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RESEARCH ARTICLE

Sampling affects the detection of genetic subdivision and conservation implications for fisher in the Sierra Nevada

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Abstract The small population of fisher (*Pekania pennanti*) in the southern Sierra Nevada is completely geographically and genetically isolated putting it at increased risk of extinction. Previous research using a clustered sampling scheme found a high amount of genetic subdivision within the southern Sierra Nevada population hypothesized to be caused by the Kings River Canyon. In this study, we use a larger and more geographically continuous set of genetic samples ($n = 127$) than was previously available to test this hypothesis and evaluate the genetic structure of the population. Both spatial and non-spatial population assignment models found three primary genetic clusters with moderate divergence between the clusters ($F_{ST} = 0.05$–0.13) at 10 microsatellite loci. These clusters appear to be associated with areas around the Kings River and Mountain Home State Demonstration Forest. One model also detected additional fine scale subdivision north of the Kings River that may be evidence of founder effects from a recent population expansion. The amount of population subdivision detected in this study is lower than previously found and indicates that while certain landscape features may reduce gene flow, these landscape features may be less of a barrier than initially thought. In the previous work, samples were collected in clusters which can inflate estimates of population structure by increasing the likelihood of oversampling related individuals. This study demonstrates how clustered sampling from a continuously distributed population can affect the assessment of population subdivision and influence conservation implications.

Keywords Fisher · *Pekania pennanti* · Isolation by distance · Population subdivision · Sampling

Introduction

Connectivity within and between populations is an important factor in population biology impacting migration (Berger et al. 2008; Wilcove and Wikelski 2008), dispersal (Willson 2004; Kojola et al. 2009), spread of disease (Greer and Collins 2008; Plowright et al. 2011), and maintenance of genetic diversity (Epps et al. 2006; Dixo

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et al. 2009). Connectivity is especially important for small populations that are already at elevated risk of extinction due to their susceptibility to stochastic demographic or genetic factors (Gilpin and Soule 1986). Assessing the genetic structure of a population is a common method for evaluating connectivity by identifying boundaries of genetic groups, quantifying the amount of gene flow between them, and distinguishing which landscape features might act to restrict gene flow (Manel et al. 2003).

Recent research has found that estimates of structure and gene flow can be strongly influenced by sampling design depending on the genetic characteristics of the population (i.e. Frantz et al. 2009; Schwartz and McKelvey 2009). If gene flow is restricted to short distances (e.g. neighbor mating), then genetic differentiation increases with increasing geographical distance between individuals, termed isolation by distance (IBD, Wright 1943). IBD results in a gradient of genetic differentiation across a landscape where groups of individuals are genetically dissimilar even though there is continuous genetic connectivity between them (Slatkin 1993; Hutchinson and Templeton 1999). In such populations, disentangling the effects of IBD from true ecological barriers is difficult and the impact of sampling design on results can be great. In particular, discontinuous sampling of a continuously distributed population characterized by IBD can lead to biased results where it appears that there is a genetic barrier on the landscape that is not really present (Schwartz and McKelvey 2009). For species of conservation concern understanding the effects of sample configuration on landscape genetic analyses and providing an accurate assessment of genetic structure is especially critical as this information can have a major impact in conservation decisions.

The southern Sierra Nevada population of fisher (*Pekania pennanti* [Koepfli et al. 2008; Sato et al. 2012], formerly *Martes pennanti*) is an example of a population for which concerns about connectivity are acute. The population is small, with an estimated size of less than 300 adults (Spencer et al. 2011), and isolated from the nearest native population by over 400 km (300 km to a recently reintroduced population). New research has shown that the southern Sierra Nevada fisher population has been genetically isolated from other fisher populations for thousands of years (Knaus et al. 2011; Tucker et al. 2012). Previous genetic analysis of this population found high amounts of subdivision ($F_{ST} = 0.51$) between two sampling areas north and south of the Kings River Canyon (Wisely et al. 2004) (Fig. 1). The two sampling areas were separated by less than 100 km, which is within the known maximum dispersal distance of the species (York 1996), and connected by fairly contiguous forested habitat transected by the Kings River. However, this distance is much greater than average dispersal distances reported in other West Coast fisher populations (6 km-female/29 km-male Aubry and Raley 2006; 16.7 km/41.3 km Weir and Corbould 2008; 1.3 km/4.0 km Matthews et al. 2013). The authors inferred that the Kings River may be a barrier to gene flow between these two sampling areas. Detection of this strong subdivision raised conservation concerns that this small population was fragmented, furthering increasing extinction risk (Center for Biological Diversity 2008).

Our overall objective was to determine if the strong subdivision detected by Wisely et al. (2004) was influenced by the sampling of a small number of individuals from two relatively limited geographic areas within the southern Sierra Nevada range (north Kings River $n = 14$, south Kings River $n = 19$). If this population is characterized by IBD, such clustered sampling may have inflated estimates of population structure and the interpretation of that structure on the landscape. In this study, we assess the genetic structure of the southern Sierra Nevada fisher population using continuously distributed samples from across the entire population (Fig. 1). We then test if sampling scheme (clustered versus continuous) strongly influenced the results.

Methods

Study area

The study area is defined as the west slope of the Sierra Nevada south of highway 120 in Yosemite National Park to the southern tip of the Greenhorn Mountains near Lake Isabella (Zielinski et al. 1995; Zielinski and Mori 2001). All sampling was conducted on federally owned lands and occurred within the known elevation range of fisher in this region (800–3,200 m: Fig. 1).

Sample collection

Genetic samples were collected from 2006 to 2009. All sampling was conducted in conjunction with the U.S. Forest Service Sierra Nevada Carnivore Monitoring Program (Zielinski et al. 2012). Sample units ($n = 223$) were distributed across the study area and co-located with points from the Forest Inventory and Analysis (FIA) sampling grid. The FIA program is a nationwide forest condition monitoring program that consists of a sampling points located within a hexagonal grid network that are on average 5.47 km apart (Roesch and Reams 1999).

