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RESEARCH ARTICLE

A carnivores' oasis? An isolated fisher (*Pekania pennanti*) population provides insight on persistence of a metapopulation

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Abstract

Landscape level species assessments are rarely available to inform conservation planning. Recent advances in multi-taxa survey techniques, however, have made them more obtainable by improving efficiency of collecting species occurrence data and genetic samples. Here, we used a multi-taxa survey technique to provide a landscape level portrait of fisher (*Pekania pennanti*) population status in a portion of the northern Rockies where the species' history has been heavily influenced by humans. From 2010 to 2014 we deployed 497 winter forest carnivore bait stations across a 23,000 km^2 study area centered on northern Idaho, United States. The stations collected remote camera images and hair samples for DNA analysis. We used 12 microsatellite loci to identify 58 individual fisher in the study area. We identified two fisher populations for which we estimated effective population size (N_e) and genetic neighborhood size (NS). We calculated local genetic diversity measures [observed (H_o) and expected (He) heterozygosity, allelic richness (Ar), fixation index (F_{ST}), and number of migrants per generation (Nm)] and mapped continuous gradients of genetic diversity [Ar and inbreeding coefficient (F_{IS})] across the study area. We identified a fisher population in the West Cabinet Mountains [N_e of 26 (15.3–55.5), NS of 50–60] which is effectively isolated from the small population we detected in the Saint Joe/Coeur d'Alene Mountains [N_e of 6.5 (2.7–15), NS of 10–25]. We determined fisher have been effectively extirpated from the Selkirk and Purcell mountains and the lack of genetic connectivity between the two small remaining populations casts doubt on long term viability. Our study suggests northern Rockies fisher populations are vulnerable to landscape barriers and successful recovery will depend on future management and augmentation. We recommend these factors be considered when determining how, and if, species recovery should proceed.

Keywords Effective population size · Fisher · Genetic connectivity · Genetic neighborhood size · Microsatellites · N_e · NS · *Pekania pennanti*

Introduction

Genetically robust, self-sustaining, populations are benchmarks of conservation success (Redford et al. 2011). However, many obstacles exist to obtaining the landscape level data necessary to measure those variables (Lindenmayer and Likens 2010). One way to circumvent those obstacles, particularly cost, is to increase efficiency of field efforts by targeting multiple species rather than just one (Robinson et al. 2017). Demonstrating whether a species meets conservation success criterion can be achieved by including that species in broad multi-taxa field survey efforts (Lucid et al. 2018; Robinson et al. 2017). Fisher (Mustelidae: *Pekania pennanti*) provide a case in point.

Fisher in the northern Rockies of the United States have a rich history of human exploitation, translocations, and management concern. Despite intense human interest in

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this species in the northern Rockies, a detailed assessment of their status is lacking. Herein, we present the first landscape level assessment of this species across a major portion of its northern Rockies range, which was made possible by their inclusion in a broad scale multi-taxa inventory (Lucid et al. 2016).

Fisher have a historical distribution that included boreal forests of Canada, the Great Lakes region and northeastern United States, a portion of the Rocky Mountains in the United States, and mountainous areas of Washington, Oregon, and California (Gibilisco 1994, Powell et al. 2003). Fisher populations declined after the early 1900s due to un-regulated trapping (Lewis and Zielinski 1996) and loss of habitat from unsustainable logging and development (Lofroth et al. 2010). Fisher were an early subject of reintroduction efforts during the past century because there were financial and recreational benefits to recovery and they have become one of the most commonly reintroduced species in North America (Drew et al. 2003).

Fisher were erroneously thought to be extirpated from the northern Rockies of the contiguous United States by 1930 (Vinkey et al. 2006). This belief led to five northern Rockies translocations between 1959 and 1991 (Vinkey 2003) and left a genetic legacy of fisher populations of mixed origin; both native and introduced (Vinkey et al. 2006; Schwartz et al. 2007). Some effort has been made to evaluate the success of specific translocations (Vinkey 2003), identify fisher habitat requirements (Sauder and Rachlow 2014), and predict climate affected habitat shifts (Olson et al. 2014). Missing from this picture is a delineation of fisher distribution on the northern Rockies landscape, and a corresponding evaluation of population genetic health.

The Idaho Panhandle and adjoining mountain ranges offer an opportunity to evaluate these factors on a substantial portion of the northern Rockies where translocations did not occur but have, nevertheless, left a legacy of introduced and native haplotypes. Fisher occurring in the Cabinet and Selkirk Mountains have been identified as being descendants of introduced animals (Lucid et al. 2016) while fisher in the Saint Joe/Coeur d'Alene Mountains (hereafter SJ/CDA) are a mosaic of reintroduction descendants and 'native' lineages (Vinkey et al. 2006; Schwartz et al. 2007; Albrecht and Heusser 2009; Lucid et al. 2016). Our study area consists of four distinct mountain ranges either in their entirety (West Cabinets) or portions of the range (SJ/CDA, Purcells, and Selkirks) (Fig. 1). The closest reintroduction occurred in Montana's East Cabinet mountains ~ 10 km from our study area 20 years and 7 fisher generations (based on a 3-year generation time, Zielinski et al. 2013) prior to our study (Roy 1991; Heinemeyer 1993; Vinkey et al. 2006). The second closest translocation consisted of three animal releases approximately 50–200 km from our study area in Idaho's Clearwater Mountains (Vinkey et al. 2006) 48 years and 16 fisher generations prior to our study (Zielinski et al. 2013).

From 2010 to 2014 we deployed 497 multi-taxa winter bait stations on a 5 × 5 km grid across a 23,000 km^2 study area. We collected fisher hair samples from these bait stations (Robinson et al. 2017) and collected tissue samples from fisher carcasses harvested incidentally from legal fur trapping. Our objective was to evaluate the status of fisher populations in four distinct but adjoining mountain ranges where fisher translocations have not directly occurred, but which also form a gradient of distance from locations of known translocations. Our goals were to (1) map current fisher distribution within the study area, (2) calculate effective population size (N_e) and genetic neighborhood size (NS), (3) calculate genetic metrics for each population to indicate genetic diversity and population connectivity, and (4) use these metrics to infer long term sustainability of these populations.

