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RESEARCH

Genetic structure in a previously extirpated population of gray wolves following reintroduction and natural recolonization

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Abstract

Genetic structuring in wildlife populations is driven by barriers that restrict gene flow as well as the history of population demography. Mechanisms driving genetic structuring can be nuanced in group-living species, such as gray wolves (*Canis lupus*). Behavioral factors, such as social affiliation and resistance, natal habitat imprinting, and trade-offs between dispersal from natal packs and territorial biding, affect habitat selection of wolves despite landscape barriers providing little resistance to their extensive dispersal capabilities. Wolves were previously extirpated from Idaho, USA, and current populations are the result of both reintroductions in 1995 and 1996 and natural dispersal from Canada. In this context we examined genetic structure of wolves in Idaho using 101 individuals genotyped at 18 nuclear DNA microsatellite loci and a subset of 38 individuals genotyped at 1019 single nucleotide polymorphism markers. We hypothesized panmictic (i.e., random mating) genetic structure in Idaho due to the long-distance dispersal abilities of gray wolves. Contrary to our hypothesis, we found three genetic clusters of gray wolves in Idaho, primarily supported by SNP markers. Microsatellite data suggested similar patterns, but permutation tests indicated these differences were not statistically significant. The extent of differentiation and evidence of gene flow, however, suggests that the three genetic clusters are not wholly isolated from one another. The distinctions between clusters spatially align with areas of reintroduction into central Idaho and Yellowstone National Park, as well ongoing natural recolonization from adjacent populations in Canada and Montana. Wolves at the periphery of analysis areas showed more admixture than those in the core, consistent with territoriality and mating behaviors contributing to genetic structuring. We demonstrate how management history, including reintroduction efforts, and animal behavior may interact and contribute to patterns of genetic structure in wild populations.

Keywords Canis lupus · Gray wolves · Genetic structure · Recolonization · Reintroduction

Introduction

Genetic structuring (i.e., patterns in the genetic variation of individuals within a population) in wildlife populations is driven by barriers that reduce gene flow and foster isolation between groups. Some such mechanisms can be structural (e.g. isolation by geographical distance, isolation by landscape barrier, and isolation by environment), while others are more behaviorally driven, such as anthropogenic-avoidance, interspecific competition, natal habitat imprinting, and social resistance (Sacks et al. 2008; Orsini et al. 2013; Armansin et al. 2019). Mechanisms driving genetic structuring can be more nuanced in group-living species and organisms with extensive dispersal capabilities. In these cases, gene flow can be affected by the interplay of kin associations, inbreeding avoidance, territoriality, and other social

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behaviors, while long-distance dispersal reduces structure overall (Cozzi et al. 2018; Blyton et al. 2015; Möller 2012).

Genetic structure can exist without explicit barriers to gene flow even in species with long-distance dispersal abilities, such as gray wolves (*Canis lupus*). While some populations of gray wolves have exhibited panmixia (i.e., random mating) across large geographical areas (Aspi et al. 2006; Đan et al. 2016), others have shown population structure associated with habitat differences and prey specialization (Jędrzejewski et al. 2012; Pilot et al. 2012; Schweizer et al. 2016). Evidence supporting natal habitat-biased dispersal has been observed across gray wolves, potentially forming the foundation for patterns of ecology-driven evolution among wolf populations (Geffen et al. 2004, Leonard 2015; Sanz-Pérez et al. 2018). At local scales, differentiation between genetic clusters of wolves can occur in adjacent but different habitat types, such as between coastal and inland wolves in British Columbia, and can also be driven by inter- and intra-specific competition and anthropogenic influences (Muñoz-Fuentes et al. 2009; Ordiz et al. 2015; Scandura et al. 2011; Stronen et al. 2012).

Gray wolves were once the most broadly distributed land mammal around the globe, but would likely have been extirpated within the contiguous USA without management interventions (Boitani 2003). US wolf populations outside of Alaska were reduced to 1% of their former range and, by the 1930s, existed solely in northern Minnesota (Fritts and Mech 1981). Endangered Species Act (ESA) protections were placed on wolves in the U.S. in 1974 and evidence of natural recolonization from Canada began to appear in areas where wolves had previously been extirpated. By 1986 a pair of gray wolves successfully bred once again in Montana (Bangs and Fritts 1996). In the following years, interest in restoring wolves to the Northern Rocky Mountain (NRM) region of the US resulted in the experimental reintroduction of gray wolves from Alberta and British Columbia (Canada) to Yellowstone National Park, Wyoming and central Idaho (USA) in 1995–1996 (Fritts et al. 2008). Restoration of a metapopulation of wolves within the NRM focused on three recovery areas: northwest Montana, central Idaho, and the Greater Yellowstone Area (GYA, including Yellowstone National Park, southwest Wyoming, and southwest Montana) (Fig. 1A; vonHoldt et al. 2010). Reintroduced wolves in both the Yellowstone and central Idaho recovery areas flourished and surpassed recovery goals by 2002 (USFWS 2009). Wolves also began recolonizing northern Idaho due to either the original reintroduction or via immigration from closer, adjacent populations in the Montana recovery area and British Columbia (Fig. 1B; USFWS et al. 2010).

