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Identification of source-sink dynamics in mountain lions of the Great Basin

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Abstract

Natural and anthropogenic boundaries have been shown to affect population dynamics and population structure for many species with movement patterns at the landscape level. Understanding population boundaries and movement rates in the field for species that are cryptic and occur at low densities is often extremely difficult and logistically prohibitive; however genetic techniques may offer insights that have previously been unattainable. We analysed thirteen microsatellite loci for 739 mountain lions (*Puma concolor*) using muscle tissue samples from individuals in the Great Basin throughout Nevada and the Sierra Nevada mountain range to test the hypothesis that heterogeneous hunting pressure results in source-sink dynamics at the landscape scale. We used a combination of non-spatial and spatial model-based Bayesian clustering methods to identify genetic populations. We then used a recently developed Bayesian multilocus genotyping method to estimate asymmetrical rates of contemporary movement between those subpopulations and to identify source and sink populations. We identified two populations at the highest level of genetic structuring with a total of five subpopulations in the Great Basin of Nevada and the Sierra Nevada range. Our results suggest that source-sink dynamics occur at landscape scales for wide-ranging species, such as mountain lions, and that source populations may be those that are under relatively less hunting pressure and that occupy refugia.

Keywords: geneflow, Great Basin, metapopulation, microsatellite, population structure, *Puma concolor*, source-sink dynamics

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Introduction

Natural geographic features, such as mountains and rivers, are known to affect the population structure of plants and animals (Slatkin 1987). In arid western North America, mountain ranges, desert valleys and expansive barren playa surfaces likely represent barriers to movement even for wide ranging fauna, such as large carnivores (Pierce & Bleich 2003). Habitat destruction, fragmentation and the presence of anthropogenic physical barriers, such as roads, also can affect movement and population dynamics of animals (Sih *et al.* 2000; Carroll *et al.* 2001; Frankham 2006). Many species also are affected by laws, management practices and other nuances of society that are unrelated to physical barriers. Harvest is one aspect of management that clearly has the potential to affect population dynamics of animals (Stoner *et al.* 2006; Cooley *et al.* 2009b; Packer *et al.* 2009; Creel & Rotella 2010). At the extreme end of this practice, bounty hunting and predator control are currently used in an effort to reduce population

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densities or even extirpate some species from specific areas, and were used in the past to extirpate them over extensive geographic areas (Berger 2006; Packer *et al.* 2009). Conversely, some species are protected, including species listed as threatened or endangered, and others that are protected from harvest. Anthropogenically imposed boundaries, such as state lines or management areas within a state, may result in instances where the same species is harvested on one side of the boundary, yet enjoys full protective status on the other side, a situation with clear potential for impacting movement patterns and population dynamics.

The concept of source-sink population dynamics was advanced by Pulliam (1988) who argued that differences in habitat quality leads to differences in birth and death rates among populations or subpopulations. In source populations where habitat quality is high, birth rates are greater than death rates and excess individuals leave the population as emigrants (Pulliam 1988). In contrast, in sink populations where habitat quality is low, death rates exceed birth rates and the population would decline towards extinction, unless 'rescued' by immigration from surrounding source populations (Pulliam 1988). Source and sink populations may be identified based on differences between emigration and immigration rates, with source populations being net exporters of individuals whereas sink populations are net importers of individuals (Pulliam 1988; Hanski & Simberloff 1997; Kawecki 2004). Although source and sink populations are typically compared in terms of relative habitat quality and consequential disparities in productivity and mortality, anthropogenic sources of mortality such as harvest, have been shown to result in source-sink dynamics when variable across the landscape (Novaro *et al.* 2005; Stoner *et al.* 2006; Beckmann & Lackey 2008; Robinson *et al.* 2008; Cooley *et al.* 2009a, b). In addition, if dispersing individuals select habitat patches of high apparent quality with high human-caused mortality, attractive sinks are created (Remeš 2000; Delibes *et al.* 2001; Novaro *et al.* 2005; Stoner *et al.* 2006; Beckmann & Lackey 2008; Robinson *et al.* 2008; Cooley *et al.* 2009b). When sink habitats are attractive to dispersers, the stability of the larger population comprising the source-sink system is particularly sensitive to changes in the proportion of sinks across the landscape (Delibes *et al.* 2001; Novaro *et al.* 2005). Moreover, although sinks can maintain large population sizes when immigration is high (Van Horne 1983; Pulliam 1988; Robinson *et al.* 2008), sinks can destabilize the system if sources are unable to sustain the continual drain of individuals imposed on them (Delibes *et al.* 2001; Kawecki 2004).