Materials and methods

Study area

The study area consisted of a 23,000 km^2 area centered on the Idaho Panhandle and containing portions of northeastern Washington, northwestern Montana, and southern British Columbia (Fig. 1). It comprises portions of the Selkirk, Purcell, West Cabinet, and SJ/CDA mountain ranges. The topography is mountainous, ranging in elevation from 702 to 2326 m with a climate characterized by mild summers and wet, moderately cold winters. The area is heavily forested and dominated by a diverse mix of conifer species.

We placed a survey grid over the four mountain ranges in our study area, consisting of 453 5 × 5 km survey cells, and deployed at least one winter multi-species bait station per cell. Bait stations consisted of a bait (ungulate quarter or frozen beaver [*Castor canadensis*]), remote camera, and 12 .30 caliber bronze rifle bore gun brushes that acted as hair snags (see Robinson et al. 2017 for details).

DNA extraction and microsatellite amplification

DNA extraction from hair samples and microsatellite amplification was performed by Wildlife Genetics International using standard protocols (Paetkau 2003; Kendall et al. 2009). Protocol descriptions include clean up, error-checking, quality threshold (Paetkau 2003), and blind checking (Kendall et al. 2009). Error-checking tested for allelic drop out as outlined by Paetkau (2003) and one replicate per sample was generated except in cases where required by the scoring criteria or error checking rules outlined in Paetkau (2003). Samples were genotyped at either eight or twelve

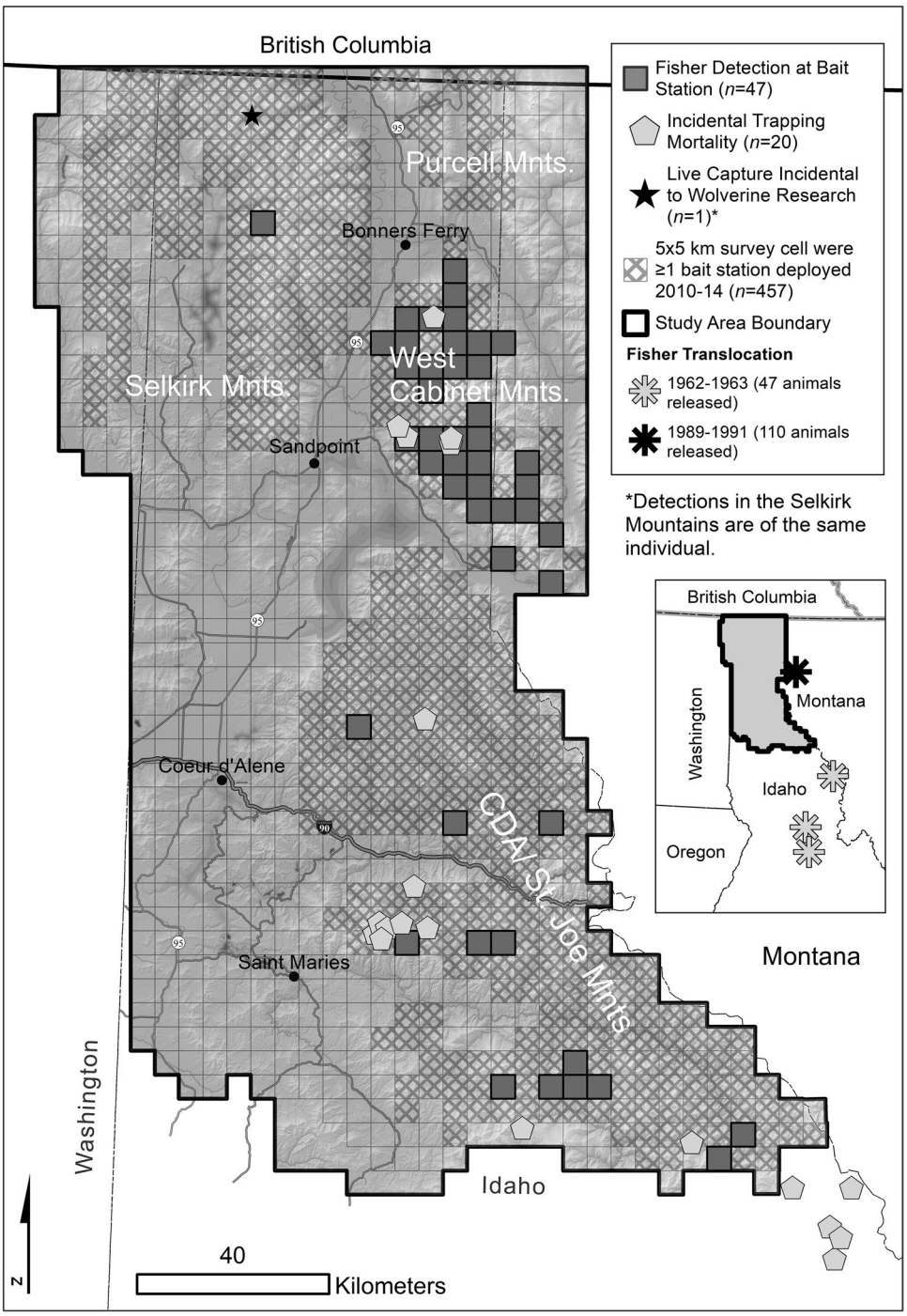

Fig. 1 Map of study area with survey results and closest documented historic fisher translocations

microsatellite loci: Ma-1, Ma-2, Ma-19 (Davis and Strobeck 1998), Mvis-072 (Flemming et al. 1999), Ggu101 (Duffy et al. 1998), MP055, MP182, MP144, MP175, MP247, MP227 (Jordan et al. 2007), plus a ZFX/ZFY gender locus.