Although reintroduced and recolonizing wolves increased in numbers, successful recovery was also ultimately contingent upon effective gene flow between recovery areas to stave off inbreeding depression (Hebblewhite et al. 2010; vonHoldt et al. 2008). Genetic diversity within recovery zones appeared high based on assessments conducted during the initial recovery period (1995–2004), and subsequent analyses also found evidence of effective migration between recovery areas (vonHoldt et al. 2010). Wolves are currently distributed widely across the three original recovery zones and met criteria for delisting in Idaho in 2011 and in Wyoming in 2017, with current census population size estimates of ~1881 (USFWS 2011, 2017; vonHoldt et al.

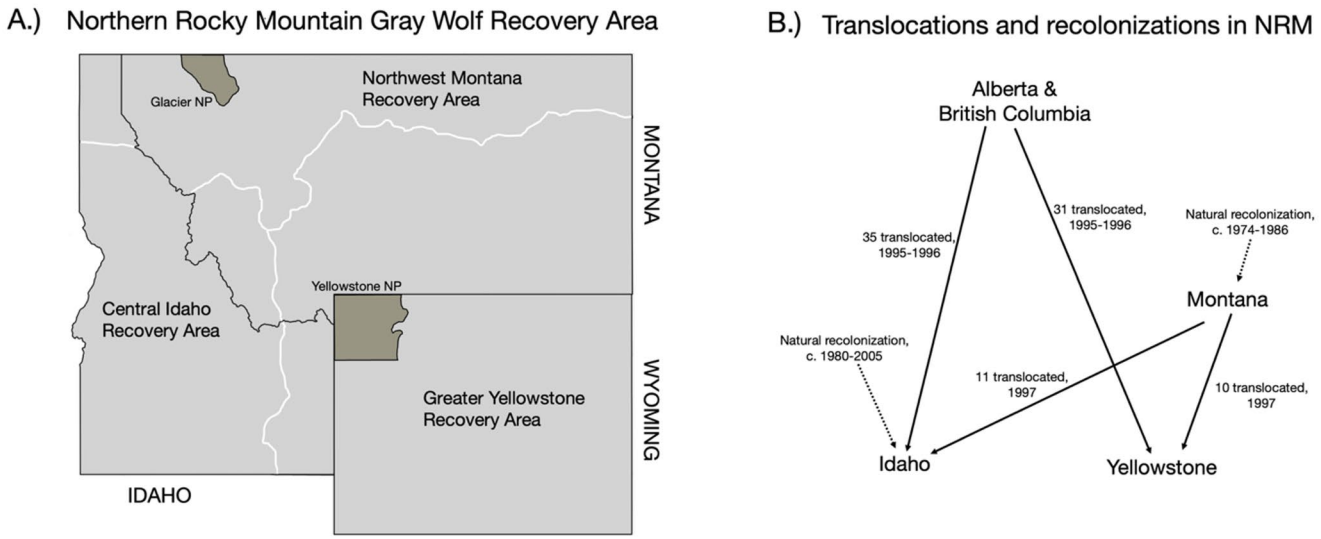

Fig. 1 (**A**) Map of the Northern Rocky Mountains (NRM) Wolf Recovery Area. (adapted from USFWS et al. 2007). Solid black borders are state boundaries, and white borders delineate the Central Idaho wolf recovery area, the Northern Montana wolf recovery area, and the Greater Yellowstone wolf recover area. (**B**) The reintroduction and recolonization history of wolves in the NRM Wolf Recovery Area. Translocations between populations are depicted by solid arrows. Natural recolonizations are depicted with hashed arrows

2024). While modeling by the Fish and Wildlife Service for the 2023 species status assessment suggested the NRM metapopulation will be robust to extirpation over the next 100 years, estimates of effective population size fall below the recommended guidelines for long-term persistence (USFWS 2023; vonHoldt et al. 2024). The on-going success of gray wolf recovery in the NRM will require continued genetic connectivity among groups within the area.