The state of Nevada, with 314 distinct mountain ranges separated by arid desert valleys, offers the most extensive example of basin and range topography in western North America (McLane 1978). Mountain lions (*Puma concolor*) are apex predators in Nevada's mountain ranges, but desert valleys separating these ranges impose an insular effect that yields patchily distributed habitats. In addition to geographic factors that affect populations, harvest pressure on mountain lions varies considerably throughout the state because of accessibility as well as hunting prohibitions in several large areas of the state. Furthermore, with the exception of depredation hunts by management officials, mountain lions are fully protected from hunting in the neighbouring state of California (Pierce & Bleich 2003).

An increasing number of demographic studies suggest that source-sink dynamics occur where immigration of mountain lions from lightly hunted source populations plays a critical role in the stability of sink populations under relatively greater hunting pressure (Sweanor *et al.* 2000; Logan & Sweanor 2001; Stoner *et al.* 2006; Robinson *et al.* 2008; Cooley *et al.* 2009a,b). In many areas it is not logistically feasible, however, to examine mountain lion population structure and movement rates in the field at the scale at which source–sink dynamics operate. Recent advances in multilocus Bayesian genetic techniques allow the estimation of population genetic structure and movement rates necessary to model source–sink dynamics operating at large spatial scales.

Genetic methods have been employed to identify genetic structure of mountain lion populations over the last decade with mixed results. Although up to half of females in some populations disperse, males are obligate dispersers (Logan & Sweanor 2001). As long distance dispersal >100 km in mountain lions is frequent (Beier 1995; Sweanor *et al.* 2000; Logan & Sweanor 2001) with reports of straight line dispersal distances up to 1067 km (Thompson & Jenks 2005), potential population structure may be limited (Frankham 2006). Indeed, a number of genetic studies failed to find structuring of mountain lion populations (Sinclair *et al.* 2001; Anderson *et al.* 2004). Nonetheless, several studies have found sub-structuring of mountain lion populations where habitat is less contiguous, likely resulting from natural or anthropogenic discontinuities of the habitat (Ernest *et al.* 2003; McRae *et al.* 2005; Loxterman 2011).

Although source and sink populations have been identified using genetic techniques for reptiles (Manier & Arnold 2005; Howes *et al.* 2009), amphibians (Martinez-Solano & Gonzalez 2008), fish (Hänfling & Weetman 2006) and small mammals (O'Keefe *et al.* 2009) at relatively small spatial scales, a recent review of landscape genetics concluded that the number of

studies addressing complex ecological questions at large spatial scales, such as source-sink dynamics, was surprisingly limited (Storfer *et al.* 2010). This research is one of the first efforts that we are aware of that examines source and sink population dynamics for a large carnivore at large spatial scales using a genetic approach. We hypothesized that desert basins limit the movement of mountain lions resulting in genetically distinct subpopulations linked through movement of individuals. In addition, we hypothesized that unequal harvest pressure throughout Nevada and between Nevada and California would result in source-sink dynamics identifiable through asymmetric rates of movement between interacting subpopulations. Accordingly, we predicted (i) mountain lion populations would be structured along the many north-south mountain ranges in Nevada and (ii) California and those areas throughout Nevada where hunting is limited would be identified as source populations.

Methods

We used Bayesian multilocus assignment methods to first identify genetically distinct mountain lion populations. These methods allow individuals to be grouped based on their genotypes without a priori delineation of populations. We then used a Bayesian multilocus genotyping method to estimate asymmetrical rates of movement between identified subpopulations. Source populations were identified as net exporters of mountain lions whereas sink populations were considered net importers following Pulliam's (1988) definition which we use throughout this article.

Sampling and DNA extraction

We obtained tissue samples from mountain lions in Nevada ($n = 709$) and eastern California within 150 km of Nevada ($n = 30$) from animals that that had been live captured for research, harvested by hunters (Nevada only), harvested for depredation, or had died because of other causes. Muscle tissue samples were taken from all mountain lions harvested in Nevada by Nevada Department of Wildlife personnel during a required check-in within 72 h of the time the animal was harvested. Samples were collected from Nevada between 2004 and 2010 and from California between 2008 and 2010. Sample locations were obtained from hunters and recorded by NDOW at the time of check-in. Samples were stored frozen until DNA was extracted. DNA was extracted using Qiagen DNeasy® Blood & Tissue extraction kits according to manufacturer's protocol.