Each sample unit consisted of an array of six track-plate boxes with barbed wire hair snares (Zielinski et al. 2006) that encompassed a 0.8 km^2 area. The use of bait (chicken) and a commercial trapping lure is thought to have extended the

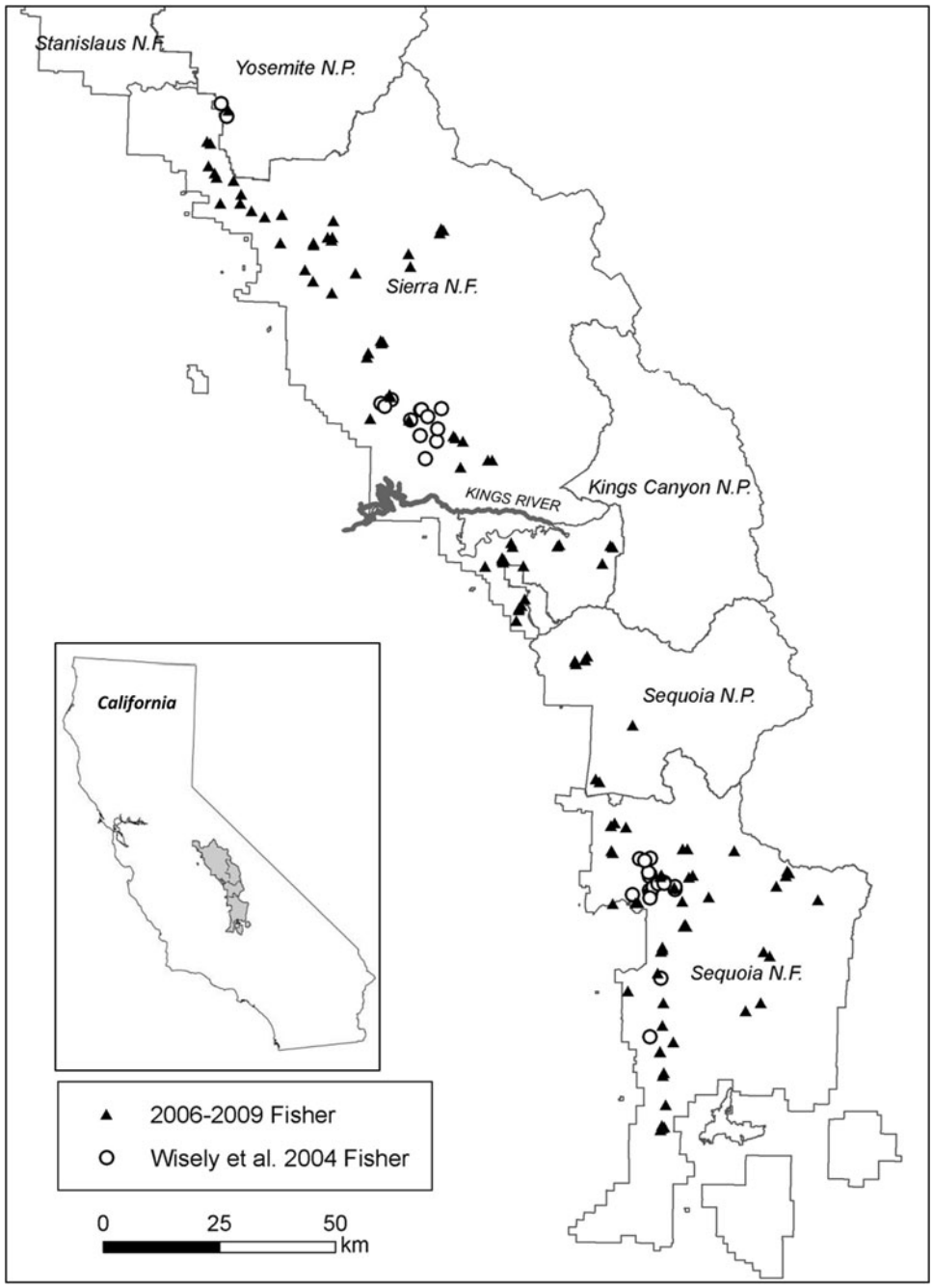

Fig. 1 Map of the southern Sierra Nevada fisher population showing the distribution of samples from Wisely et al. (2004) (*open circles*) and from the 2006 to 2009 sampling for this study (*black triangles*)

effective survey area of the sample unit to ~ 1.22 km^2 (Zielinski and Mori 2001). Positive identification of fisher from track data has been well established (Zielinski and Truex 1995) and only hair samples from stations that detected fisher via tracks were genetically analyzed. Hair samples were collected and stored in prescription vials with a silica gel desiccant at room temperature to minimize DNA degradation.

Because we were concerned that gaps in sample distribution can bias analyses of population genetic structure, we opportunistically deployed hair snares in Sequoia, Kings-Canyon, and Yosemite National Parks, as these areas were not included in the aforementioned sampling network. For this opportunistic sampling, track-plate boxes with hair snares were installed every 500–1,000 m along established roads or trails. Stations were placed at least 50 m from the edge of the road or trail to reduce any potential disturbance effects from close proximity to these anthropogenic features.

Laboratory analysis

DNA was extracted from hair samples using the Dneasy Tissue Kit (Qiagen, Valencia, CA) with modifications for

hair samples. Up to 10 hairs were used in each DNA extraction to maximize the probability of obtaining a high quantity of DNA. Samples were analyzed at ten microsatellite loci. *MP059*, *MP144*, *MP175*, *MP197*, *MP200,* and *MP247* were developed from tissue samples from the southern Sierra fisher population (Jordan et al. 2007). *MA1*, *GGU101, GGU216*, and *LUT 733* were developed in other mustelid species and have also been found to be variable in the southern Sierra fisher population (Davis and Strobeck 1998; Duffy et al. 1998; Dallas and Piertney 1998). The reaction volume (10 µl) contained 1.0 µL DNA, 1× reaction buffer (*Applied Biosystems*), 2.0 mM $MgCl_2$, 200 µM of each dNTP, 1 µM reverse primer, 1 µM dye-labeled forward primer, 1.5 mg/ml BSA, and 1 U *Taq* polymerase (*Applied Biosystems*). The PCR profile was 94 °C/5 min, [94, 55 °C/1 min, 72 °C/30 s] × 36 cycles). The resultant products were visualized on a LI-COR DNA analyzer (LI-COR Biotechnology). Hair samples that successfully genotyped were analyzed for sex using the Y-linked marker *DBY-3* (Hedmark et al. 2004).

We used the multi-tubes approach to address the potential for genotyping error in non-invasive samples in which each sample is analyzed a minimum of three times per locus with that locus accepted as accurate only if the samples produced consistent genotypes (Eggert et al. 2003; McKelvey and Schwartz 2004). If the genotype at a locus differed in one or more of these amplifications, we conducted an additional round of three amplifications. If a consistent genotype could not be determined after multiple amplifications then that locus was removed from the dataset. Samples that amplified at fewer than seven loci were removed from further analysis.

We checked for genotyping errors using the examining bimodabilty (EB test) in the software DROPOUT (McKelvey and Schwartz 2005), which tests for bimodal peaks in the distribution of allele frequency differences among individuals that is indicative of genotyping error. We also used the program MIRCOCHECKER to assess the potential for null alleles at each locus (van Oosterhout et al. 2004).