Gray wolves are a wide-ranging, highly mobile generalist species, and neither distances nor landscape features between groups in the NRM region are expected to act as barriers to dispersal (Forbes and Boyd 1997). Although human development and high rates of anthropogenic sources of mortality may create some resistance to dispersal, these forces alone seem unlikely to create significant genetic substructure among gray wolf populations. For instance, coyotes (*C. latrans*) exhibit many similar traits, and, despite the long history of divergence between northern and southern lineages in North America, panmictic population structure was found after the eastwardly-colonizing fronts of these two lineages converged in the Mid-Atlantic contact zone (Bohling et al. 2017; Monzón 2014). This pattern, however, has not been universally observed—in other cases, genetic substructure has been found among coyotes in association with environmental heterogeneity and between urban and rural populations (Damm et al. 2015; Sacks et al. 2008). It is unclear whether the differences in environmental conditions and demographic histories among gray wolves reintroduced from Alberta and British Columbia and those that recolonized north Idaho naturally are significant enough to generate lasting, observable genetic structure.

We examined the genetic structure of gray wolves in Idaho, part of an expanding population with prior evidence of regional gene flow and extensive dispersal abilities (vonHoldt et al. 2010). We hypothesized panmictic (i.e., random mating) genetic structure in Idaho due to the long-distance dispersal abilities of gray wolves, regardless of recolonization or translocation history. To test the effect of different genetic marker types on inferences of population structure, we compared results using a panel of previously developed microsatellite loci and single nucleotide polymorphisms (SNPs) discovered by RAD sequencing.

Methods

Study area

The state of Idaho (216,632 km^2) includes a wide variety of habitats and ecosystems. Northern Idaho has a maritime climate and is dominated by western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) whereas southern Idaho has a continental climate and is dominated by Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*; Nadeau et al. 2009). Elevations range from 457 m to over 3,650 m, annual precipitation ranges from <20 cm at low elevations to >250 cm at high elevations, and temperatures ranges from −34° C in winter to 38° C in summer (Western Regional Climate Center 2019). The majority of southern Idaho is private agricultural lands, central Idaho contains 3 contiguous wilderness areas and several highly productive prairies of mixed native and agricultural lands, and northern Idaho is predominantly public forests and private corporate timber holdings. The primary prey species for wolves in Idaho are largely elk (*Cervus elaphus*) and white-tailed deer (*Odocoileus virginianus*) with moose (*Alces alces*) and mule deer (*O. hemionus*) also present in the diet (USFWS 1994).

Sampling

Personnel from Idaho Department of Fish and Game collected tissue samples from gray wolves harvested during 2014 and 2015 and individuals from long-term study packs as part of a genetic monitoring program. Hunters and trappers are required to report harvested wolves within 10 days and provide the hide and skull as voucher specimen. Dentition analysis of premolars was used to identify young of the year (YOY; i.e., individuals born in the current year). The estimated population census size was 770 in 2014 and 786 in 2015, with 104 and 108 packs estimated respectively; our sampling represented one individual YOY per pack for 52 of 55 known reproductively-successful packs from 2014, and 63 of 69 known reproductively-successful packs from 2015 (Clendenin et al. 2020).

Genotyping

Population structure inferences are not always concordant between studies using different genetic markers; thus we assessed genetic structure using 18 microsatellites for 118 individuals and single nucleotide polymorphism (SNP) loci for 98 individuals from the sampled wolves. The 18 microsatellite loci were previously developed for genetic monitoring as described in Stenglein et al. (2010), Stansbury et al. (2014), and Clendenin et al. (2020). The SNP loci were identified in our samples using and updated RADseq protocol (Ali et al. 2016).

For the microsatellite genotyping, we extracted DNA from 20-mg tissue samples using Qiagen DNeasy Blood and Tissue kits (Qiagen, Valencia, CA, USA). Negative controls were included to test for sample contamination, and each multiplex polymerase chain reaction (PCR) was run with a negative control to test for reagent contamination. 18 dye-labelled nuclear DNA microsatellite loci were combined into 2 PCR multiplexes with a product size of <300 base

pairs (AHT103, AHT109, AHT121, AHT200, C05.377, C09.173, C37.172, Cxx.119, Cxx.250, FH2001, FH2004, FH2010, FH2054, FH2088, FH2137, FH2611, FH2670, FH3725; Holmes et al. 1994, Breen et al. 2001, Guyon et al. 2003, Salim et al. 2007, Ostrander et al. 2017). Both multiplexes contained 3.5ul of 1.5× concentrated Qiagen Master Mix, 0.7 uL of 0.5× concentrated Qiagen Q Solution, and 2 uL DNA extract (Clendenin et al. 2020). We used an Applied Biosystems 3130xl capillary machine to separate PCR products (Applied Biosystems, Foster City, CA, USA), and scored genotypes with GENEMAPPER 5.0 (Applied Biosystems). We ran samples in duplicate or triplicate when necessary to resolve genotypeinconsistencies or to address failure due to sample preservation quality. We only retained samples with consensus genotypes. (i.e., alleles independently identified at least twice) at 90% or more of the loci, and coded non-consensus genotypes as missing data.