Microsatellite analysis

Thirteen microsatellite loci were amplified with primers developed specifically for mountain lions by Kurushima *et al.* (2006; Table 1). Loci were amplified using a single-nested polymerase chain reaction (PCR) method using forward primers with fluorescently labelled M13(-21) attached to their 5′ ends (Schuelke 2000). Reverse primers were 'PIG-tailed' to improve genotype scoring (Brownstein *et al.* 1996). We performed five multiplex reactions for each individual and conducted fragment analyses on PCR products at the Nevada Genomics Center using an Applied Biosystems (ABI) 3730 DNA Analyzer and associated GENEMAPPER software (version 3.7). We genotyped individuals using GENEMAPER, checked for genotyping errors using MICROSATELLITE TOOLKIT version 3.1.1 (Park 2001), and tested for null alleles, large allele drop-out, and genotype scoring errors associated with stutter using MICRO-CHECKER version 2.2.3 (van Oosterhout *et al.* 2004).

Genetic clustering analyses

We assessed genetic population structure across the landscape using Bayesian genotype assignment analyses. Use of both non-spatial and spatial approaches to examine the same dataset has been suggested to validate results (Chen *et al.* 2007). To this end, we used a combination of non-spatial (STRUCTURE software: Pritchard *et al.* 2000; Falush *et al.* 2003) and spatial (TESS software: Chen *et al.* 2007; Durand *et al.* 2009b) model-based Bayesian clustering techniques to probabilistically assign q individuals to k populations (where k is

Table 1 Locus name, number of alleles for each of the five populations assigned by TESS, and total number of alleles for 13 loci analysed for 739 mountain lions. Central ($n = 110$), West ($n = 155$), North ($n = 208$), South ($n = 76$), and East ($n = 190$)

Locus	Central	West	North	South	East	Total Alleles
PcoB316w	3	4	3	4	3	4
PcoC010w	3	3	3	3	3	3
PcoB010w	5	7	6	5	6	8
PcoC209w	3	3	3	4	4	4
PcoA106w	3	4	3	3	4	5
PcoD012w	3	5	3	4	4	5
PcoB210w	7	7	7	5	7	7
PcoC112w	4	5	4	4	4	5
PcoB203w	3	5	3	4	5	6
PcoC108w	3	4	3	3	3	4
PcoA208w	4	4	4	4	4	4
PcoD217w	4	5	4	3	3	5
PcoB207w	3	6	5	3	4	6

unknown). These methods assign individuals to populations and do not require subjective delineation of populations a priori (Pritchard *et al.* 2000; Chen *et al.* 2007; Durand *et al.* 2009b; Francois & Durand 2010).

We used the program STRUCTURE (Pritchard *et al.* 2000; Falush *et al.* 2003) first to evaluate population genetic structure without consideration of geographic locations of samples. We used the admixture model and allowed for correlated allele frequencies (Falush *et al.* 2003). We ran STRUCTURE with a burn-in period of 100 000 Markov chain Monte Carlo (MCMC) generations followed by 200 000 iterations for $k = 1$ through $k = 10$ with ten replicates for each k. We evaluated the logarithm of the probability of the data ($\ln P(D \mid K)$; Pritchard *et al.* 2000) and estimates of Δk (Evanno *et al.* 2005) using the program STRUCTURE HARVESTER (Earl 2009) to determine the most likely number of distinct genetic clusters. We averaged each individual's admixture proportions over the 10 replicates for the best k using program CLUMPP (Jakobsson & Rosenberg 2007) then assigned each individual to the population for which its average inferred ancestry was greatest.

In addition to STRUCTURE, we used the program TESS 2.3.1 (Chen *et al.* 2007; Durand *et al.* 2009b) to evaluate population genetic structure across the landscape. Like the program STRUCTURE, TESS is implemented with an MCMC algorithm, but uses the geographic coordinates of the samples as prior information (Durand *et al.* 2009b; Francois & Durand 2010). We ran TESS, with the geographic distance option, initially with the no-admixture model to estimate an upper bound on the number of distinct genetic clusters, as recommended by Durand *et al.* (2009a). We ran the model for 200 000 iterations after a burn-in period of 100 000 iterations for $k = 2$ through $k = 10$ with ten replicates for each k. To identify the most likely k, we plotted the deviance information criterion (DIC; Spiegelhalter *et al.* 2002) computed by TESS against k and chose the k that corresponded to the plateau of the DIC curve (Durand *et al.* 2009a,b; Francois & Durand 2010). We then ran 10 replicates of the admixture model with the same parameters as above for the most likely k identified (Durand *et al.* 2009a,b) and used the program CLUMPP (Jakobsson & Rosenberg 2007) to average each individual's admixture proportion over those 10 replicates. Each individual was assigned to the genetic group for which its average inferred ancestry was the greatest.