Data analysis

We tested microsatellite genotypes for departures from Hardy–Weinberg proportions at each locus using Fisher's exact test in Genepop 4.0 (Raymond and Rousset 1995; Rousset 2008). Gene diversity (H_E) (Nei 1973), F_{IS}, number of alleles (A), allelic richness (A_R) and gametic disequilibrium for each pair of loci were calculated using FSTAT 2.9.3 (Goudet 1995, 2001). The amount of genetic diversity present in the sample groups was compared using paired t tests of A_R and arcsine-transformed H_E (Archie 1985). We used sequential Bonferroni corrections to correct for multiple comparisons when assessing statistical significance (Rice 1989). We assessed the statistical power of the microsatellite panel to identify individuals by calculating the probability of identity (P_{ID}), the probability of two unrelated individuals randomly drawn from the population sharing the same multilocus genotype, using the method of Paetkau and Strobeck (1994). As shared ancestry and population subdivision can bias P_{ID} we also calculated P_{SIB} which is the probability of two siblings sharing the same genotype. P_{SIB} defines the upper limit for the range of P_{ID} in a population when there is bias due to shared ancestry (Taberlet and Luikart 1999). Both P_{ID} and P_{SIB} were calculated in the software GenAlEx 6.4 (Peakall and Smouse 2006).

Spatial autocorrelation

We tested for the presence of IBD using Mantel tests of pairwise geographic versus genetic distance between individuals and spatial autocorrelation analysis in GenAlEx 6.4 (Peakall and Smouse 2006). For spatial autocorrelation analysis we used the genetic autocorrelation coefficient (r) as defined by Peakall and Smouse (2005) (closely related to Moran's I) to measure the genetic similarity between pairs of individuals in defined distance classes. We quantified spatial autocorrelation in the data by binning genetic distances between individuals into classes defined by geographic distance. We conducted this analysis using three different geographic bin sizes of 4, 6, and 10 km to assess the effect of bin size on the results. We then visualized the data graphically using correlograms that illustrate the behavior of the autocorrelation as a function of distance (Manel et al. 2003). To define statistical significance an autocorrelation coefficient representing no spatial structure was generated by randomly shuffling all individuals among geographic locations and calculating the autocorrelation coefficient over 1,000 random permutations.

Population subdivision

Population structure was assessed using two individual based approaches that allow for the evaluation of genetic structure without defining a priori populations. One approach, implemented in the program STRUCTURE 2.3.3 (Pritchard et al. 2000), does not include geographic coordinates in its analysis, whereas the second approach, implemented in GENELAND (Guillot et al. 2005), incorporates specific spatial information for individuals in population assignments. The spatial approach assumes that some degree of spatial dependence is present among individuals and that the probability of any two individuals belonging to the same population decreases with the geographical distance between them in accordance

with Wright's IBD model (Guillot et al. 2005). We chose GENELAND for spatially based analyses as it has been shown to perform well for detecting boundaries of genetic clusters, especially with semi-permeable edges (Safner et al. 2011).

In STRUCTURE we used the admixture model in which each individual has mixed ancestry and draws some fraction of its genome from each of the K populations, and ran both the independent and correlated allele frequency models (Pritchard et al. 2000; Falush et al. 2003). We also used the LOCPRIOR model (Hubisz et al. 2009) that incorporates location information by allowing for the a priori grouping of samples based on sample location as this model found to improve inference when working with lower levels of divergence or less data (Hubisz et al. 2009). We determined K using two different methods: the maximum likelihood value (ln[Pr($X|k$)]), and the ΔK method which is based on the second order rate of change of ln[Pr($X|k$)] between consecutive values of K (Evanno et al. 2005).

In GENELAND we conducted analyses using both the uncorrelated (similar to the independent model in STRUCTURE) and correlated allele frequency models. We chose to compare the results of both models because while the correlated model has been found to be more powerful at detecting subtle structure, it is also more sensitive to model assumptions and can overestimate K (Guillot et al. 2005). We used the spatial uncertainty option in GENELAND which allows for the locations of individuals to vary within a specified distance from the sample location and mimic the movement of an individual. This added variation addresses the problem of assigning individual genotypes to stationary points for mobile animals and has been found to increase the precision in detection of true population boundaries (Guillot et al. 2005) (Supplementary material, Appendix 1).

For both STRUCTURE and GENELAND we investigated two different cutoff probabilities (q-values) of 0.60 and 0.80 to infer population membership for each individual. Individuals assigning <0.80 may be considered as admixed between populations (Lecis et al. 2006; Vähä and Primmer 2006; Bergl and Vigilant 2007). We verified the F_{ST} values between genetic clusters identified by STRUCTURE and GENELAND using Genepop 4.1 (Raymond and Rousset 1995; Rousset 2008) according to the method of Weir and Cockerham (1984).

We calculated an F_{ST} value between samples north and south of the Kings River to assess the a priori hypothesis, based on the Wisely et al. (2004) results, that the Kings River may be a major barrier to gene flow in the southern Sierra Nevada. We also attempted to recreate the sampling scheme of Wisely et al. 2004 by taking a subset of the 2006–2009 samples in the closest geographic proximity possible to the Wisely et al. (2004) samples. However, the 2006–2009 samples were collected at much lower spatial density than the Wisely et al. (2004) study and therefore, an equivalent number of samples covered a much greater spatial area. The differences in the spatial extent of sampling were so great that our subset was not an accurate reflection of the sampling design used in the Wisely et al. (2004) study and therefore, we could not meaningfully compare the two studies directly in this manner.

Hierarchical analysis

Hierarchical population structure, in which genetic groups are made up of clusters of further differentiated populations, has been detected in many previous studies (Evanno et al. 2005). Therefore, after determining the primary population subdivision using the methods described in the previous section, we conducted a hierarchical analysis for IBD by analyzing each of the identified genetic clusters separately. Because of the relatively small size of each subpopulation we used reduced geographic bin sizes of 3 km and 5 km for within subpopulation spatial autocorrelation analysis. We also conducted hierarchical population subdivision analyses using STRUCTURE and GENELAND to investigate the potential for additional subdivision within identified genetic clusters.

Results

Genotyping

We successfully genotyped 247 hair samples from which we identified 127 unique genotypes representing different individuals. While the majority of genotypes ($\sim$70 %) were obtained from field samples containing 5–10 hairs, some genotypes were from samples consisting of 1–4 hairs. Not all samples amplified at all 10 loci with 85 % of samples amplifying at 10 loci, 9 % at 9 loci, 3 % at 8 loci and 3 % at 7 loci. We detected more males ($n = 72$) than females ($n = 48$), and had seven individuals for which we could not determine sex due to inconclusive results at the sexing locus.