Genetic analysis of "a priori" defined populations

We used Arlequin v3.5 (Excoffier and Lischer 2010) to calculate locus-by-locus observed (H_o) and expected (H_e) heterozygosity for the West Cabinets and SJ/CDA populations separately. The per-locus number of alleles and mean allelic richness were also calculated for both populations with FSTAT v2.9.3 (Goudet 1995). We tested for per locus heterozygote deficiency or excess (both deviations from Hardy–Weinberg equilibrium), and for pairwise linkage disequilibrium between loci in both populations using a Markov-chain method in GENEPOP 3.4 (Raymond and Rousset 1995), with 10,000 dememorization steps, 500

batches, and 10,000 subsequent iterations. To test the discrimination power of the 11 microsatellite set, we computed the probability of identity (PID) using GIMLET (Valière 2002). The conservative PID for full-sibs (PIDsib) was estimated as an upper limit to the probability that pairs of individuals would share the same genotype. Pairwise relationships were estimated between loci. We used Coancestry v1.0.1.2 (Wang 2011) to generate pairwise relatedness values based on Queller and Goodnight's Estimator (1989). Rarefaction corrected average allelic richness and private allelic richness for each population were obtained using the program HP-RARE (Kalinowski 2005).

We assessed genetic structure present in the data without a priori constraints using a Bayesian clustering approach with STRUCTURE v2.3 (Pritchard et al. 2000). We performed individual analyses for $K = 1$–10, and 10 replicate runs at each value of K, with 10,000,000 MCMC iterations after a burn in of 1,000,000, using the correlated allele frequencies and admixture model. Each value of K specifies a subset of allele frequency estimates, identified in the data, to characterize each cluster. Individuals are assigned to a cluster according to membership probabilities based on the allele frequency estimates (Porras-Hurtado et al. 2013). Then, the likelihood of the data given K, $\Pr(X|K)$, is calculated for a range of K values (see Pritchard et al. 2000 equations 12–14). The maximal value of $Pr(X|K)$, called '*Ln P(D)*' in STRUCTURE output, is accepted as the most likely number of genetic clusters in the data. To corroborate inferences from the STRUCTURE analysis, we conducted a principal component analysis (PCA), which clusters individual microsatellite genotypes. The PCA was implemented in the R statistical language (R Development Core Team 2013) with the adegenet package (Jombart 2008).

Per locus pairwise F_{ST} values (Weir and Cockerham 1984) were estimated between the two pre-defined populations using GENEPOP 3.4 (Raymond and Rousset 1995). Theoretically, assuming finite subpopulations of size N_e and a proportion, m, migrants into each subpopulation each generation, $FST = 1/(4N_em + 1)$ (but see Whitlock and McCauley 1999). However, F_{ST} estimates rely on simplifying population models, and we therefore used a second approach to estimate migration rates with the program migrate-n (Beerli and Felsenstein 1999; Beerli 2009), which can account for different immigration rates and different population sizes. Migrate-n jointly estimates the mutation-scaled migration rate ($M = m/\mu$; where m and μ are the migration and mutation rates, respectively), and the mutation-scaled N_e $\left(\theta = 4N_e\mu\right)$. The number of migrants per generation into each population is thus estimated by $\theta * M = 4N_em$. We estimated starting values of θ and M with an F_{ST} calculation and used uniform priors (for θ, minimum = 0.0, maximum = 50.0, delta = 1.0; for M, minimum = 0.0, maximum = 50.0, and delta = 1.0). Analyses were conducted using four replicates, four static-heated chains (1.0, 1.5, 3.0, 100,000.0) ran for 20,000,000 generations with sampling every 100 (burn-in = 20,000). We inspected posterior distribution plots of estimated M and θ values (bin number = 1500) to assfisess convergence. We converted estimates of M and θ to the effective number of migrants per generation (Nm) moving from population X to population Y via $Nm = (\theta_X \times M_{Y\rightarrow X})/4$.

We estimated N_e using a bias-corrected version of the linkage disequilibrium method by Waples and Do (2008) as implemented in the Ne Estimater v2 software (Do et al. 2014). The software uses a correlation coefficient, r, which is a measure of linkage disequilibrium LD between pairs of alleles at two loci (see Lewontin 1988 and; Devlin and Risch 1995), as the basis for estimating N_e. More commonly, the square of the correlation coefficient (r^2) is calculated (see Waples and Do 2008, Eq. 1), and N_e is estimated from the overall mean $\hat{r}^2$ averaged across multiple loci and alleles. Specifically, $\widehat{N_e} = \left(0.308 + \left(0.94864 - (2.08)\hat{r}^{2\prime}\right)^{1/2}\right)/2\hat{r}^{2\prime}$, where $\hat{r}^{2\prime} = \hat{r}^2 - E(\hat{r}^2)$. The expected value $E(\hat{r}^2)$ is a function of N_e, the weighted harmonic sample size (S), the recombination rate between loci, and the mating system (see Waples and Do 2008, Table 1). In general, this approach is reliable if the data set is based on 10 or more loci and sample sizes of 30 or more.