SNP discovery for 98 YOY harvested in Idaho during the 2014-2015 season was conducted using an updated RADseq protocol as described in Clendenin (2019). RADseq library preparation for individuals genotyped with SNPs entailed equally dividing the 98 samples between two plates, including 6 technical replicates. Standardized samples were digested with the restriction enzyme Sbf-I and RAD libraries were prepared using the protocol of Ali et al. (2016). Libraries were sent to University of California, Berkeley, genomics core facility for sequencing using a single high-output lane on an Illumina HiSeq 4000 machine with paired-end 150bp reads.

Reference-aligned SNP discovery using the dog genome, CanFam 3.1, was conducted using STACKS v. 1 (Broeckx et al. 2014; Catchen et al. 2013). We used a protocol modified from Mastretta-Yanes et al. (2015) to optimize STACKS parameter settings by minimizing genotyping error between replicates. The optimized parameters included setting the minimum coverage, i.e., the number of raw reads required to call a locus, to 3. The SNP calling model, which specifies the chi square significance level required to call a heterozygote or homozygote (alpha) and the upper bound for epsilon, the error rate (bound high), were optimized with an alpha value of 0.01 and the upper bound of epsilon at 0.1. Loci genotyped in fewer than 40 percent of individuals were removed. The minimum minor allele frequency accepted for loci was 0.1 and the maximum threshold of heterozygosity at a locus was 0.5. We removed reads from mitochondrial DNA and the X chromosome. After optimizing parameters, a final set of 1019 SNPs were used in analyses. Individuals with more than 95% missing data were excluded, leaving 50 individuals after filtering.

We used the program ML-RELATE to estimate relatedness between individuals from their microsatellite genotypes (Kalinowski et al. 2006). When pairs of individuals surpassed an r-value threshold of 0.4, we excluded one individual per pair from analyses because related individuals have been shown to bias results from Bayesian clustering analyses (Schwartz and McKelvey 2009; Rodríguez-Ramilo and Wang 2012). Using this threshold to remove related individuals left 101 individuals in the microsatellite dataset and 38 in the SNP dataset.

Evaluation of genetic substructure

We used the Bayesian model-based program, STRUCTURE v2.3.4 to test the hypothesis of panmixia and identify genetic clusters based on both microsatellite and SNP genotypes (Pritchard et al. 2000). We used the general admixture model with the number of potential genetic clusters ranging from one to ten (K = 1–10), without a priori assumptions about sample locations. Each K was run with 5 independent iterations, each with 500,000 Markov chain Monte Carlo (MCMC) repetitions following a burn-in of 100,000. To obtain the most likely value of K, we used STRUCTURE HARVESTER to summarize log-likelihood values and estimate ΔK (the rate of change in the likelihood curve) using the Evanno method (Earl and vonHoldt 2012; Evanno et al. 2005).

Genetic differentiation between clusters was evaluated using Weir and Cockerham's F_{ST} (Weir and Cockerham 1984) and visualized through principal component analysis (PCA). Clustering of individuals was assessed by two methods. In the first, assignment was based on individual majority ancestry from STRUCTURE. In the other, individuals were assigned to clusters geographically; where geographic clusters overlapped at their perimeters, majority ancestry was used to determine individual assignment. PCA plots were generated for both assignment schemes. Pairwise F_{ST} values within each scheme were calculated using the R package hierfstat (Goudet 2005). Missing genotypes were retained as missing in all F_{ST} analyses, with no imputation prior to estimation or testing. Mean imputation was applied only for PCA visualization.

For microsatellite loci, statistical significance of population differentiation was tested via permutation. Observed F_{ST} values were compared to null distributions generated by randomly permuting individuals among populations (5,000 permutations) using the test.between() function. This preserves multilocus genotypes and allele frequencies, and p-values reflect the probability of observing F_{ST} values equal to or greater than those empirically observed under the null hypothesis of no structure.