We detected limited movements in the 42 individuals that were recaptured multiple times. The majority of both within year and between year recaptures occurred within the same sample unit or at other units in close proximity. We recaptured 12 individuals at more than one sample unit; 11 of these 12 recaptures were male. The largest movement we found was a male detected in sample units 20 km apart over a three month time period.

The 10 microsatellite loci had an average of 3.5 alleles per locus with an observed heterozygosity (H_O) of 0.51 and H_E of 0.56. The P_{ID} ranged from 0.00008 (7 loci) to 0.000002 (10 loci), and P_{SIB} from 0.01 (7 loci) to 0.002 (10

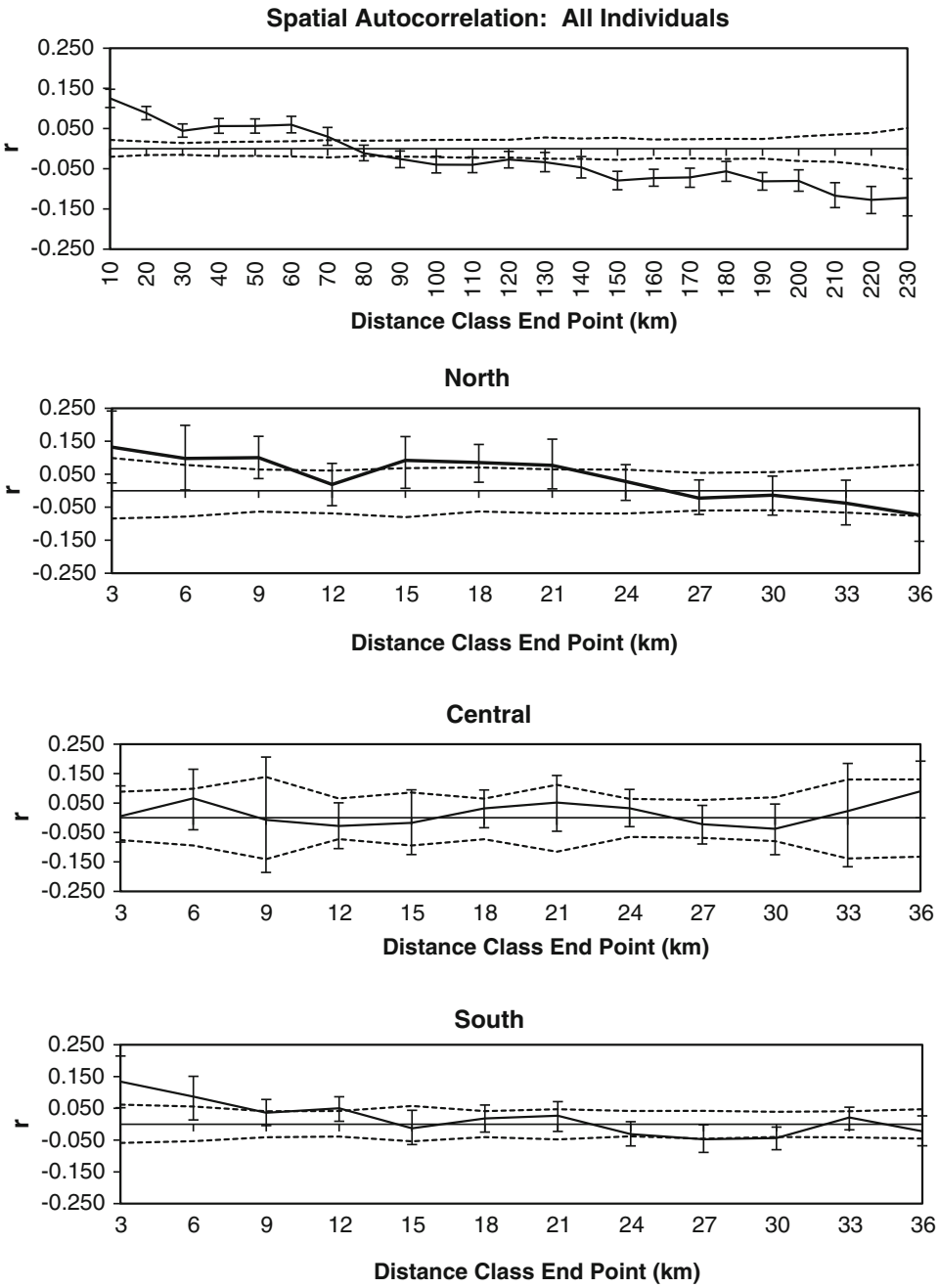

Fig. 2 Correleograms indicating the results of hierarchical spatial autocorrelation analysis showing the correlation coefficient *r* (*solid line*) as a function of distance with 95 % confidence interval error bars and a 95 % confidence interval (*dotted line*) around the null hypothesis of no spatial structure. For all individuals combined and for each of the three genetic clusters identified in population subdivision analyses (North, Central, South)

loci) which are within the values of 0.01–0.001 recommended for reliable identification of individuals (Waits et al. 2001). Two of the 10 loci were out of Hardy–Weinberg proportions, both of which had a significant deficit of heterozygotes (F_{IS} MP59 = 0.202, MP200 = 0.172), and were identified as potential null alleles by MICROCHECKER. Significant gametic disequilibrium was detected for 17 of the 45 loci pairs ($P < 0.05$), 15 more than the two that would be expected by chance alone. After correcting for multiple comparisons using a sequential Bonferroni correction, three loci pairs remained significant. However, all loci were in Hardy–Weinberg proportions and gametic equilibrium after accounting for the population subdivision described in the following sections, indicating that the heterozygous deficit we detected was the result of underlying population subdivision and not null alleles (Wahlund 1928).

Isolation by distance

Across all samples, the Mantel test of geographic versus genetic distance was statistically significant ($P < 0.001$) indicating IBD, with a Mantel correlation coefficient (Mantel *r*) of 0.25. We also detected IBD in spatial

autocorrelation analyses with significant autocorrelation between individuals at distances up to 70 km ($r = 0.045$, $P < 0.001$). The autocorrelation coefficient r decreased as geographic distance increased, declining from $r = 0.191$ for individuals 10 km apart to $r = -0.173$ for individuals 230 km apart (Fig. 2).