Spatial patterns of genetic diversity

We used sGD (Shirk and Cushman 2011, 2014) to calculate local measures and map continuous gradients of genetic diversity within each of the four study areas. Diversity indices are typically calculated from the multilocus genotypes of all individuals sampled within discretely defined habitat patches or larger regional extents. Importantly, discrete population approaches do not capture the clinal nature of populations genetically isolated by distance or isolation by landscape resistance. Shirk and Cushman (2011) developed spatial Genetic Diversity (sGD) to estimate genetic diversity based on grouping individuals into potentially overlapping genetic neighborhoods that match the population structure, whether discrete or clinal. When the population does not meet the assumptions of an island model, patch and regional sampling generally overestimates local heterozygosity, inbreeding and allelic diversity (Shirk and Cushman 2014). In addition, sGD reveals fine-scale spatial heterogeneity in genetic diversity that is not evident with patch or regional sampling. Shirk and Cushman (2014) extended the sGD analysis capability to estimating spatial patterns of population size. The classical approach to estimate N_e from genetic data involves grouping sampled individuals into discretely defined subpopulations assumed to be panmictic. Importantly, this assumption does not capture the continuous nature of populations genetically isolated by distance. Shirk

and Cushman (2014) modified Wright's (1946) neighborhood concept, which was defined as the number of interacting individuals inside a circle with radius two times the standard deviation of dispersal distance within the average lifespan of the individual, to produce spatially-explicit estimates of local *NS* from genetic data in continuous populations isolated by distance or resistance.

We created a resistance surface for use in sGD by combining landcover and elevation. Landcover classes were taken from the National Landcover Database (NLCD) and were reclassified to reflect expected increase in resistance to movement by fishers in non-forest habitats. Forest was given a resistance of 1 and non-forest areas were given increasingly high resistance with increasing contrast to forest habitat (e.g., Vergara et al. 2017) with the highest resistance value of 20 given to water bodies and urban areas. Elevation cost was defined using an inverted Gaussian function, as has been done for bears (Cushman et al. 2006) and martens (Wasserman et al. 2010) in the study area. The approach enables the resistance to elevation to have a inimical optimum, with the lowest resistance, and increasing resistance as you move either higher or lower from that optimal elevation. Resistance due to elevation was modeled as a Gaussian function with minimum 1 at an elevation of 1200 m, and a standard deviation of 1000 m, increasing to a maximum of 10.

We used a neighborhood search radius of 40,000 cost units to define genetic neighborhoods, which reflects a dispersal distance of approximately 15 km through average resistance values on the landscape, corresponding to the dispersal distances used in past sGD analysis of American marten genetic diversity in this region (Wasserman et al. 2012). We calculated two measures of local genetic diversity, allelic richness (Ar) and inbreeding coefficient (F_{IS}; Shirk et al. 2012), and calculated the focal estimate of *NS* in the genetic neighborhood surrounding each sampled individual.

Results

A total of 204 hair samples were successfully genotyped, of which 58 unique genotypes were identified as representing different individuals. We detected 38 individuals in the West Cabinets, 19 individuals in the SJ/CDA, 1 individual in the Selkirks, and 0 individuals in the Purcells. We detected 30 males and 27 females and one individual with inconclusive results at the sexing locus. For the non-sexing loci, we obtained genotypes at 11 loci for 30 individuals, 10 loci for three individuals, eight loci for two individuals, and seven loci for 23 individuals. The mean PIDsibs for each locus across all individuals was approx. 0.06, meaning that 1 individual in 60 siblings is expected to share, by chance, an identical genotype with another individual. Across the study area pairwise relatedness between individuals averaged −0.01866 (−0.6059 to 0.8591) with lower values in the SJ/CDA (mean = −0.08276, range −0.8167 to 0.7669) then the WC (mean = −0.02715, range −0.5965 to 0.6803).

Genetic analysis of "a priori" defined populations

Of 38 individuals from the West Cabinets, there are 45 alleles at 11 loci with 17.46% missing data. Likewise, of 19 individuals from the SJ/CDA, there are 39 alleles at 11 loci with 13.4% missing data. Average H_o and H_e were 0.72 and 0.69 for the West Cabinets and 0.52 and 0.54 for the SJ/CDA, whereas average number of alleles and allelic richness was 4.1 and 3.81 for the West Cabinets and 3.55 and 3.48 and SJ/CDA. The West Cabinet population showed one locus (MP247) that deviated from Hardy–Weinberg equilibrium, while the SJ/CDA population showed two (MP175 and Ma-19) (Table 1). Linkage disequilibrium was found among three pairs of loci in the West Cabinet population (1 and 4, 1 and 11, and 4 and 11) and five pairs of loci in the SJ/CDA population (1 and 3, 5 and 6, 1 and 7, 3 and 7, and 2 and 8).

The optimum number of clusters, *K*, from the STRUCTURE analysis was $K=3$ ($Ln\ P(D)=-1264.21$), although $K=2$ showed a comparable value, $Ln\ P(D)=-1268.63$. With both $K=3$ and $K=2$ there is a clear division between West Cabinet and SJ/CDA individuals (Figs. 2, 3). Only a single individual from the West Cabinets showed appreciable admixture between West Cabinets and SJ/CDA clusters (Sparv1k). The results from $K=3$ showed the West Cabinet population having distinct genetic structure, whereas the SJ/CDA showed little structure. Similarly, the PCA analysis separated the West Cabinet and SJ/CDA into two distinct genetic clusters (Fig. 4).

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Average pairwise F_{ST} between West Cabinet and SJ/CDA was 0.17105. This suggests the number of successfully breeding migrants between groups is $N_em = 1.22$, using the F_{ST} indirect measures of gene flow criterion. From the migrate-n analyses, the mutation-scaled migration rates were estimated to be $1.396_{\mathrm{WC}\rightarrow\mathrm{SJ/CDA}}$ (0.233–2.533) and $1.194_{\mathrm{SJ/CDA}\rightarrow\mathrm{WC}}$

Table 1 Diversity statistics for the West Cabinet (WC) and Saint Joe/Coeur d'Alene (SJ/CDA) fisher populations using 11 microsatellite loci