Source-sink dynamics

To identify source and sink populations, we used the program BIMR 1.0 (Faubet & Gaggiotti 2008) to estimate recent rates of movement (while allowing for the possibility of asymmetrical rates) between the genetic groups identified with the Bayesian clustering analyses. BIMR uses the multilocus genotypes of descendents of recent migrants to infer the proportion of the population that immigrated during the last generation by measuring gametic disequilibrium generated by migration (Faubet & Gaggiotti 2008). As BIMR assumes that sampling has taken place before migration, we used the genetic assignment of individuals from the TESS analysis instead of geographically delineated groups to define populations. BIMR allows for departures from Hardy–Weinberg equilibrium (HWE) within populations and uses a model (the F-model) which allows consideration of admixture that may have taken place before the last generation of migration. The F-model improves estimation of allele frequencies when genetic differentiation is weak which allows BIMR to estimate rates of migration between populations that are weakly differentiated ($F_{ST} > 0.01$) and those that incur substantial migration rates (Faubet & Gaggiotti 2008).

We ran 20 replicates, a total of 17 020 000 iterations each. For each of the 20 replicates, we first ran each MCMC for 20 short pilot runs of 1000 iterations each, in which incremental values were tuned by the program in an effort to obtain acceptance rates between 25% and 45%. The next 15^6 burn-in iterations were also discarded for each replicate. We then collected 20 000 samples from each of the 20 replicates using a thinning interval of 100 iterations. Following Faubet *et al.* (2007) and Faubet & Gaggiotti (2008), we then chose the run with the lowest Bayesian deviance, in particular the assignment component of the total deviance (D_{assign}) calculated by BIMR, to extract parameter estimates. We examined 95% HDPIs to assess significance of asymmetry for pair-wise migration rate estimates. In addition to assessing 95% HDPIs, estimates of migration rates were examined for significant asymmetry between population pairs by examining (for each pairwise comparison) the proportion of times a given estimate was greater or less than the other population migration rate estimate at each step in the post-burn-in MCMC (Fordyce *et al.* 2011). This proportion is interpreted as the probability that a particular parameter value (migration in one direction) is higher than another value (migration in the second direction).

Descriptive statistics of TESS assigned genetic groups

We used MICROSATELLITE TOOLKIT version 3.1.1 (Park 2001) to calculate allele frequencies, allelic richness and average expected and observed heterozygosity. As uneven sample sizes can bias estimates of allelic richness, we also produced unbiased estimates by conducting rarefaction using the program HP-Rare to account for unequal sample sizes (Kalinowski 2005). FSTAT 2.9.3.2

(Goudet 2002) was used to compute all other population genetic analyses of groups that were identified using the Bayesian assignment analyses. We tested for linkage disequilibrium between all pairs of loci in each genetic group using the log likelihood ratio G-statistic (Goudet 2002). We assessed deviations from HWE within genetic groups by permuting alleles among individuals within genetic groups and used F_{IS} to compare the observed vs. randomized datasets in FSTAT (Goudet 2002). We tested for allelic and genotypic population differentiation using the log-likelihood G statistic in FSTAT. We also conducted tests of genotypic differentiation for each population pair using the overall G-statistic in FSTAT (Goudet 2002). Pairwise F_{ST} values were estimated (Weir & Cockerham 1984) to evaluate the degree of differentiation between genetic groups.

Population bottlenecks

We tested for evidence that populations had experienced recent genetic bottlenecks using the program BOTTLENECK (Piry *et al.* 1999). Populations that have experienced severe reductions in effective population sizes exhibit reduced numbers of alleles and heterozygosity of loci, however alleles are expected to be lost faster than heterozygosity (Luikart & Cornuet 1998; Piry *et al.* 1999). We therefore used the program BOTTLENECK to test for heterozygosity excess using a Wilcoxon signed-rank test (Cornuet & Luikart 1996) under a two-phase model of microsatellite evolution (DiRienzo *et al.* 1994) parameterized conservatively as suggested by Gazra & Williamson (2001) with 90% single step mutations and a variance among multiple steps of 12 (Hundertmark & VanDaele 2009). We ran BOTTLENECK for 10 000 iterations. Piry *et al.* (1999) suggest that the Wilcoxon signed-rank test is the most appropriate and powerful for analysis of <20 loci. We also used the program BOTTLENECK to determine if a mode shift in the distribution of allele frequencies, which is characteristic of recent severe bottlenecks, had occurred (Luikart & Cornuet 1998).

Results

All 13 loci were polymorphic with 3–8 alleles and a mean of 5.1 alleles per locus. MICRO-CHECKER indicated, however, that locus PcoB207 had possible null alleles with consistent patterns across the landscape. PcoB207 was therefore discarded and all other loci were retained.