Permutation-based significance testing of F_{ST} is appropriate for multiallelic microsatellite loci, but can be unreliable for large biallelic SNP datasets. Rather than generating p-values, uncertainty in SNP-based F_{ST} was assessed via

bootstrap resampling of loci with replacement, generating confidence intervals around pairwise F_{ST} estimates. Bootstrap confidence interval width stabilized after approximately 150–200 replicates, so 300 replicates were used in all analyses.

Results

The results of our analyses using 18 microsatellite loci for 118 individuals and 1019 SNP loci for 38 individuals were consistent with genetic substructure, rather than panmixia, for wolves in Idaho. Estimates based on likelihood and ΔK from both the microsatellite dataset and the SNP dataset suggest at least 3 genetic groups are present, with varying amounts of admixture between them (Figure S1). Our hypothesis of a single genetic group (K = 1) was not supported. Despite a peak at 4 in the microsatellite-based ΔK plot, the likelihood curve peaks at K = 3 genetic groups (Figure S1A) and is the preferred indicator of K (Evanno et al. 2005). For SNP loci, the likelihood curve continues to increase up to K = 10, but the ΔK value supports K = 3 (Figures S1C and S1D). These clusters are congruent between marker types, and geographically concentrated in northern Idaho, central Idaho, and the southeast portion of the state adjacent to Yellowstone National Park (Figs. 1, 2 and 3). We subsequently refer to these groups as the northern, central, and southeastern clusters respectively.

While there is evidence for multiple genetic groups and substructure among wolves, there is also evidence for gene flow among regions. In the microsatellite dataset, a substantial proportion of individuals with the majority of their ancestry assigned to the southeastern cluster were distributed geographically within the central cluster, as well as a few within the northern cluster. The PCAs of the microsatellite genotypes show these individuals clustering by majority ancestry in distinct contrast to their geographic location (Figures S2A and S2B). PCAs show consistent differentiation of the three groups in the SNP dataset using both individual assignment methods, with minimal changes between them (Figures S2C and S2D). Overall, many individuals show mixed ancestry across multiple groups (Figs. 2 and 3), and there is mixed ancestry within regions.

Analysis of genetic differentiation among clusters using Weir and Cockerham's F_{ST} revealed generally low levels of divergence across both marker sets. Pairwise F_{ST} values were highest between the northern and central clusters, though rankings among other pairs varied. F_{ST} values differed between datasets (microsatellites vs. SNPs) and between assignment methods (majority ancestry from STRUCTURE vs. geographic location).

In the microsatellite dataset, F_{ST} values based on ancestry assignment were consistently higher than those based on geography (ancestry: northern–central 0.046, northern–southeastern 0.030, central–southeastern 0.036; geography: northern–central 0.024, northern–southeastern 0.012, central–southeastern 0.017). However, permutation tests indicated that these differences were not statistically significant overall ($p = 0.165$ and 0.161 for ancestry and geography, respectively), suggesting that microsatellite differentiation, while nonzero, is weak and should be interpreted cautiously.

For SNPs, F_{ST} values were lower but more consistent across assignment methods (ancestry: northern–central 0.012, northern–southeastern 0.012, central–southeastern 0.009; geography: northern–central 0.012, northern–southeastern 0.012, central–southeastern 0.007). Uncertainty in SNP-based F_{ST} estimates was assessed using locus-bootstrap resampling, which generated 95% confidence intervals excluding zero for all pairwise comparisons, indicating that SNP differentiation was statistically supported.