Locus	WC						SJ/CDA						F_{ST}
	N	H_o	H_e	A	A_r	F_{is}	N	H_o	H_e	A	A_r	F_{is}	
[1]Ma-1	38	0.79	0.72	5	4.22	−0.09	19	0.53	0.68	4	3.95	0.23	0.17
[2]MP055	19	0.79	0.7	4	3.63	−0.13	12	0.42	0.54	3	3	0.24	0.27
[3]MP182	18	0.72	0.74	5	4.67	0.03	12	0.5	0.41	3	3	−0.23	0.15
[4]Mvis72	38	0.63	0.66	4	3.32	0.04	19	0.32	0.4	3	2.98	0.21	0.2
[5]MP144	20	0.7	0.69	4	3.94	−0.02	12	0.58	0.59	5	5	0.01	0.22
[6]MP175	38	0.74	0.69	4	3.95	−0.07	19	**0.58**	**0.73**	4	3.99	0.21	0.13
[7]Ma-19	38	0.55	0.58	3	3	0.05	19	**0.84***	**0.61***	3	3	−0.40	0.04
[8]Ma-2	38	0.63	0.65	3	3	0.03	19	0.47	0.53	4	3.86	0.11	0.11
[9]MP247	22	**0.86**	**0.64**	3	3	−0.35	12	0.67	0.66	4	4	−0.02	0.11
[10]Ggu101	38	0.82	0.8	6	5.25	−0.03	19	0.11	0.1	2	1.87	−0.03	0.36
[11]MP227	38	0.74	0.69	4	3.93	−0.06	19	0.68	0.65	4	3.63	−0.05	0.06

Number genotypes (N), observed (H_o) and expected (H_e) heterozygosity, number of alleles (A) and allelic richness (A_r), inbreeding coefficient (F_{is}), and the fixation index (F_{ST}). Bold values are significant at the 0.05 level and bold* values at the 0.01 level

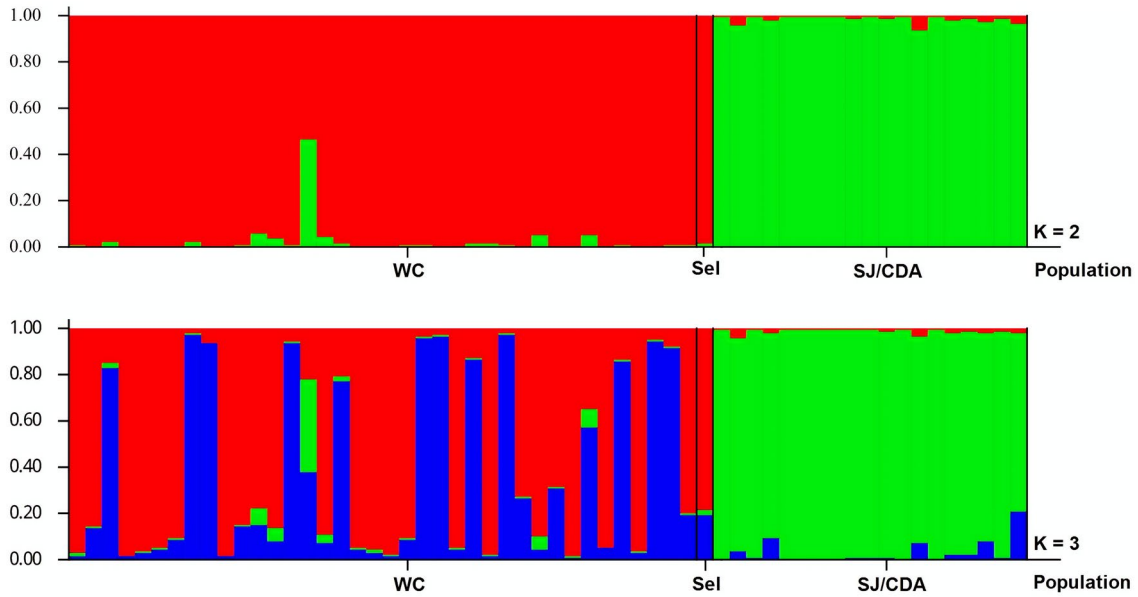

Fig. 2 STRUCTURE output of the West Cabinet (WC) and Saint Joe/Coeur d'Alene (SJ/CDA) populations for K = 2 and K = 3 models

(0.167–2.167). The mutation-scaled N_e were estimated to be 2.25 (1.167–2.283) and 2.728 (1.53–2.75) for West Cabinet and SJ/CDA, respectively. Thus, the effective number of migrants per generation (N_em) are 0.672 for West Cabinet → SJ/CDA and 0.95 for SJ/CDA → West Cabinet. In general, N_em values < 1 indicate that the effect of genetic drift is greater than the effect of migration (Mills and Allendorf 1996). Lastly, N_e calculated with NeEstimator based on the linkage disequilibrium method (Hill 1981) indicated and N_e of 26 (15.3–55.5) for the West Cabinet and an N_e of 6.5 (2.7–15) for the SJ/CDA.

Patterns of spatial genetic diversity

Using the sGD program, we observed clear patterns of genetic diversity and the local effective population size across the study area. Allelic richness was much higher in the central Cabinet mountains than in any part of the SJ/CDA (Fig. 5). Allelic richness appeared to be slightly lower on the edge of the Cabinet population than in the center, and was nearly twice as high in the center of the Cabinets than in any part of the SJ/CDA. A generally similar pattern was seen in the inbreeding coefficient (Fig. 5), with generally larger

