations	**H_o**	**H_e**	**LDN_e**	**TpN_e**	**F_{IS}**	**A_r**	**Private Alleles**
BOR British Columbia, Canada (n = 25)	0.64	0.67	647.5 (66.9–∞)	N/A	0.05*	4.78	6
COL British Columbia, Canada (n = 31)	0.57	0.63	778.3 (89.6–∞)	N/A	0.08*	4.29	0
MID Montana and Idaho, USA (n = 48)	0.61	0.62	35.2* (26.3–49.5)	40.7* (24.3–74.8)	0.01	4.42	8
BC-CLR Montana and Idaho, USA (n = 260)	0.53	0.56*	146.6* (116.7–188.6)	105.8* (43.2–381.3)	0.05*	4.16	5

We observed the greatest observed and expected heterozygosity (H_o and H_e), effective population size (TpN_e and LDN_e), and mean allelic richness (A_r) in the BOR genetic cluster. We observed the greatest number of private alleles in MID but a higher coefficient of inbreeding (F_{IS}) in COL. Asterisks were ascribed if bootstrapped confidence (F_{IS}) and jackknifed credible intervals (N_e) of population genetic estimators did not bound 0 or reach infinity. Asterisks were also prescribed for H_e values if *P*-values < 0.01 across all "hs.test" results with a given genetic cluster (H_e).

significantly different than expected heterozygosity in all genetic clusters (Table 2). MID and BOR had the highest observed heterozygosity (H_o = 0.61 and 0.64, respectively), while BC-CLR had the lowest (H_o = 0.53; Table 2). The linkage disequilibrium (LDN_e) and temporal (TpN_e) estimators of effective population size (Ne) were lowest in MID (Table 2). We observed greater LDN_e in BOR and COL compared to either the MID or BC-CLR (Table 2). Broadly, BOR and COL fishers had higher observed heterozygosity and LDN_e than MID or BC-CLR fishers. The exceptions were MID fishers that had high observed heterozygosity but low estimates of LDN_e (Table 2). Although F_{ST} values between the MID and BC-CLR were substantial from one another during each time period, there was less differentiation within either genetic cluster between any time periods (Supplementary Data SD11). We did not detect any significant changes in allelic richness nor any differences in expected heterozygosity within either MID nor BC-CLR fishers over time (Supplementary Data SD11).

Genetic ancestry assignment and evaluation of translocation success.

We used 15 microsatellite loci and 356 fishers ("reference" set) to test our ability to assign individual fishers to a genetic cluster (Fig. 4). We removed 8 individuals from our simulation, leaving 348 fishers in our "reference" set because they represented collections with low sample sizes (n < 3) or had a low probability of reassignment to the genetic cluster from which they were sampled (posterior probability for reassignment <0.85). We were able to reassign simulated mixtures of Fisher genetic ancestries from the "reference" set back to their true genetic cluster with high confidence (posterior probability of assignment >92%; Supplementary Data SD12) but mostly not their sampling location (Supplementary Data SD13).

We ultimately assigned the genetic ancestry of 41 fishers with unknown ancestry in the "mixture" set including 8 fishers removed from the "reference" and the 33 that could not be assigned to a population in genetic structure analyses, with high confidence (posterior probability >0.9; Supplementary Data SD14). Four of the 8 fishers in the "mixture" set sampled in the United States had a significant portion of their genetic ancestry assigned to BOR or COL genetic clusters in British Columbia (Fig. 4C; Supplementary Data SD14). Three of the 4 fishers were sampled in the Cabinet Mountains, with 2 fishers containing genetic ancestry from COL and one from BOR. The other 4 fishers came from the Clearwater Mountains and had mixed genetic ancestry from the BC-CLR and COL genetic clusters (Fig. 4C).