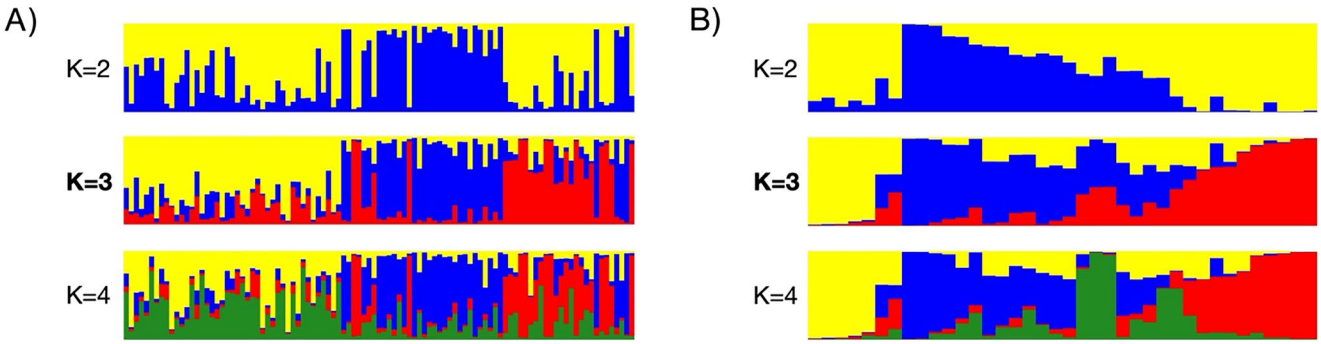

Fig. 2 Results from genetic structure analysis of gray wolves in Idaho that were assigned to genetic clusters (K) based on wolves sampled between 2014–2015. Bar graphs include the proportion of individual genetic ancestry determined for each individual based on microsatellite (**A**) and SNP (**B**) genotypes. Each vertical bar depicts an individual, with colors representing separate genetic group. K = 2 through K = 4 are depicted, while K = 3 (in bold) was the most probable number of clusters. In the K = 3 plot, red represents the cluster referred to as northern, blue represents the cluster referred to as central, and yellow is used for the southeastern cluster

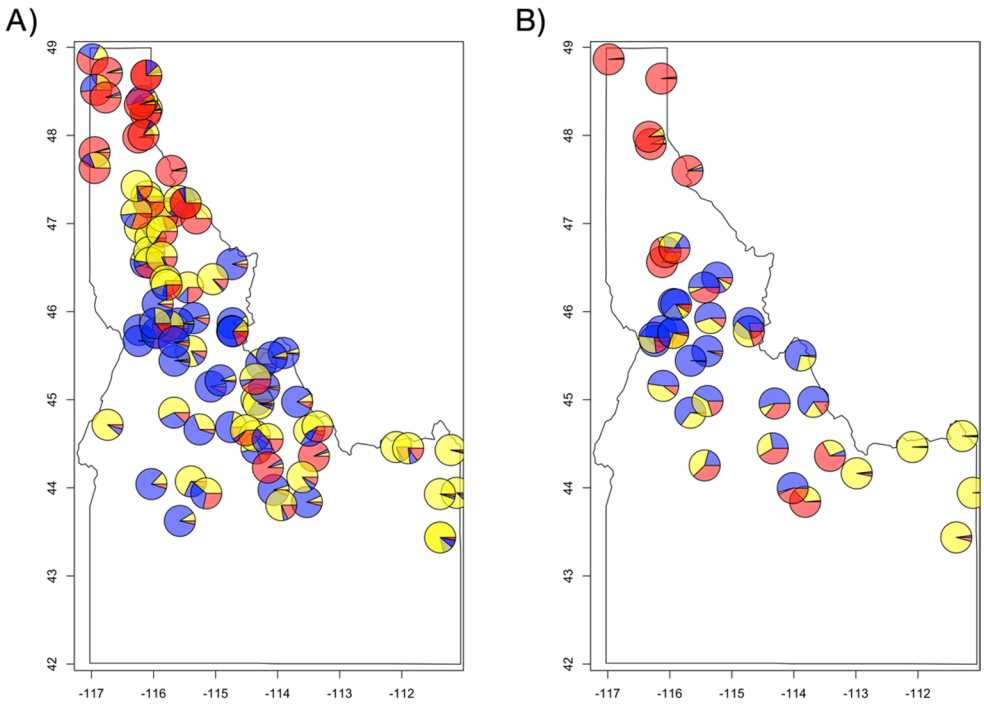

Fig. 3 Individual ancestry of gray wolves in Idaho, USA, sampled between 2014–2015. Map A displays results based on microsatellite genotypes, while map B displays results based on SNP genotypes. Each sampled individual is represented as a pie-chart depicting the proportion of their ancestry assigned to each genetic cluster. Red represents the cluster referred to as "northern," blue is for the "central" cluster, and yellow for the "south-eastern" cluster. Each individual point has been plotted based on the corresponding GPS coordinates reported to Idaho Department of Fish and Game at the time of collection

Discussion

Contrary to our hypothesis of a panmictic population of wolves, we found three genetic clusters of gray wolves in the state of Idaho, supported primarily by SNP markers. Microsatellite data suggested similar patterns, but permutation tests indicated these differences were not statistically significant. The extent of differentiation and evidence of gene flow suggests that the three genetic clusters are not wholly isolated from one another and wolves regularly move and breed among the clusters (Table 1; Fig. 3; vonHoldt et al. 2010). These groups are spatially aligned with areas of reintroduction of gray wolves from Alberta and British Columbia into central Idaho (i.e., the central cluster, represented in blue in Figs. 2 and 3) and Yellowstone (south-eastern cluster, represented in yellow in Figs. 2 and 3), as well as ongoing natural recolonization from adjacent populations in Canada and Montana (northern cluster, represented in red in Figs. 2 and 3). Genetic structure without obvious barriers has been observed in other populations of gray wolves in association with habitat variation, prey preference, inter- and intra-specific competition, and demographic history (Aspi et al. 2006; Hindrikson et al. 2017).