Genetic clustering

The Δk method we used to determine the number of distinct genetic clusters from the STRUCTURE analysis

identified two populations at the highest level of genetic structuring with a total of five subpopulations at the lowest levels of substructure (Figs 1A and 2). Five genetic clusters were also identified by lnP(D|K) as the most likely k (Fig. 1B). The DIC scores from the no-admixture model implemented in TESS suggested that
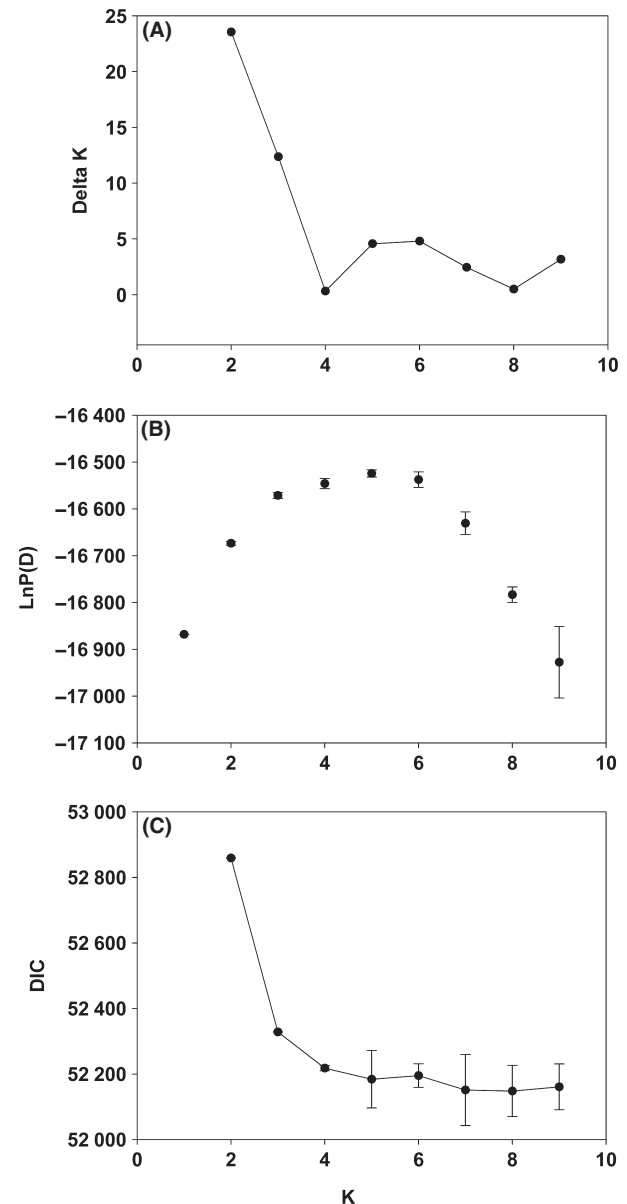

Fig. 1 (A) Delta k (Δk) of Evanno *et al.* (2005) across 10 replicates of STRUCTURE, where $k = 2$ is shown as the best fit of the data for the highest level of hierarchical genetic structure followed by $k = 3$, and $k = 5$ at lower levels of structuring. (B) The mean lnP(D|K) and SD of 10 replicates of STRUCTURE runs for each k where the model of $k = 5$ is indicated as the best fit. (C) The deviance information criterion (DIC) scores computed by the TESS no-admixture model plotted against k, where $k = 4$ is indicated as the model that best fits the data.
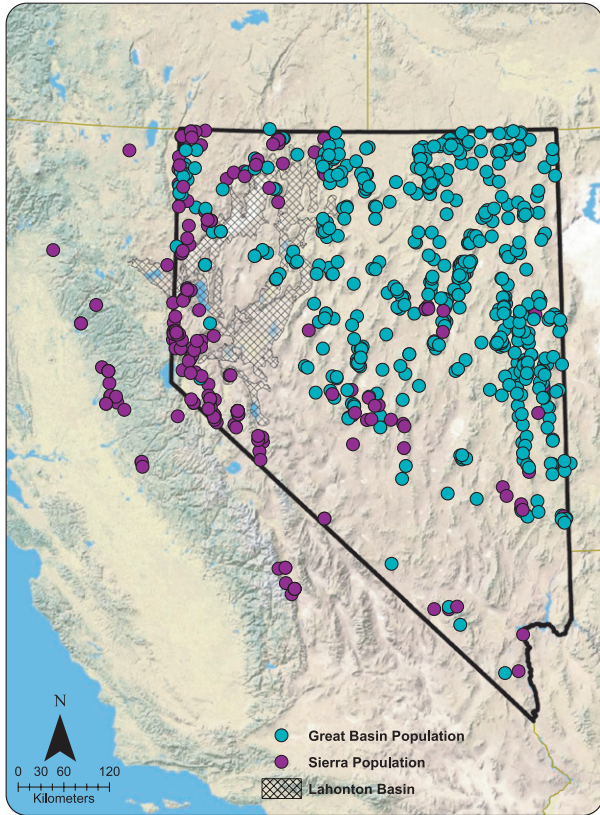
Fig. 2 Map illustrating mountain lion sample locations and the two main populations associated with the Sierra Nevada range and the Great Basin as assigned by TESS clustering. Samples were collected between 2004 and 2010 for Nevada and between 2008 and 2010 for California.