Discussion

We assessed how historic, mixed-source Fisher translocations may have affected the genetic composition and diversity of fishers in the Northern US Northern Rocky Mountain population over 3 decades after translocation. We found high levels of genetic structure and differentiation between fishers sampled in the Cabinet Mountain

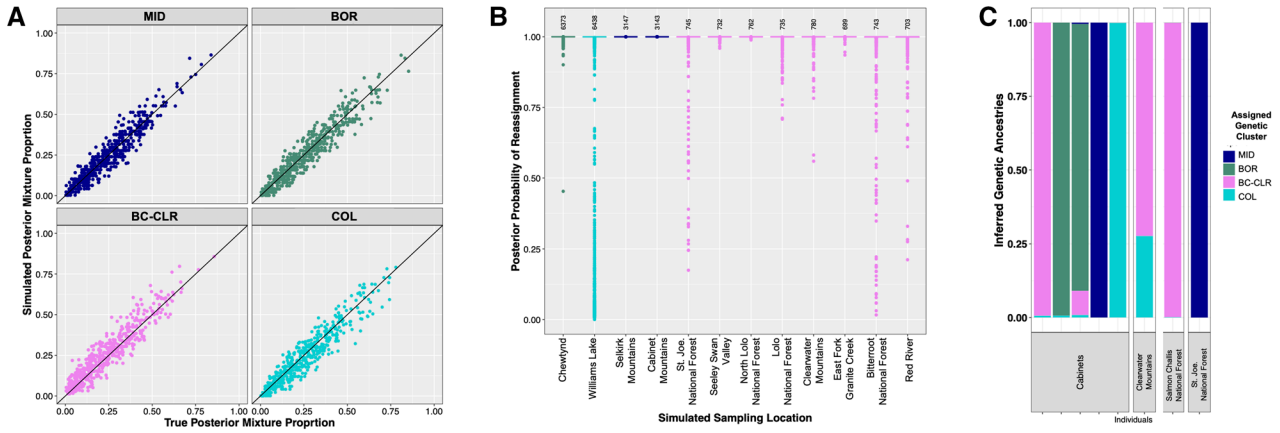

Fig. 4. We observed a high correlation between the genetic mixture proportions of the microsatellite genotypes from simulated individuals from each genetic cluster (A), but not sampling location (B). These results suggested a high likelihood of reassigning individuals in our reference set back to their true genetic cluster. (C) Five out of the 8 individuals that could not be assigned to a single genetic cluster had some genetic ancestry assign to British Columbia reference populations. Two individuals were assigned to BOR and COL respectively, with 2 individuals showing admixture between COL and BC-CLR and BOR and BR-CLR. Finally, 2 individuals were assigned to MID, but 1 that was sampled in the St Joe National Forest, South of I-90.

range in Northern Idaho and Montana (MID) and the fishers sampled outside of these mountains in North-central Idaho and Western Montana (BC-CLR). MID fishers shared genetic ancestry, private microsatellite alleles, and mitochondrial haplotypes with the Midwestern fishers that were translocated into the Cabinet Mountains. BC-CLR fishers showed limited evidence of genetic substructure, evidence of IBD, and high frequencies of British Columbia and endemic US Northern Rocky Mountain mitochondrial haplotypes. Fishers in the BC-CLR genetic cluster also showed evidence of lower genetic diversity when compared with the source populations in British Columbia, where the translocated fishers were originally sourced. While we saw no evidence of admixture between the MID and BC-CLR genetic clusters, we identified some relict genetic ancestry from BOR and COL in the contemporary US Northern Rocky Mountain Fisher population.