Due to similar anthropogenic influences, Europe's recolonizing wolves can provide insights into the potential drivers of genetic division observed in Idaho. In Europe, the most notable distinction is genetic variation along a north-south axis associated with the expansion of former remnant populations in eastern and southern Europe (Hindrikson et al. 2017). Finer-scale genetic structure also emerged as these remnant populations recolonized different regions and experienced serial founder effects and population bottlenecks (Fabbri et al. 2014; Aspi et al. 2006; Jansson et al. 2012). Fine-scale genetic structure is also associated with natural landforms, such as mountain ranges, avoidance of interspecific conflict, intraspecific territoriality and spatial stability, prey and habitat preferences, and anthropogenic influences, such as habitat alteration and hunting pressure (Aspi et al. 2009; Scandura et al. 2011; Stronen et al. 2013; Milanesi et al. 2018; Ordiz et al. 2015). Our findings in Idaho suggest patterns consistent with similar mechanisms for genetic clustering; founder effects from reintroductions

Table 1 F_{ST} values using microsatellite and SNP markers for pairwise comparisons between clusters of wolves in Idaho

Marker type	Assignment method	Northern to Central	Northern to Southeastern	Central to Southeastern
SNP	Ancestry majority	0.011	0.010	0.008
SNP	Geographic	0.011	0.012	0.006
Microsatellite	Ancestry majority	0.046	0.030	0.036
Microsatellite	Geographic	0.017	0.012	0.023

Weir and Cockerham's F_{ST} was calculated between each pair of clusters for wolves genotyped using SNPs and microsatellites. Individuals were grouped into three clusters (northern, central, and southeastern) using two assignment methods for each marker set, determined either by the ancestry majority from the STRUCTURE analysis, or by geographic location. F_{ST} values are listed under the description of the corresponding pairwise comparison.

and more recent natural recolonization events, and perhaps anthropogenic and landscape features (albeit not explicitly measured in our study) dampening dispersal and limiting population panmixia.

Overall, the levels of differentiation we observed between genetic clusters are low and admixture is observed across the state, with many individuals showing mixed ancestry across groups (Figs. 2 and 3; Table 1). Previously, vonHoldt et al. (2010) found similar evidence for gene flow in wolves in the northern Rocky Mountains. PCAs using SNP data showed high congruence between geographic location and majority ancestry, while the PCAs using microsatellite data indicated clearer distinction among the clusters when individual cluster assignment was based on majority ancestry rather than geographic location (Fig. S2A-D). We observed less admixture among individuals sampled within the geographical cores of clusters and admixture among all groups was more evident at the peripheries of each cluster and in intermediate areas. This may be indicative of wolves' territoriality and mating behaviors, which limit admixture in the core of saturated habitats. Alternatively, it may indicate a preference for inheriting natal territories or establishing territories in habitat similar to natal territories, with more admixture occurring among individuals who have dispersed beyond these core areas.

Pairwise differences between genetic clusters based on Weir and Cockerham's F_{ST} were not consistent between marker panels (Table 1). The greatest differentiation was observed between the central and northern clusters in SNP data, while microsatellite F_{ST} values were not statistically significant. The northern cluster may be genetically distinct as a result of a serial founder effect among naturally recolonizing wolves. This is further supported by recent work showing that wolves in northern Idaho had lower heterozygosity and wolf groups were more related to one another than the historically reintroduced wolves in central Idaho (Ausband and Waits 2020). Additionally, it is possible that genes from the coastal wolf ecotype identified in the adjacent state of Washington may contribute to distinctiveness among northern Idaho wolves (Hendricks et al. 2019). Discrepancies between marker panels may reflect differences in mutation rates or sample sizes. While microsatellite F_{ST} values were higher in some pairwise comparisons, these differences were not statistically significant, suggesting lower power of microsatellites in detecting subtle differentiation in this system.