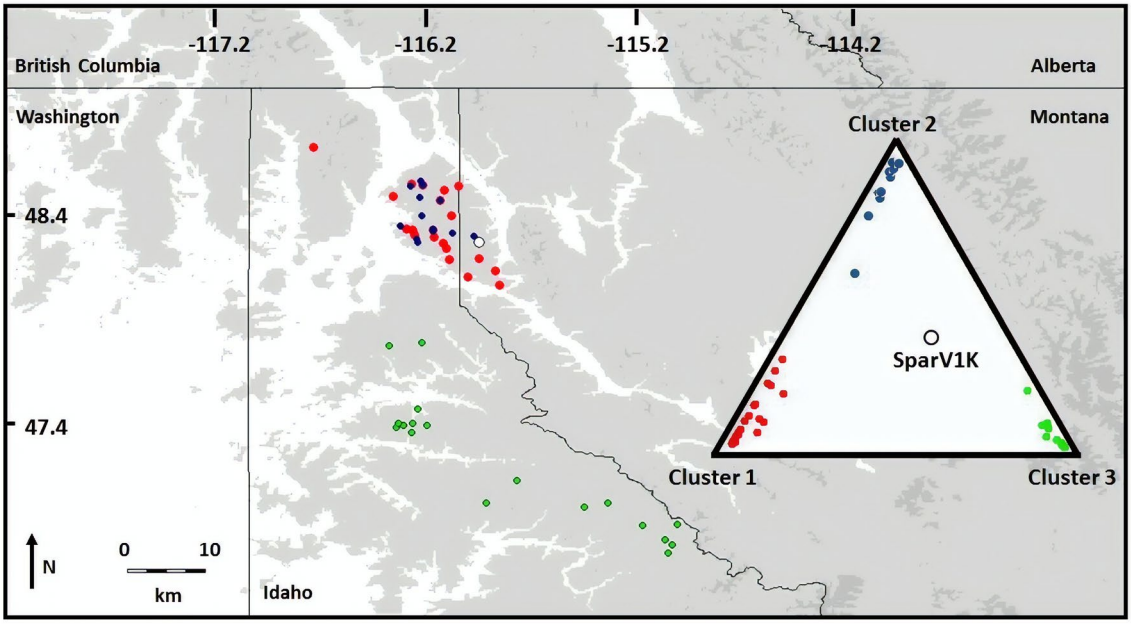

Fig. 3 Geographic clustering of genotypes under the K = 3 model. Cluster 1 and 2 show subdivision within the WC population and between the SJ/CDA Cluster 3. SparV1K, the only individual showing admixture between populations, is shown in white

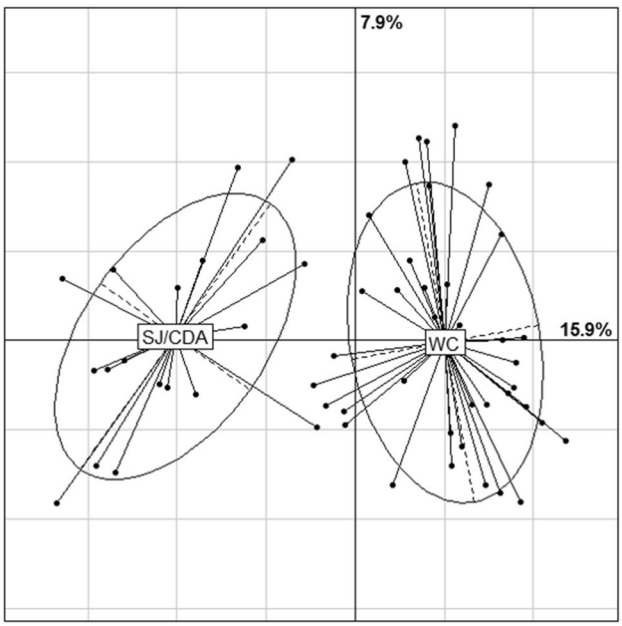

Fig. 4 PCA output comparing West Cabinet (WC) and Saint Joe/Coeur d'Alene (SJ/CDA) fisher populations

negative F_{IS} values in the Cabinets than in the SJ/CDA. The exception is for the two individuals on the northern end of the SJ/CDA, which have relatively small negative F_{IS} values. This indicates lower inbreeding of these individuals, probably because of genetic exchange with the Cabinet subpopulation. Inbreeding coefficient becomes increasingly negative toward the southern part of the SJ/CDA. Local N_e estimated within focal genetic neighborhoods surrounding each fisher genotype followed the same pattern. Local *NS* was estimated within the 50–60 individual range for the entire Cabinet ecosystem, but was much lower (10–25) across the SJ/CDA. sGD was unable to estimate local neighborhood size in the farthest southern part of the SJ/CDA due to sparsely distributed samples.

Discussion

Selkirk and Purcell extirpation

Although hair snare surveys reliably detected small numbers of fisher in the Selkirks and Purcells in the first decade of the 2000's (McCall et al. 2006; Cushman et al. 2008; Knetter and Hayden 2008), we only detected a single male in the Selkirks, which had first been observed during the previous surveys in 2005 (K. Pilgrim, U.S. Forest Service, personal communication). We detected this male in 2010 approximately 2 km from the 2005 detection location and again in 2011 when it was incidentally live-captured in a wolverine (*Gulo gulo*) research trap 23 km to the north (Fig. 1). This was well outside of what would be the limits of the mean northern Rockies male fisher home range of 98.2 km^2 (Sauder and Rachlow 2014). A concurrent British Columbia survey (Hausleitner and Kortello 2016) did not detect fisher in the Canadian Selkirk or Purcell Mountains. Thus, the only