there were four distinct genetic clusters. We observed comparable patterns of genetic clusters across the landscape from the spatial and non-spatial Bayesian assignment analyses run with $k \leq 3$ (Fig. 3A, B). Although roughly similar patterns across the landscape could be discerned by both STRUCTURE and TESS at lower levels of population structure, TESS provided much more distinct

populations at $k = 4$ and $k = 5$ than did STRUCTURE (Fig. 3C). Those five genetic groups assigned by TESS, corresponding to the Sierra Nevada mountain range and western Nevada, northern Nevada, central Nevada, eastern Nevada and southern Nevada were therefore used for subsequent analyses (Fig. 4).

Source-sink dynamics

We initially encountered difficulty obtaining efficient parameter mixing with the program BIMR, and subsequently removed one locus at a time to determine if mixing issues were loci dependent. Removing loci PcoD217w, PcoB010w and PcoB210w resulted in efficient mixing and were therefore excluded from BIMR analyses. Mean migration rates were very consistent across 16 of the 20 BIMR runs with the lowest Bayesian deviances (difference in means across those 16 runs: average = 1.72, min = 0.08, max = 5.3). The run with the lowest Bayesian deviance (D_{assign}), indicated mean migration rates between the five populations ranged from a low of 1.4% with almost no migration into the North population from the West population, to a high of 39.7% (proportion of the population that immigrated within the last generation) from the South population to the East population (Table 2). We identified significant asymmetric movement from the South population into the East population (no overlapping 95% HDPIs; Table 2 and Fig. 4). Although the 95% HDPIs overlapped for all other pairwise estimates, we observed evidence of asymmetrical movement from the East into the North population ($P = 0.0001$), from the Central to the West ($P < 0.01$), and into the Central population from the North population ($P < 0.05$; Table 2). The South population was identified as the largest net provider of immigrants, indicating it was the most substantial source population, whereas the West population had the largest net immigration indicating it was the largest relative sink population (Fig. 5).
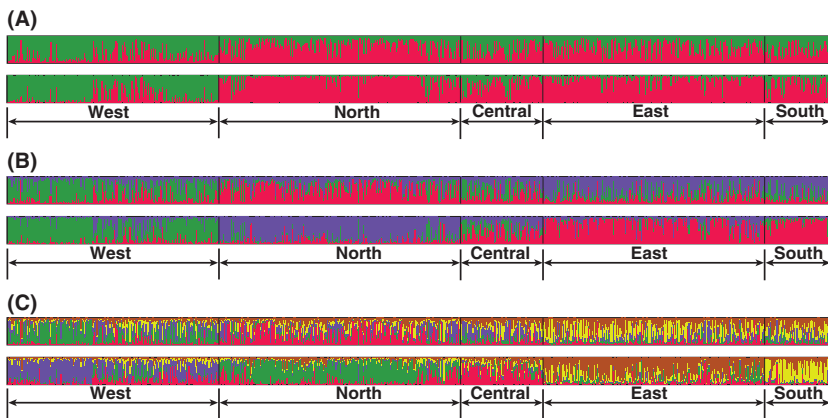