Population subdivision

Bayesian clustering methods detected a moderate amount of subdivision within the southern Sierra Nevada fisher population. Both the independent and correlated models in STRUCTURE, found $K = 3$ using the maximum ln[Pr($X|k$)] value, and $K = 2$ using the ΔK method (Evanno et al. 2005) (Fig. 3). The correlated model showed greater mixing among populations than the independent model. The correlated and independent models in STRUCTURE had an average admixture value (α) of 2.54 suggesting a high degree of admixture as large α values (>1) indicate most individuals in the population are admixed. The mean α for $K = 3$ (1.72) was much lower than for $K = 2$ (3.35) indicating less admixture in individuals when the population was partitioned into three versus two populations. The variance in α over multiple iterations was also much lower for $K = 3$ than $K = 2$. In simulation studies low variance in α has been found to be indicative of the true value of K (Pritchard et al. 2000).

The uncorrelated model in GENELAND also found $K = 3$ and this value of K was consistent across all 20 runs and all three levels of spatial uncertainty (Fig. 4a). The geographic delineation of the clusters identified by STRUCTURE for $K = 3$ were the same as found for $K = 3$ in GENELAND. In both GENELAND and STRUCTURE for $K = 3$ the identified genetic clusters roughly correspond to the area north of the Kings River (North), between the Kings River and the Mountain Home Demonstration State Forest (Central), and south of Mountain Home Demonstration State Forest (South) (Fig. 5). Pairwise F_{ST} values between the clusters estimated in GENELAND were North–Central = 0.083, Central–South = 0.054, North–South = 0.127. Testing the hypothesis of population division along the Kings River Canyon we found an F_{ST} value of 0.087 between samples north and south of the Kings River.

When $K = 2$ in STRUCTURE the North and Central populations were combined into a single larger population, with its boundary to the South population nearly identical to when $K = 3$. In GENELAND for k = 3, 98.4 % of individuals assigned with greater than a 0.60 probability to a population, while in STRUCTURE only 84.3 % of individuals assigned at this probability threshold. Assignment rates remained high (89.0 %) for GENELAND models even when using a stricter 0.80 threshold for probability of population assignment, but dropped considerably (53.5 %) for the STRUCTURE models. Twelve of

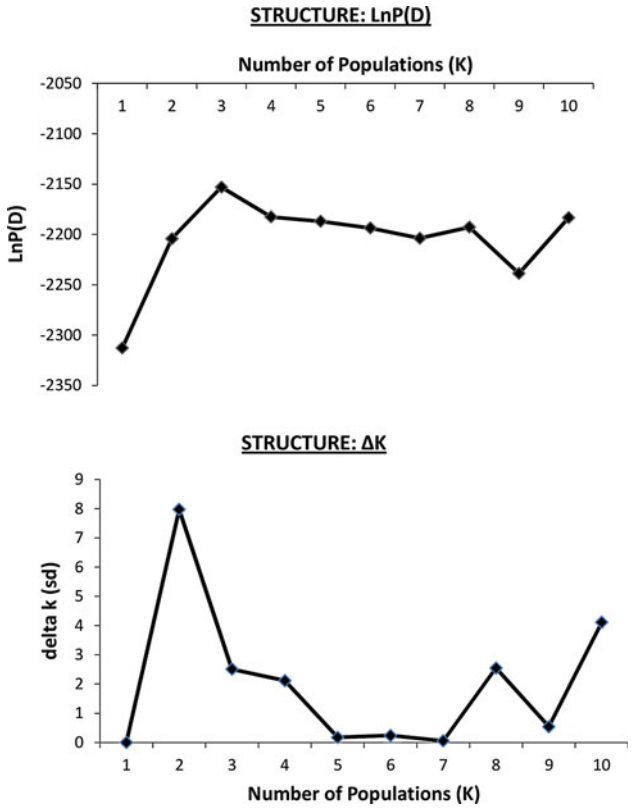

Fig. 3 Results of the admixed–correlated model in STRUCTURE showing the modal value of $K = 3$ for the maximum likelihood method and $K = 2$ for the ΔK method. Results were similar for the admixed–independent and LOCPRIOR models

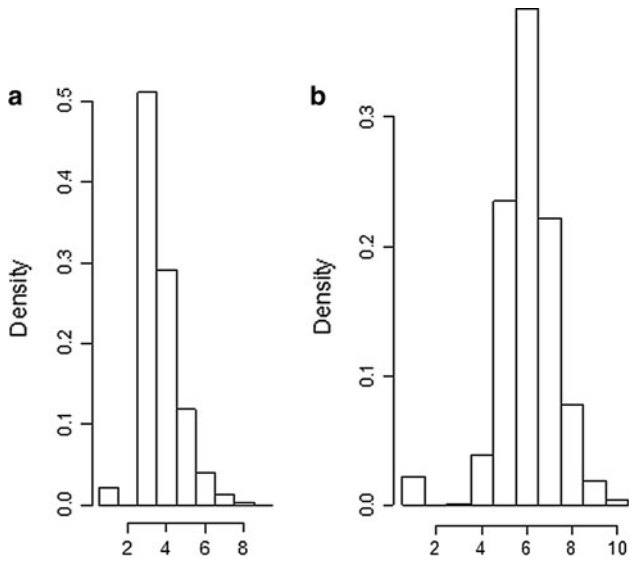

Fig. 4 Histogram of the distribution of simulation results over 500,000 iterations for the number of populations (K, x-axis) for the GENELAND **a** uncorrelated and **b** correlated models