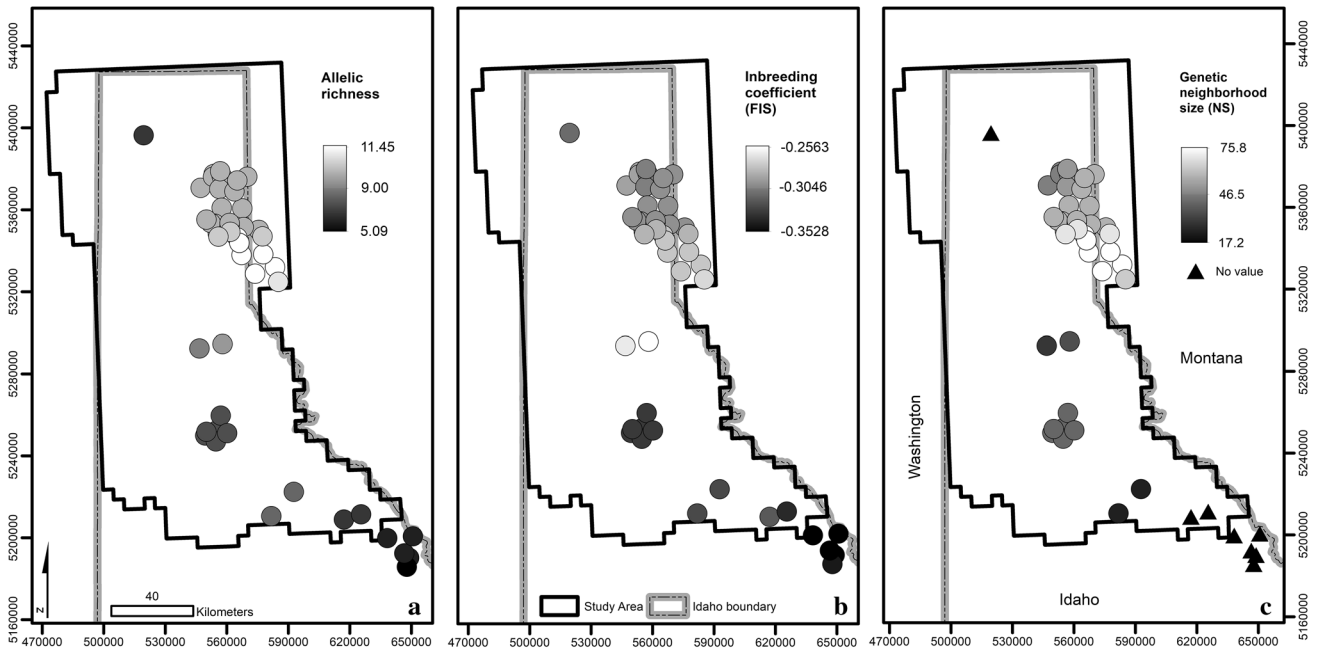

Fig. 5 sGD output showing allelic richness, inbreeding coefficients, and genetic neighborhood size mapped continuously across the study area

fisher detected in either range from 2010 to 2014 was a single male, which was ≥ 6 years old at its last detection in 2011. Therefore, it appears fisher have been effectively extirpated from both the Selkirk and Purcell Mountain Ranges.

Possible reasons for the extirpation include: (1) an unidentified mortality source in the Selkirks and/or Purcells, (2) modeled habitat (Olson et al. 2014) is not actually suitable, (3) the West Cabinet fisher population is not at carrying capacity and surplus individuals are not available to disperse, and/or (4) the Selkirk-West Cabinet MacArthur wildlife corridor (Davidson 2003; Cushman et al. 2006; Schwartz et al. 2009) or other potential corridors are not permeable by fisher.

West Cabinet island population

The small population we identified in the West Cabinets leads us to assume animals from 1989 to 91 releases were able to move west across the Bull River and Montana State Highway 56 and successfully colonize the more suitable habitat (Olson et al. 2014) in the West Cabinets.

We determined the West Cabinets comprise a fisher 'hotspot' within our study area where we found a population with distinct genetic structure, high genetic diversity, consistent allele numbers, allelic richness, and heterozygosity values (Table 1). The average per-locus H_o and H_e in the West Cabinets were 0.72 and 0.69, respectively. In comparison Carr et al. (2007) and Hapeman et al. (2011) found similar H_e values (0.6–0.68 H_e and 0.52–0.56 H_e respectively) in fisher populations in northeastern North America. However, Wisely et al. (2004) found lower H_e values in fragmented fisher populations along the west coast of North America (0.2–0.42 H_e). The average per-locus allelic richness in the West Cabinets was 3.81, which fell between the northeast populations (4.50–6.88 Carr et al. 2007 and; Hapeman et al. 2011) and the west coast fisher populations (1.4–2.6, Wisely et al. 2004). Based on these parameters, our estimates of genetic diversity are comparable to values observed for presumably viable northeastern populations but greater than those observed for genetically depauperate west coast populations. In addition, from our population-level approach, there was no detectable inbreeding in the West Cabinets (average per-locus $F_{IS} = -0.05$; Table 1). The two distinct clusters of individuals may be a result of descendants from disparate augmentation ancestry (Lucid et al. 2016).

Fishers in northern Idaho, like most wild populations, mate and disperse over limited distances relative to the extent of the population. For this reason, this population is not panmictic, but likely structured by some form isolation by distance or isolation by landscape resistance. Therefore, in addition to population-based estimates that assume panmixia in two parts of the study area, we employed a second approach that models populations continuously as a gradient phenomenon. Neel et al. (2013) and Shirk and Cushman (2014) found that assuming panmixia when populations are continuous produces biased and unreliable estimates that do not reflect *Ne* for the global population nor the local *NS*. Moreover, the single estimate for an entire sampling area may mask substantial spatial heterogeneity in the local *NS*. In this study, the population-based and gradient-based

measures of genetic diversity and N_e gave qualitatively similar results. Both found relatively high genetic diversity and lower inbreeding in the West Cabinet population than in the population to the south in the SJ/CDA watersheds. Our estimate of genetic neighborhood size in the West Cabinets region was somewhat higher than the *Ne* estimate obtained from the same area, which is a pattern also reported from simulations by Shirk and Cushman (2014), suggesting the true fisher population in that region may be slightly larger than would be estimated from *Ne* calculations assuming a panmictic population. Conversely, our spatial estimates of inbreeding are substantially higher that those obtained from a population based approach.

Genetic connectivity between West Cabinet and SJ/CDA populations

Our *NS* estimates in the southern SJ/CDAs are very low, but again slightly higher than the *Ne* estimates, reflecting that panmictic assumptions might systematically underestimate true population size (e.g., Shirk and Cushman 2014). Regardless of this potential underestimate, the agreement of the two approaches in terms of finding that the fisher population in the southern part of the study area is very small, with low genetic diversity and elevated inbreeding coefficient is clear.