Fig. 3 Bar plots from STRUCTURE (top) and TESS (bottom) for (A) $k = 2$, (B) $k = 3$ and (C) $k = 5$.
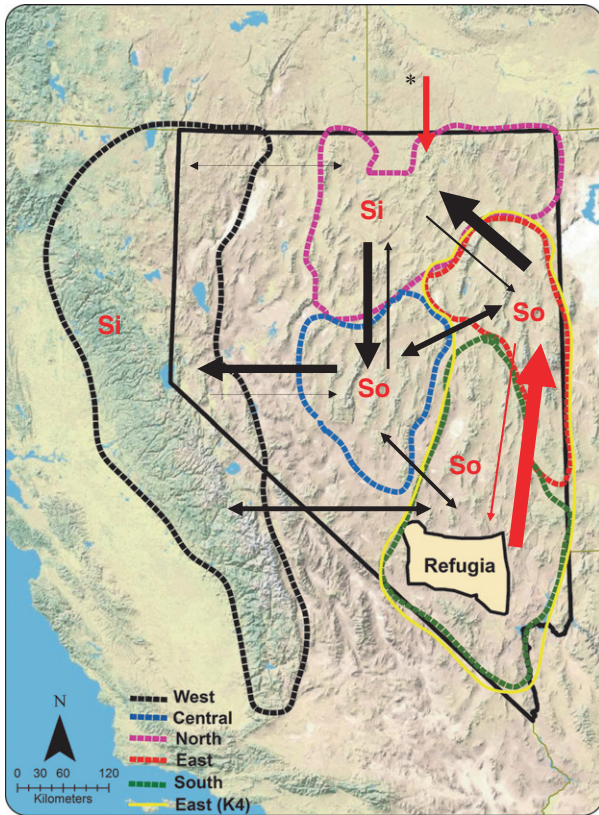
Fig. 4 Genetic populations and migration rates at $k = 5$. Polygons represent roughly delineated populations for ease of interpretation. Arrows indicate direction and rate (thickness) of recent migration rates estimated with BIMR. Pairwise estimates with non-overlapping 95% HDPIs indicating significant asymmetry in migration are indicated with two unidirectional red arrows. Pairwise estimates showing significance based on the Fordyce *et al.* (2011) method are indicated with two unidirectional black arrows. Non-significant asymmetry of migration rates are represented with double headed black arrows. Source (So) populations are net exporters of mountain lions whereas sink (Si) populations are net importers of individuals. Samples were collected between 2004 and 2010 for Nevada and between 2008 and 2010 for California. *Migration rate estimate between Idaho and Nevada from Loxterman (2011).

Descriptive statistics of TESS assigned genetic groups

After Bonferroni correction for multiple comparisons, none of the pairwise tests for linkage disequilibrium were significant suggesting that loci were unlinked. Similarly, none of the tests for Hardy–Weinberg departures were significant after Bonferroni correction. Average expected heterozygosity ranged from 0.50 in the East and Central to 0.57 in the South population (Table 3). The total number of alleles ranged from 45 in the Central population to 56 in the West population whereas the average number of alleles per locus (after rarefaction) ranged from 3.8 in the Central, North and South populations to 4.7 in the West population

(Table 3). Mountain lions from the five genetic groups identified by TESS differed in both allele and genotype frequencies. The null hypotheses of uniform allelic and genotype frequencies were rejected for all populations ($P < 0.001$) and all population pairwise tests ($P < 0.0001$). All population pairs were significantly different at the 1% nominal level after Bonferonni correction for multiple comparisons. Pairwise F_{ST} values ranged from 0.05 between several populations to 0.09 between the West and North populations (Table 4). Although F_{ST} values differed slightly from those values when only the sub-set of nine loci were used (Table 4), the three test results for population differentiation were the same.

Population bottlenecks

When assessed with the Wilcoxon signed-rank test, the South population showed significant heterozygote excess after Bonferroni correction for multiple comparisons ($P = 0.007$) which is characteristic of populations that have gone through a recent bottleneck. None of the five populations showed evidence of a mode shift that is often found in populations that have undergone recent severe bottlenecks.

Discussion

Genetic structure

Results from both the model-based Bayesian assignment analyses and descriptive statistics support our hypothesis that mountain lion populations in our study area exhibit genetic structure. We observed a total of five genetically distinct subpopulations occurring in two main populations associated with the Sierra Nevada range and the Great Basin. As we predicted, mountain lion populations in Nevada are structured around mountain ranges in a generally north-south direction indicating that genetically effective movement and dispersal patterns most often follow the topography of the numerous mountain ranges that are separated by desert basins. This north-south structure is particularly evident in the West, South and East populations and at $k = 4$ (Fig. 4). The North population may be the exception to this hypothesis because it is the only population that extends further to the east and west than the north and south, however, the North population contains mountain ranges with more east–west directionality than the rest of the state (Fig. 4).

The Lahontan Basin, a basin that corresponds to the Pleistocene Lake Lahontan and is now dominated by three vast desert playas, appears to be the major barrier responsible for limiting movement between the two main populations (Fig. 2). Similarly, barriers limiting

Into/From	Central	East	North	South	West
	Mean/mode/95% HDPI				
Central	0.641	0.086	0.212[a]	0.043	0.018[b]
	0.644	0.048	0.211	0.011	0.005
	[0.426; 0.877]	[0.008; 0.339]	[0.023; 0.490]	[0.014; 0.302]	[0.006; 0.163]
East	0.161	0.390	0.027[c]	0.397[d]	0.025[b]
	0.164	0.392	0.010	0.403	0.011
	[0.023; 0.375]	[0.171; 0.566]	[0.001; 0.148]	[0.191; 0.577]	[0.002; 0.141]
North	0.041[a]	0.367[c]	0.525	0.054	0.014
	0.024	0.381	0.535	0.024	0.004
	[0.007; 0.205]	[0.069; 0.583]	[0.316; 0.735]	[0.001; 0.250]	[0.005; 0.128]
South	0.092	0.025[d]	0.147	0.587	0.150
	0.077	0.006	0.139	0.594	0.143
	[0.016; 0.392]	[0.006; 0.181]	[0.013; 0.477]	[0.277; 0.834]	[0.021; 0.382]
West	0.176[b]	0.191[b]	0.015	0.059	0.559
	0.170	0.193	0.004	0.044	0.556
	[0.007; 0.387]	[0.022; 0.468]	[0.003; 0.125]	[0.011; 0.243]	[0.329; 0.725]