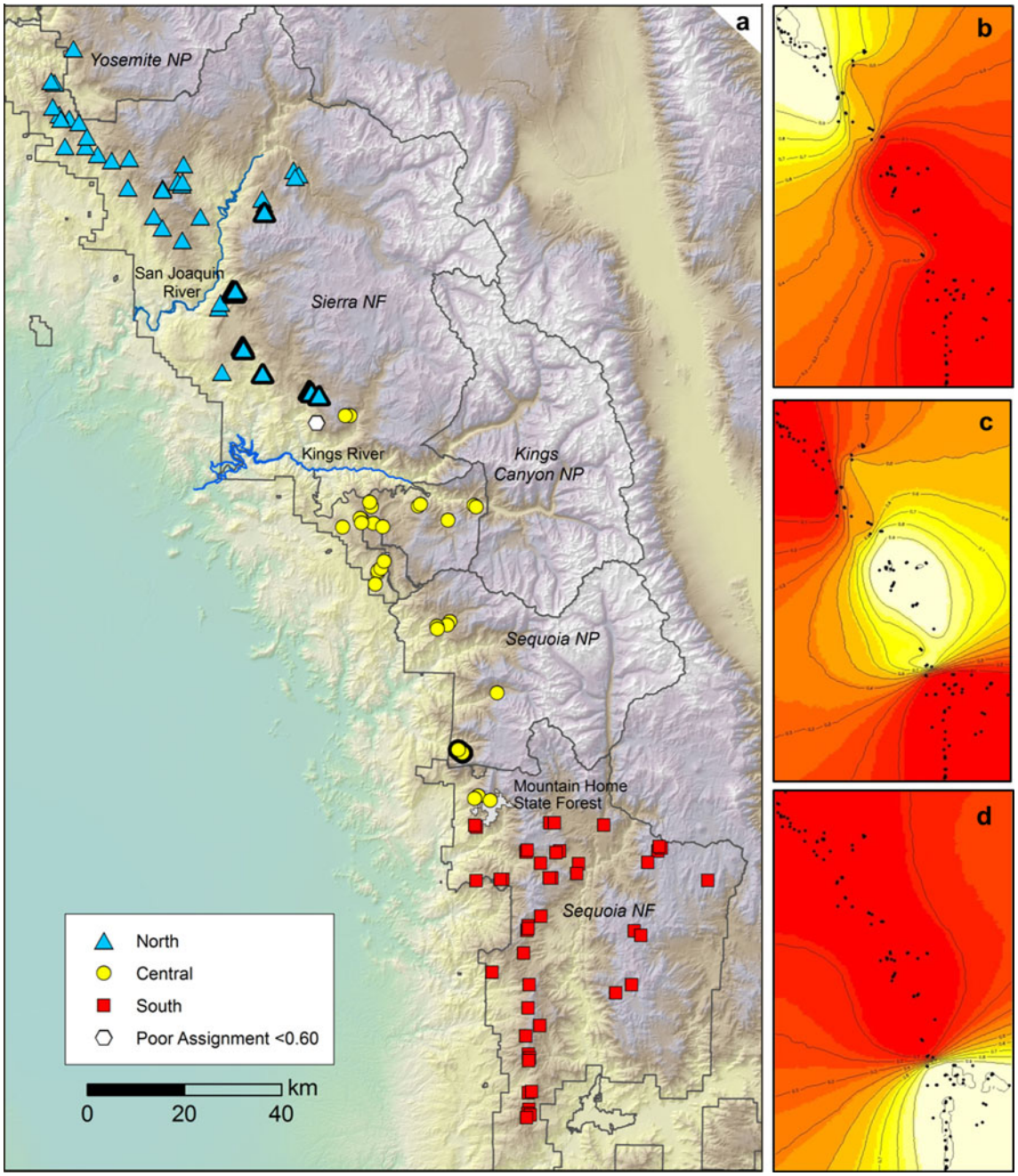

Fig. 5 **a** Map showing the assignment of individuals to each of the identified genetic clusters using GENELAND for the uncorrelated model ($K = 3$). Individuals that assigned with a probability of <0.80 to any one population are highlighted in black. **b**–**d** Maps showing the posterior probabilities of cluster membership to **b** North, **c** Central, and **d** South genetic groups: individuals in areas with *white shading* indicate fisher that had a high probability of assignment to that genetic group

the 14 individuals that assigned with relatively low probability (0.60–0.80) were found in the southern portion of the North population, between the San Joaquin and King River (Fig. 5a). The value of H_E was significantly lower at a 0.1 significance level in the North group than the Central and South. There was no significant difference between groups in A_R. (Table 1).

The correlated model in GENELAND found $K = 6$ in the majority of simulations, with a minority of simulations finding $K = 5$ (Fig. 4b). The proportion of simulations showing $K = 5$ decreased with increasing spatial uncertainty (1,000 m = 20 %, 2,000 m = 10 %, 5,000 m = 5 %). The correlated model showed similar genetic clustering as the uncorrelated model in the South and Central

Table 1 Expected heterozygosity (H_E), F_{IS}, and allelic richness (A_R), of the North, Central, and South genetic groups and the total population

Group	*n*	H_E	F_{IS}	A_R
North	44	0.474	0.043	2.78
Central	32	0.552	0.061	2.80
South	51	0.561	0.024	2.95
Entire SSN	127	0.565	0.101	3.04

areas, but subdivided the North group into four smaller clusters (Fig. 6). Pairwise F_{ST} values between the Central and the South group remained the same, but values between the Central group and the four North subgroups varied considerably ranging from moderate (0.042) to very high (0.169) (Table 2). However, the probability of assignments to three of these four North subgroups (Fig. 6: North 2–4) was very low >0.60 with a great deal of admixture between these clusters. The exception was the northernmost subgroup (Fig. 6: North-1) in which all but two individuals assigned with >0.90 probability.

Hierarchical analysis

Mantel tests for IBD were non-significant within each of the identified subpopulations for K = 3 and K = 6. For K = 3, there was no significant spatial autocorrelation found in the Central cluster, and relatively weak but significant spatial autocorrelation up to 21 km in the North, and up to 12 km in the South (Fig. 2). For K = 6, in which additional groupings were found within the North cluster, the sample sizes in two of the four northern groups were too small to permit further analysis (Fig. 6: North-2, North-3) and the other two did not show any significant spatial autocorrelation. No additional population subdivision was detected by either STRUCTURE or GENELAND within the North, Central or South clusters.

Discussion

Population subdivision

We found the southern Sierra Nevada population to have a moderate amount of genetic subdivision that appears to be associated with a number of geographic features or administrative areas including Little Shuteye Peak, the San Joaquin River, Kaiser Wilderness, Kings River Canyon and the Mountain Home Demonstration State Forest (Fig. 6). The most consistently detected genetic clusters, found in both STRUCTURE and GENELAND models, were three clusters with boundaries associated with the Kings River, and Mountain Home Demonstration State Forest. Results of this study contrast with Wisely et al. (2004) in the amounts of genetic subdivision; our results indicate areas of resistance to gene flow rather than major barriers, as evidenced by moderate F_{ST} values and the detection of a number of highly admixed (q = 0.60–0.80) individuals between populations. During the four year study period we detected very limited movement among recaptured individuals with the majority of recaptures either at the same or adjacent sample units, possibly indicating that long distance movements are relatively rare and that effective dispersal distance is likely much less than maximum dispersal capability (Kyle et al. 2001).