We identified significant genetic structure in the US Northern Rocky Mountain Fisher population that appeared to be heavily influenced by translocation history. Fishers in the MID genetic cluster were primarily sampled from around the Cabinet Mountain range in Northern Idaho and Montana and appeared to be descendants of fishers translocated from the Midwest (Minnesota and Wisconsin) to the Bull River site (Fig. 1; Vinkey 2003). These fishers were genetically distinct from those sampled in the rest of Idaho and Western Montana (BC-CLR) and did not exhibit any genetic substructure. BC-CLR fishers appear to form a single panmictic population encompassing mitochondrial haplotypes from both British Columbia and endemic US Northern Rocky Mountain genetic ancestry (Drew et al. 2003; Schwartz 2007; Knaus et al. 2011). Our genetic structure results are similar to previous work monitoring fishers in subregions of the US Northern Rocky Mountain Fisher population in the years preceding translocation using both mitochondrial (Drew et al. 2003; Vinkey et al. 2006; Schwartz. 2007) and microsatellite (Lucid et al. 2016, 2019) data. While MID fishers appear as far North and West as the Selkirk Mountains (107 km from the translocation site), there seems to be little expansion of MID fishers beyond major highways, including South of Interstate 90 (I-90) or East of Highway 2 (42 and 49 km from the translocation site, respectively). We observed only a single instance of a male MID Fisher (Fig. 4) detected in the St Joe National Forest (113 km from the translocation site). Similarly, we detected only 1 BC-CLR Fisher that immigrated North across I-90 into the Cabinet Mountains (Fig. 4). One possible explanation is that the I-90 and Clark Fork River corridor restrict physical movement between fishers in the Cabinet Mountains and those in the Lolo and Idaho Panhandle National Forests. However, fishers to the East of the Cabinet Mountains, also North of I-90, in Northwestern Montana also assign to BC-CLR (Fig. 2). Although these fishers persist in low density, they harbor mitochondrial haplotype 12, believed to be endemic to Idaho and Montana (Schwartz 2007) and do not exhibit substructure suggestive of differentiation from other BC-CLR fishers.

Lack of movement and gene flow between BC-CLR and MID fishers in the past 35 yr (~7 to 11 generations) may suggest that sufficient time has not passed for dispersal to have occurred since initial translocation or that populations have not built up to high enough numbers for propagule pressure to occur. Variance in dispersal of translocated fishers across North America has been attributed to translocation conditions, including the composition of the source population (size, sex, and genetics), time since translocation, and suitable habitat surrounding the translocation site (Aubry and Lewis 2003; Lewis et al. 2012; Matthews et al. 2013; Hapeman et al. 2017). While studies suggest that juveniles can disperse >100 km in optimal habitat, less work has been done quantifying dispersal in suboptimal habitat or in the early stages of population establishment (Powell and Zielinski 1994; Greenhorn et al. 2018). For example, 1 juvenile male Fisher captured in a trap in January 2005 was incidentally detected in June 2006 in a hair-snare device 91.5 km from the original trap site, across the Selway-Bitterroot Wilderness (Schwartz et al. 2013). Over 3 decades after translocation, fishers in the Southern Cascades of Oregon also did not appear to disperse significantly from their initial translocation sites (Aubry and Lewis 2003; Drew et al. 2003). Today, we see evidence of admixture with the Southern Cascades population, though this is from Klamath fishers from the Klamath-Siskiyou Fisher populations that have dispersed North rather than those derived from the translocated population moving South (Murdoch et al. 2020). Fishers from British Columbia to the Olympic Peninsula, in contrast, expanded into wilderness edge habitat rather than dense, mature coastal forest as managers expected within 8 yr of introduction (Happe et al. 2017, 2020). Given that the earliest translocations from British Columbia into Idaho occurred ~66 yr ago, insufficient time does not seem to be the most likely explanation. Alternatively, slow dispersal of fishers following a translocation could be the result of a mismatch between habitat of the source population and their novel habitat after translocation. The lack of genetic admixture detected between the BC-CLR and MID fishers could thus be the consequence of evolutionary divergence between the Western (*P. p. pacifica* and *P. p. columbiana*) and Midwestern Fisher subspecies (*P. p. pennanti*) and the endemic subspecies (*P. p. columbiana*; Aubry and Lewis 2003; Drew et al. 2003; Lewis et al. 2012). Admixture may be

occurring, but lower fitness and high mortality may result in pre- or post-zygotic selection against admixed offspring.