Another important insight from the spatial analysis of genetic diversity and *NS* provided by sGD is the edge effect that appears at the periphery of a population. If a population is genetically structured, the theoretical expectation is for reduced gene flow, *NS*, and neutral genetic diversity near the periphery relative to the core (Caughley 1994; García-Ramos and Kirkpatrick 1997), though variation in local population densities and resistance could create more complex patterns. This expectation has been empirically observed in both plant and animal populations, though not consistently (Eckert et al. 2008). We saw this here both in terms of lower genetic diversity on the edge of the West Cabinet subpopulation and declining genetic diversity heading southward through the SJ/CDA Mountains. This demonstrates how heterogeneous landscapes and variable population density can create complex spatial patterns of *NS* (and concomitant spatial variation in management implications) that can only be elucidated with a spatially explicit approach.

To achieve long-term genetic diversity, the loss of variation needs to be balanced by new mutations, recombination, or genetic input from neighboring populations (Allendorf and Ryman 2002). Much uncertainty exists regarding the N_e or census population sizes necessary for long term (> 100 years) species persistence. Franklin (1980) and Soulé (1980) proposed a minimum effective size of 50 is required to avoid inbreeding depression in the short term, though some reports consider the minimum number to be greater (Reed and Bryant 2000). In this example, both population and gradient-based measures of N_e found that the Cabinet Mountains region holds a population either smaller [N_e of 26 (15.3–55.5)] than this size or slightly larger (*NS* of 50–60). Additionally, this population is largely isolated, and the very small and quite distant population identified in the SJ/CDA is unlikely to provide demographic or genetic rescue. Conversely the West Cabinet population does not appear to be subsidizing the SJ/CDA population to any considerable degree.

We found minimal genetic evidence of migration between the two ranges. One West Cabinet individual (Sparv1k) showed genetic admixture between the West Cabinet and SJ/CDA populations (Figs. 2, 3) The spatial F_{IS} analysis identified genetically introgressed individuals, possibly the product of repeated backcrossing of inter-population hybrids, on the northern end of the SJ/CDA between these two areas with lower inbreeding. Our F_{ST} value (0.17) falls between F_{ST} values reported for fisher in other study areas. Kyle et al. (2001) reported a mean F_{ST} of 0.14 for 13 fisher populations from northeastern North America. Wisely et al. (2004) reported a F_{ST} value of 0.45 for six west coast fisher populations. Although these results suggest some genetic exchange between the WC and SJ/CDA populations, our genetic estimates of migration were low (migrate-n indicated $N_em < 1$ while the traditional calculation from F_{ST} was 1.22). Natural populations may need as many as 10 migrants per generation to maintain diversity (Mills and Allendorf 1996) and without a substantial increase in population sizes or migration between the West Cabinets and SJ/CDA, it is unlikely that gene flow will have an impact on the maintenance of genetic diversity for either population. In addition, Shirk and Cushman (2014) noted that the periphery of a population can be at risk of decline, even though the core might initially remain viable and that the decline of the edge neighborhoods may contract the population inward, lowering *NS* in areas adjacent to the original periphery, and potentially creating a wave of inbreeding depression that could threaten even the centermost neighborhoods. Therefore, maintaining a sufficiently large *NS* in the periphery is an important conservation target to avoid a greater threat to the entire population.

Conservation implications

Both *Ne* and *NS* indicate a very small fisher population in the SJ/CDA and a slightly larger population in the West Cabinets. Using the rule of thumb that *Ne* is generally 20–50% of the census population size (Allendorf and Ryman 2002), and applying that rule liberally to *NS*, there may be 52–300 fisher in the West Cabinets, 13–88 fisher in the SJ/CDA, and 65–388 fisher in the study area.

Keeping in mind that perceived reintroduction success is sometimes actually recolonization (Stewart et al. 2017);

it does appear the 1989–1991 fisher augmentation was successful in terms of establishing a small, reproductive fisher population in the West Cabinets. However, the potential for this relatively small and highly isolated population to persist in the long-term is uncertain. Future population assessments will be required to clarify if the population is stable, increasing, or decreasing. Assuming the West Cabinets can support a contiguous fisher population, their ~ 2000 km^2 area could support a $N_e \geq 50$ (this study; Sauder and Rachlow 2014). However, a N_e of at least 100 and possibly 500 is necessary to facilitate long term (> 100 year) population persistence (Allendorf et al. 2013) and an overall loss of fisher habitat by 2090 is predicted to occur in the West Cabinets under all climate scenarios examined (Olson et al. 2014). By this line of reasoning, the West Cabinets may not be able to independently support a fisher population large enough to have low long-term extinction risk. By the same line of reasoning it is unlikely the SJ/CDA population is large enough to facilitate long term population persistence.

Our results suggest the small and highly isolated nature of northern Rockies fisher populations will not reach a sufficient level of gene flow without human intervention. It is likely a 'filling in the gaps' type of approach would be most effective which would include augmentations to strategic locations in multiple mountain ranges to maximize stepping-stone connectivity. This would need to be coupled with addressing identified threats to the species including habitat connectivity maintenance and restoration, reductions in human caused mortality, and evaluations of why some populations (e.g., Selkirk and Purcell Mountains) disappear (IDFG 2017; WDFW 2015).

Directing resources to the recovery of a species often comes at the expense of other species and it is imperative that recovery plans consider the costs, benefits, and feasibility of recovery (Martin et al. 2018). Our study suggests the genetic connectivity of northern Rockies fisher populations is vulnerable to landscape barriers, un-likely to persist without human intervention, and successful recovery will be dependent on future management and augmentation. This costly process would demand resources from already overburdened natural resource management agencies. However, incorporation of fisher recovery into multi-species management actions may help alleviate some of the time and financial burden. We recommend these factors be considered when determining how, and if, species recovery should proceed.

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