The highest levels of subdivision were found between a number of small genetic clusters north of the Kings River that were detected only by the correlated model in GENELAND. The strongest genetic clustering was north of Little Shuteye Peak (Fig. 6: North-1) to which individuals assigned with high probability. F_{ST} values between this subgroup (North-1) and the other three North subgroups ranged from 0.137 to 0.164. This is a surprising amount of subdivision considering the North-1 group is within 30 km of the other four northern subgroups. However, based on low assignment probabilities (q < 0.60), there appears to be considerable admixture among the other three northern subgroups (Fig. 6: North 2–4). It is possible that the additional genetic subdivision detected in the North group is the result of multiple founder events within this area during a recent population expansion. The reduction in H_E in the North compared to the Central and South groups is consistent with the genetic signature expected to be generated by recent founder events (Nei et al. 1975; Hawley et al. 2006), but the lack of difference in allelic richness between the groups is at odds with this hypothesis. However, survey data supports the idea of a recent population expansion. In the 1990s surveys routinely detected fisher in the central and southern portion of the study area, but rarely in the northern portion (Zielinski et al. 1995, 2005). From 1991 to 1994 fishers were detected only once at track-plate surveys in the Sierra National Forest (which encompasses the entirety of the North genetic group) whereas this study detected 44 individuals within this area. From 1996 to 2002 only two fishers were detected in Mariposa and Madera counties within the North genetic group (Zielinski et al. 2005), while this study detected 25 individuals from these same two counties.

Compared to other closely related North American mustelids such as the wolverine (*Gulo gulo*) and American marten (*M. americana*), fisher have been found to have high genetic structure. Studies of wolverine and marten have shown little genetic divergence among populations in the northern portions of their ranges (wolverine global F_{ST} = 0.04, marten global F_{ST} = 0.02; Kyle et al. 2000, 2002, Kyle and Strobeck 2001, 2003). In comparison,

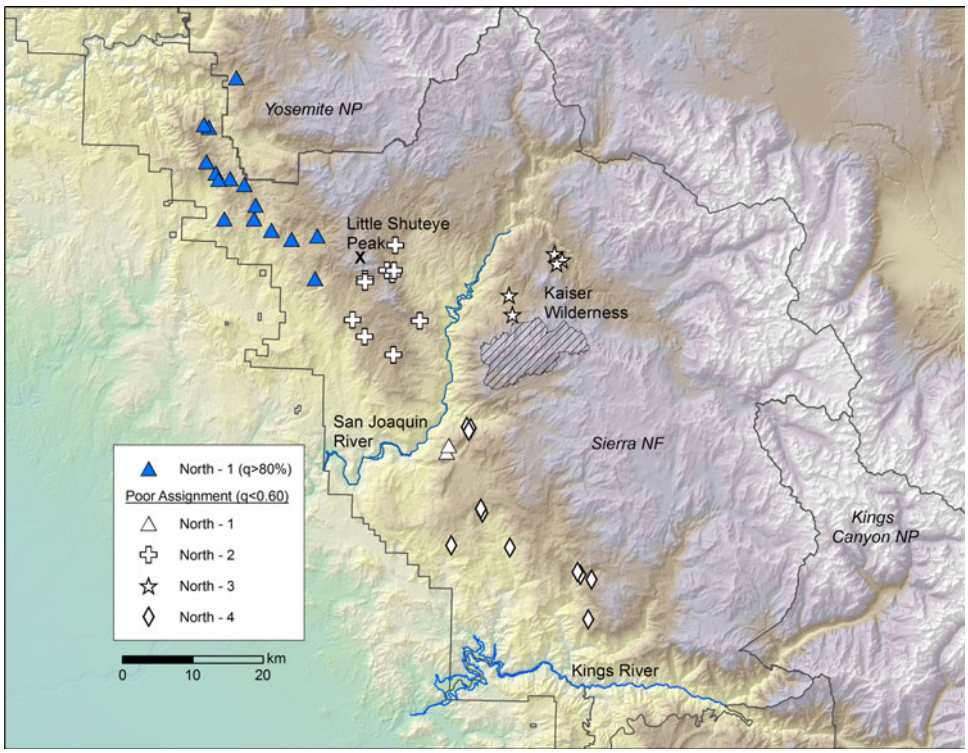

Fig. 6 Map showing the modal population assignment of individuals to each of the identified genetic subgroups within the North population using the correlated model in GENELAND. Individuals that assigned poorly ($q < 0.60$) are shown in *white*

fisher populations across Canada were found to have a much higher global $F_{ST} = 0.136$ (Kyle and Strobeck 2001). The greater subdivision found in fisher compared with wolverine is unsurprising given wolverine's ability for long distance dispersal (Gardner et al. 1986; Copeland 1996) but the greater subdivision in comparison to marten is more unexpected considering that martens have smaller dispersal distances than fisher (Broquet et al. 2006; Aubry and Raley 2006). The difference in genetic divergence between these species may indicate that fishers' habitat requirements for gene flow are more specific than for martens, or are the result of smaller effective population sizes and therefore increased genetic drift.

Isolation by distance

Isolation by distance can confound the assessment of population subdivision by creating spurious signals of population structure (Schwartz and McKelvey 2009; Meirmans 2012). But the converse can also occur where hierarchical population structure can produce a false signal of IBD (Meirmans 2012). We detected IBD across the entire southern Sierra Nevada fisher population with significant Mantel tests and long distance positive spatial autocorrelation between individuals up to 70 km. IBD has been reported in other fisher populations across its range in both individually based analyses (Hapeman et al. 2011 $r_{Mantel} = 0.19$) and population based analyses (Kyle et al. 2001 $r_{Mantel} = 0.75$; Carr et al. 2007 $r_{Mantel} = 0.38$; Garroway et al. 2008 $r_{Mantel} = 0.44$) with the magnitude of Mantel's r varying considerably across studies. The magnitude of IBD found in this study ($r_{Mantel} = 0.25$) is near the low end of this range and similar to the magnitude of IBD reported in the individually based Hapeman et al. (2011) study.

Table 2 F_{ST} values for the population assignments identified in the GENELAND correlated frequencies model

	North-1	North-2	North-3	North-4	Central
North-1	–				
North-2	**0.137**	–			
North-3	**0.164**	0.023	–		
North-4	**0.138**	**0.079**	**0.055**	–	
Central	**0.169**	**0.096**	0.042	**0.056**	–
South	**0.198**	**0.104**	**0.074**	**0.137**	**0.054**

Values significantly different from zero at $p < 0.05$ are indicated in bold

However, Mantel tests for IBD within each cluster were non-significant. Furthermore, spatial autocorrelation was detected in only two of the three clusters and this autocorrelation was only over small distances (12–21 km). This indicates that gene flow is relatively spatially unrestricted within clusters and that the IBD signal detected across the entire population is likely created by population subdivision. These results support the idea that the genetic clusters

identified reflect real population subdivision and are not a spurious result generated by IBD.

Factors contributing to the assessment of population subdivision

Similar to Wisely et al. (2004) we detected a subpopulation break in the area of the Kings River, but we detected a much lower amount of population subdivision. Based on the magnitude of our F_{ST} estimates the Kings River Canyon does not appear to be a major barrier to gene flow. The main difference between the studies which likely accounts for the quantitative difference in F_{ST} values is the sampling design (see below).