Despite being a generalist species, gray wolves have also been found to exhibit genetic structure associated with habitat and diet differences. For instance, wolves in British Columbia show distinct habitat and prey preferences associated with coastal or forest habitat and also exhibit physiological adaptations to these habitats (Muñoz-Fuentes et al. 2009; Hendricks et al. 2018). Genome-wide association studies in Europe looking for signs of local adaptation identified candidate loci associated with genes linked to temperature regulation and other functional genes (Stronen et al. 2015). Genetic subdivision associated with dietary differences has been observed in other areas, such as Poland and eastern Europe, some of which have been supported by stable isotope analysis of the prey composition of wolves' diets (Jędrzejewski et al. 2012; Milakovic and Parker 2011; Pilot et al. 2012). Similarly, a study of the genetic structure of gray wolves in part of the Canadian Rockies identified two differentiated groups that corresponded to either dense or open coniferous forest, suggesting either prey preference or natal habitat affinity (Cullingham et al. 2016). Several studies have suggested that habitat and prey preferences, even in the absence of local adaptation, may be imparted during the natal period through learned foraging behaviors or other mechanisms, such as imprinting (Sanz-Pérez et al. 2018; Pilot et al. 2006; Milleret et al. 2019). Such an effect could be present in Idaho where wolves' primary prey may vary spatially (e.g., deer in north Idaho and elk in central Idaho). Additionally, habitats in north Idaho receive more precipitation, are generally more forested, and more productive overall than other areas in Idaho. Such differences in habitat and dominant prey species may influence dispersal behavior in wolves and be associated with some of the genetic structure patterns we observed. Lastly, there are potential landscape barriers (i.e., interstate highway, large river system; Salmon River) to movement between the north subpopulation and others considered in Idaho. We note, however, that radio-collared wolves have routinely crossed such obstacles.

Genetic structure may also be attributed to social resistance, especially under circumstances where preferred habitat is monopolized by founders and their offspring (Armansin et al. 2019). In wolves, social resistance can inhibit movement and gene flow across landscapes via territorial aggression (vonHoldt et al., 2008; Cassidy et al. 2016). Wolves survey their territories for incursions from wolves outside their own packs, and confrontations that occur can be deadly (Schlägel et al. 2017; Cassidy et al. 2016). In this fashion, interspecific conflict acts as a major source of adult mortality and has been documented as means of regulating density in Yellowstone National Park (Cubaynes et al. 2014). Although adoption of unrelated dispersers into packs has sometimes been documented, genetic studies in Idaho have generally only found dispersers accepted into packs as breeders (Ausband et al. 2017). Under instances of high spatial stability and habitat saturation, delayed dispersal and linear inheritance of territory may influence relatedness and genetic structure (Koenig et al. 1992; Scandura et al. 2011; Sparkman et al. 2011).

Wolf harvest within Idaho and the resulting disruption of social structure may have unclear impacts on maintaining genetic structure (Ausband et al. 2017). In these cases, territories seem to be rapidly re-established by nearby wolves, which may be occupying suboptimal territories or delaying dispersal within natal packs (Ausband et al. 2017). Similar observations of this type of territorial biding have been seen in coyotes in an urban-rural landscape matrix, which avoid urban environments unless they are avoiding conspecifics (Mitchell et al. 2015). In these instances, less-preferred habitat is selected for movement during dispersal or as transient territory during bouts of biding for higher-quality territory (Morin and Kelly 2017). While it seems likely that wolves claiming nearby vacant territories will be genetically related to previous occupants, these openings also provide opportunities for wolves dispersing over greater distances to enter roles as breeders (Jimenez et al. 2017). Additionally, these conditions also appear to encourage alternate breeding strategies, such as polyandrous mating within packs with transient sneaker males, which may also undermine the strength of genetic structure formed by territorial behavior (Ausband 2018, 2019).

Concluding statements

We found genetic structure among gray wolves within the state of Idaho, primarily supported by SNP genotype data. This structure exists within wolf dispersal ranges and without clear physical barriers. Genetic clusters spatially align with locations of reintroduction (near central Idaho and adjacent to Yellowstone National Park) and natural recolonization in the northern Idaho panhandle from Canada, though other factors may explain these groupings. The mechanisms behind the observed genetic structure can be tested over time in Idaho. Patterns may emerge over time if genetic structure is influenced by territorial inheritance and social resistance. For example, if wolves adjust their dispersal and mating behaviors in response to breeder turnover, increased human harvest, or changes in population density. If the observed genetic structure is driven by habitat preferences and remains stable over time, differences in selective pressures (e.g., anthropogenic influences, habitat and prey differences, alternate reproductive strategies) could lead to heritable adaptive differences. Presently, levels of gene flow between groups and genetic diversity suggest that the observed genetic clusters are not isolated and wolves move and breed, at least somewhat, between clusters.

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Data availability Sample metadata are the property of the state of Idaho and are unavailable for publication.

Declarations

Competing interests The authors declare no competing interests.

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