While the MID genetic cluster appears to be composed of ancestors of the Midwestern Fisher translocation, the source of the genetic ancestry in the BC-CLR genetic cluster is more ambiguous. BC-CLR appears to be a panmictic population composed of mitochondrial haplotypes from relict, endemic US Northern Rocky Mountain fishers (Vinkey et al. 2006; Schwartz 2007) as well as British Columbia populations (Drew et al. 2003; Knaus et al. 2011; Weir et al. 2024). While genetic structure analyses primarily distinguish contemporary British Columbia populations from BC-CLR, we detected 5 fishers sampled near historic translocation sites that shared genetic ancestry with these potential source populations (Fig. 1A). Translocations from British Columbia may have been more successful than originally thought and yielded greater admixture historically between endemic US Northern Rocky Mountain and translocated British Columbia fishers. Previous genetic studies of fishers in the St Joe and Idaho Panhandle National Forests identified 3 genetic clusters and suggested that substructure may be due to relict ancestry from these initial translocation events from British Columbia (Lucid et al. 2016, 2019). If this were the case, then we may expect to see more shared genetic ancestry between BC-CLR and contemporary British Columbia source populations ~11 generations after the earliest translocations. Neither genetic structure nor IBT analyses detected significant relationships between Fisher genetic ancestry and translocation history that would suggest shared genetic ancestry among most BC-CLR fishers. One alternative explanation for the detection of British Columbia genetic ancestry in the BC-CLR genetic cluster is that fishers could have naturally re-established after population declines in the 1800s, as has been seen in other Fisher reintroduction studies in Eastern Canada (Stewart et al. 2018) and in the Midwest (Hapeman et al. 2017). This seems unlikely, however, because the closest Fisher population to the US Northern Rocky Mountain population in British Columbia is roughly ~400km North and is genetically distinct from BC-CLR (Vinkey et al. 2006; Lofroth et al. 2010; Weir et al. 2024). Additional genetic substructure may exist, but we may not be detecting it with microsatellite and mitochondrial haplotype genetic data sets. Mitochondrial haplotypes are maternally inherited, and thus may be detected today, but could have been derived from historic introgression events that predate both range contractions and translocations (Schwartz 2007). Due to the high mutation rate of microsatellite loci and susceptibility to homoplasy, genetic substructure may be obscured, making the BC-CLR population appear more genetically homogenous when substructure from translocations may exist (Zimmerman et al. 2020).

We did not detect temporal changes in genetic diversity within MID nor BC-CLR (Supplementary Data SD11). Differences between translocations from the Midwest and British Columbia including variable numbers of animals, frequency of translocation events, and number of source populations translocated into Idaho and Montana may have influenced the number of surviving animals able to contribute to the next generation (Vinkey 2003; Vinkey et al. 2006; Schwartz 2007). We predicted that low survivorship of translocated individuals might lead to declines in genetic diversity in MID fishers today relative to the founders. Lower effective population sizes (TpNe and LDNe) and a greater number of private alleles in MID relative to BC-CLR may also be the consequence of lower genetic variation of the Midwestern fishers translocated into the Cabinet Mountains in 1989 (Table 2). While we included tissues from 6 of the Midwestern founder fishers in our data set, documentation of the source populations for the remaining 104 individuals was limited and tissues were not available. However, evaluating genetic structure at $K>2$ resulted in separation of the Midwestern founders as distinct, suggesting significant genetic differentiation and allelic diversity of Midwestern source populations. Fishers in Southwestern Oregon are similarly thought to have retained high genetic diversity and allelic richness due to translocations from divergent source populations (Kyle et al. 2001; Drew et al. 2003). These fishers were translocated into Crater Lake, Oregon from the Midwest and British Columba in 1960 to 1981 and similarly exhibited little evidence of gene flow with the endemic Klamath-Siskiyou Fisher population located South of the translocation site (Wiseley et al. 2004; Murdoch et al. 2020). Significant mortality of the Midwestern translocated individuals could have led to diminished genetic diversity in founders that otherwise could have successfully contributed to concurrent generations beyond what we could genotype.