Sampling design

The difference in the results here and Wisely et al. (2004) is primarily attributable to (1) the geographic location of the samples available and (2) the possible sampling of close relatives. The influence of sampling design in the analysis of population structure has been addressed in a number of previous studies which have found that sampling can have a large impact on results (Rosenberg et al. 2005; Schwartz and McKelvey 2009; Frantz et al. 2009). Sampling at a small scale will cause estimates of between group differentiations to be overestimated by minimizing within group variation and emphasizing between group variation (Schwartz and McKelvey 2009). To minimize this error, genetic samples should be representative of the entire population by including samples across the geographical range. The samples used for the Wisely et al. (2004) study were from two relatively small and geographically disparate areas within the southern Sierra Nevada range ($\sim$98 km apart) and we would expect such clustered sampling to result in higher estimates of subdivision than a more continuously distributed sample.

The majority of samples in Wisely et al. (2004) were from two very small areas: 12/14 samples in the north and 17/19 of the samples in the south were collected from within 87.1 and 49.9 km^2 areas respectively (minimum convex polygon area of sample locations). Considering home range sizes of fisher in the southern Sierra Nevada (Zielinski et al. 2004) the Wisely et al. (2004) samples are likely an almost complete census of individuals within each area. Fishers have been shown to have male-biased dispersal and female philopatry with mean dispersal distances of males found to be five times greater than that of females (Aubry et al. 2004; Aubry and Raley 2006). Consequently, the dense sampling of individuals from these small areas likely had a high degree of relatedness, especially among females, resulting in an inaccurate estimate of allele frequencies compared to the overall population.

Sample size can influence the assessment of population subdivision with the sample size required to precisely estimate F_{ST} being dependent on the amount of subdivision present (Kalinowski 2005; Yang et al. 2005). However, large sample sizes are only required to precisely estimate F_{ST} when the amount of subdivision between populations is very low (Kalinowski 2005). Considering that the amount of subdivision detected between genetic groups in this study was moderate (0.054–0.127) and high (0.51) in Wisely et al. (2004), the smaller sample size used by Wisely et al. (2004) did not likely contribute significantly to the difference in results between the studies.

Genetic diversity of loci

The amount of genetic variation within loci can also influence estimates of subdivision. The maximum F_{ST} value is directly related to the heterozygosity (H_E) of markers such that the maximum $F_{ST} = 1 - H_E$ (Hedrick 1999). Consequently, when using loci with higher heterozygosity the maximum possible F_{ST} value is lower. The eight loci examined by Wisely et al. (2004) were developed in stoats (*Martes ermina*) and marten (*Martes americana*). These loci had extremely low variability in the southern Sierra Nevada fisher population likely due to ascertainment bias (Ellegren et al. 1995; Cooper et al. 1998), with H_E values of 0.16 and 0.20 north and south of the Kings River respectively and some loci fixed in the Sierra Nevada population. In 2007, a new suite of microsatellite loci were developed for fisher in California which have a much higher diversity (Jordan et al. 2007). Consequently, the lower F_{ST} detected in this study could result from a decrease in maximum possible F_{ST} due to the increased heterozygosity of the markers ($H_E = 0.56$). We calculated G'_{ST} according to Hedrick (2005) which standardizes F_{ST} by sample heterozygosity. The estimates of divergence were still very different (G'_{ST} [Wisely et al. 2004] = 0.76, G'_{ST} [this study] = 0.31) and thus differences in heterozygosity of the loci used only partially account for the difference in the results.

Considerations for population subdivision analyses

While the ΔK and maximum likelihood methods in STRUCTURE yielded different values of $K = 2$ and $K = 3$ a number of factors indicate that $K = 3$ better reflects the genetic population structure of this population. We found a lower mean α for $K = 3$ indicating individuals assigned with more certainty to each population compared to when $K = 2$. The variance in α was much lower for $K = 3$ than $K = 2$ which is indicative that $K = 3$ better represents the true population structure (Pritchard et al. 2000). Additionally, the STRUCTURE population

assignments for $K = 3$ agreed with those from the uncorrelated GENELAND model which also found $K = 3$.

An important consideration in attributing population subdivision to landscape features is the temporal dynamics between the two factors. Landguth et al. (2010) found there were lag times between either the establishment or removal of a genetic barrier and the detectability of the resulting genetic structure. Depending on the dispersal and movement characteristics of a species it can take tens to hundreds of generations until the genetic data reflects either the appearance or loss of a barrier. Consequently, it can be difficult to discern whether the observed subdivision is due to historical or contemporary landscape elements. This problem is minimized for species with relatively long distance dispersal. Landguth et al. (2010) found using simulations that it takes less than 10 generations to lose 50 % of the barrier signal if maximum dispersal distance is >30 km. Considering the maximum recorded dispersal distance for fisher is ~100 km (York 1996) the population subdivision observed in this study is likely attributable to relatively recent landscape conditions rather than historical conditions. However, considering fisher's generation interval is approximately five years, the observed structuring may be the result of landscape conditions over the last few decades rather than current conditions.

Conclusions

We found that the southern Sierra Nevada fisher population is not characterized by high subdivision as previously thought. This landscape can be characterized as having areas that are resistant to gene flow but without major barriers. However, the limited movement distances we found among individuals recaptured across multiple years suggest that long distance movements may be uncommon in this population. We found the genetic subpopulations to be connected by moderate amounts of gene flow that may actually help to counteract the effects of genetic drift due to small population size and help maintain genetic diversity within the southern Sierra Nevada population over time. Perhaps most importantly, this study provides an empirical example of the influence that sampling can have on population genetic analyses.

While the magnitude of subdivision we detected was different between studies, both studies indicate that gene flow in fishers may be sensitive to landscape features. Maintaining connectivity within this population will rely on determining what specific landscape elements are acting to restrict gene flow within the population. Identifying these landscape features is critical to prevent creation or expansion of anthropogenically influenced landscape elements that may further restrict gene flow and to plan for shifts in connectivity due to predicted changes in the landscape from climate change.

The comparison between these two studies, and the realized differences between their results and associated conservation implications, provides a clear example of the need to reassess other early genetic studies for species of conservation concern. Technological advances in laboratory analysis make marker development less expensive and easier, and the advent of new analytical methods in the emerging field of landscape genetics allow for more quantitative analyses of landscape features. These advances, combined with the ability to noninvasively collect genetic samples of populations on a large scale, allow the next generation of conservation genetic work to obtain a clearer picture of a species' population structure than was previously possible. As this comparative study shows, such a reexamination can have important implications in the management and conservation of a species.

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