In conclusion, while the main objective of historic Fisher translocations was species recovery, managers today continue to be interested in how augmentation affects genetic diversity and composition of the species. A critical concern with translocating either mixed source or evolutionarily divergent lineages is often extirpation of 1 or both lineages due to outbreeding depression or reduced fitness (Whiteley et al. 2015; Bell et al. 2019). Thus, research on historic translocation efforts can often help address how to select source populations to aid in population re-establishment, recovery of genetic diversity, and in increasing the evolutionary capacity of Fisher populations (Pacioni et al. 2019). Contemporary efforts to augment or reintroduce fishers across their historic range have explicitly incorporated genetic tools in the consideration of source populations and monitoring plans (Lewis and Hayes 2004; Wiseley et al. 2004; Hayes and Lewis 2006; Callas and Figura 2008; Happe et al. 2017, 2020). However, understanding how diverse factors such as geographic origin, population size, and genetic variation of the source population(s) of past translocation efforts have impacted contemporary populations continues to be a critical knowledge gap that would inform future Fisher translocation efforts. As genotyping and sequencing costs continue to decrease, genetic tools are more commonly employed to assess the movement, occupancy, and reproductive success of translocated fishers from tissue, hair, scat, and eDNA. We successfully used microsatellite genotypes and mitochondrial haplotypes to assess the impacts of mixed translocations on the US Northern Rocky Mountain Fisher population. Historic translocation efforts had variable success, but genetic ancestry from diverse lineages persists in this Fisher population and drives genetic structure today. One major caveat to this study was that samples were mostly collected opportunistically from historic, legal trapping, or ad hoc via monitoring for numerous carnivore species (Vinkey et al. 2006; Albrecht and Heusser 2009; Schwartz et al. 2013; Lucid et al. 2016; Olson et al. 2024). To effectively assess the implications of lack of gene flow and dispersal of the MID fishers throughout the US Northern Rocky Mountains, future work should evaluate what limits admixture between local BC-CLR and MID fishers. Monitoring immigration and emigration of fishers from the Cabinet Mountains to the St Joe, Lolo, and Idaho Panhandle National Forests will provide insight into the potential mechanisms limiting gene flow between these Fisher populations. Future research is also needed to pair live trapping of fishers with genomic methods that can assess the extent and directionality of admixture to disentangle contemporary from historic gene flow among US Northern and Canadian Rocky Mountain Fisher populations.

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Author contributions

Alexandra K. Fraik (Data curation, Formal analysis, Investigation, Writing—original draft, Writing—review & editing), Kristine L. Pilgrim (Data curation, Methodology, Project administration, Resources, Supervision, Writing—review & editing), Cory E. Mosby (Data curation, Funding acquisition, Investigation, Resources, Writing—review & editing), Richard Weir (Writing—review & editing), Cameron L. Heusser (Data curation, Writing—review & editing), Nathan Kluge (Data curation, Writing—review & editing), and Michael K. Schwartz (Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing—review & editing)

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1. Summary of sampling locations and time periods for all 397 samples included in this study. The final column represents all mitochondrial haplotypes detected from each sampling location, with the nomenclature denoted as previously described in Drew et al. 2003.

Supplementary Data SD2. Detailed methods regarding model construction, selection, and parameterization for evaluating the role of Euclidean distance (IBD) and distance to translocation sites (IBT) on Fisher genetic structure.

Supplementary Data SD3. STRUCTURE results for all fishers from the U.S. supported K = 2, with smaller changes in the likelihood values (ΔK) indicative of lower model support at K > 2 (ΔK2 = 1996.36, ΔK3 = 47.51, ΔK4 =2.31). Each vertical bar represents an individual. Individual sampling locations organized latitudinally along x-axis and summarized by grey bars. Colors represent a distinct genetic cluster (K). Proportions of colors represent the global ancestry proportions for each distinct genetic cluster assigned to each individual. STRUCTURE was run not allowing for admixture as we expect there is no ongoing gene flow.

Supplementary Data SD4. We conducted discriminant analysis of principal components (DAPC) to evaluate genetic structure of the fishers sampled from the U.S. Northern Rocky Mountain population. DAPC supported an elbow between K = 2-5 as shown by the BIC plot (A). Increasing K to 3 (B) and then 4 (C) separated Midwestern individuals from other individuals sampled in the Cabinet Mountains in Northern Idaho and Montana. At K = 5, we began to observe substructure among fishers sampled outside of the Cabinet Mountains in Idaho and Montana (D), however assignment to each genetic cluster varied across DAPC runs.

Supplementary Data SD5. We conducted discriminant analysis of principal components (DAPC) to evaluate genetic structure of fishers in the British Columbia reference populations. DAPC supported an elbow at K = 2 as shown by the BIC plot. Increasing K from 3-5 (B-D) increased the BIC (suggestive of lower model support) and did not appear to explain additional genetic structure.

Supplementary Data SD6. STRUCTURE results for all fishers from British Columbia supported K = 2, with smaller changes in the likelihood values (ΔK) indicative of lower model support at K > 2 (ΔK2 = 24.45, ΔK3 = 10.36, ΔK4 =2.57). Each vertical bar represents an individual. Individual sampling locations organized latitudinally along x-axis and summarized by grey bars. Colors represent a distinct genetic cluster (K). Proportions of colors represent the global ancestry proportions for each distinct genetic cluster assigned to each individual. STRUCTURE was run not allowing for admixture as we expect there is no ongoing gene flow.

Supplementary Data SD7. (A) Three genetic clusters were separated in our Principal Coordinates Analysis (PCOA) along PCOA Axes 1 and 2 using the 364 fishers that were assigned to genetic clusters. BOR and COL were not very distinguishable in the PCOA, while the MID and BC-CLR genetic clusters split clearly along PCOA Axis 1. (B) The genetic distance (DPS; 1 minus the proportion of shared alleles) between MID and the other 3 genetic clusters explained > 50% of the variance amongst all population.

Supplementary Data SD8. STRUCTURE allowing for admixture among all fishers supported K =3 (genetic cluster) with small changes in likelihood values (ΔK) indicative of lower model support at K =2 and K =4 (ΔK2 = 548.36, ΔK3 = 822.82, ΔK4 =2.15). Each vertical bar represents an individual. Individual sampling locations organized latitudinally along x-axis and summarized by grey bars. Colors represent a distinct genetic cluster (K). Proportions of colors represent the global ancestry proportions for each distinct genetic cluster assigned to each individual.

Supplementary Data SD9. We observed significant evidence of isolation by distance (IBD) using a mantel test between all U.S. Northern Rocky Mountain fishers (excluding the individuals originally translocated from the Midwest; A) and between all BC-CLR fishers (B). Results from permutation testing supported statistically significant correlations between genetic distance and Euclidean geographic distance between all U.S. Northern Rocky Mountain fishers (C) and just the BC-CLR fishers (D).

Supplementary Data SD10. Generalized linear model results testing the explanatory power of Euclidean Distance metrics (IBD) compared to distance to a translocation site (IBT) among all pairs of individuals sampled in the U.S. (excluding the individuals originally translocated from the Midwest). The best model based on AIC was the full model, with the second-best model being Chamberlain Basin.

Supplementary Data SD11. We observed genetic differentiation between the MID and BC-CLR genetic clusters across all time periods we sampled using pairwise FST (A). Within populations, however, we found little evidence of genetic differentiation (A), allelic richness (B) or heterozygosity (C) over time. Expected heterozygosity is displayed in grey and observed heterozygosity is displayed in blue.

Supplementary Data SD12. Simulations performed on the reference individuals across sampling locations reflected high accuracy of reassignment back to their true, reference genetic cluster. Bolded values represent the highest mean posterior probability of assignment (> 85%) to a particular genetic cluster.

Supplementary Data SD13. There were mixed results with the probability of reassigning simulated individuals back to their known sampling location. As a result, we chose not to continue testing the probability of reassignment based on sampling location.

Supplementary Data SD14. The posterior probabilities of assignment to a genetic cluster from RUBIAS for fishers from the "mixed" data set. The inferred sampling location indicates where the fishers were sampled, the time period indicates when they were sampled and the mitochondrial haplotype they were genotyped with. Bolded posterior probabilities and the corresponding "tested" genetic clusters indicate which genetic cluster RUBIAS assigned an individual to. Individuals with mixed posteriors could indicate either poor probability of assignment or poor probability of assignment to a single genetic cluster (mixed ancestry).

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Conflict of interest

None declared.

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