Table 2 Migration rates between five mountain lion subpopulations throughout Nevada. Estimates are based on posterior means and modes

Probability that the pairwise estimate is equal to or greater than the corresponding pairwise estimate [a]$P < 0.05$, [b]$P < 0.01$, [c]$P < 0.0001$, [d]$P < 0.00001$.

geneflow between the North, East, Central and South populations appear to be desert basins that comprise low quality habitats to mountain lions and their prey, such as barren desert playas and large expanses of salt desert scrub. Nevertheless, it is likely that continuous mountainous habitat facilitates movement in a north and south direction as much as, or to a greater extent than, barriers impede movement. Distributions of prey populations, particularly mule deer, which are concentrated along mountain ranges, also are likely to be partially responsible for the spatial structure of these subpopulations.

TESS identified the Sierra Nevada range as a single genetic group which partially supports the findings of Ernest *et al.* (2003) who also reported high geneflow north and south throughout much of the Sierra Nevada range. However, Ernest *et al.* (2003) found some evidence for additional population substructure in the Sierra Nevada range using assignment methods (STRUCTURE) and, particularly east and west of the Sierra Nevada crest in the southern part of the range, using traditional geographic analysis of genetic data (F_{ST}, genic differentiation, etc.).

Source-sink dynamics

Our goal was to estimate the amount of asymmetrical effective movement of mountain lions between populations to identify source and sink dynamics (Pulliam 1988). We observed significant asymmetrical movement rates among subpopulations, which provides support for our hypothesis that source-sink dynamics occur

among these subpopulations. Although the West population was not identified as a net source of dispersing individuals as we had predicted, the most notable asymmetry in movement rates did occur out of a population that was under substantially less hunting pressure (Table 5). Identification of the South population as the largest net source of dispersing individuals can be explained by several very large de facto refuges, where mountain lions are not removed for sport or management, located inside the boundaries of this genetically delineated population. These refuges are the Desert National Wildlife Refuge (5700 km^2), which is
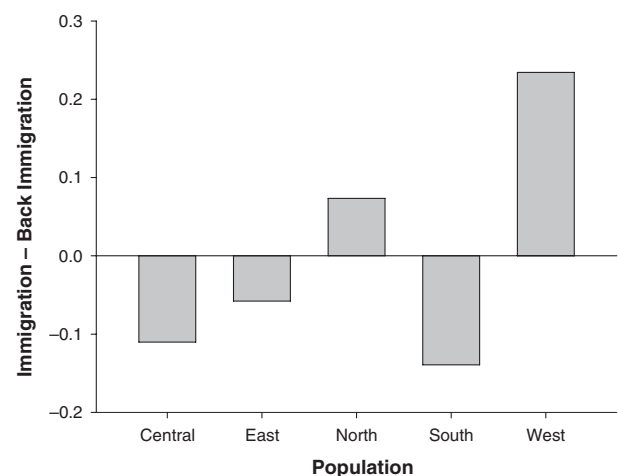

Fig. 5 Immigration asymmetry (immigration—back immigration) estimated from recent migration rates (BIMR) with $k = 5$. Bars indicate the differences between mean immigrant and emigrant estimates in each population.

Table 3 Measures of genetic diversity across the five genetic populations in Nevada and eastern California identified with TESS assignments

Population	n	Average % H_O (SD)	Average % H_E (SD)	Total number of alleles	Average number alleles per locus†	Bottleneck P-value‡
West	155	51 (1.2)	52 (4.4)	56	4.7	0.898
North	208	50 (1.0)	51 (3.8)	46	3.8	0.088
Central	110	51 (1.4)	50 (4.3)	45	3.8	0.190
South	76	57 (1.7)	57 (2.7)	46	3.8	0.007
East	190	52 (1.1)	50 (3.9)	50	4.2	0.633

†Rarefaction estimates of allelic richness for even sample sizes.
‡Wilcoxon ranked-sign test (1-tailed) testing for heterozygote excess using the program BOTTLENECK.

Table 4 Pairwise F_{ST} values between the 5 TESS genetic populations with 12 loci (below diagonal) and 5 TESS genetic populations the 9 loci (above diagonal) used for BIMR analysis

Region	West	North	Central	South	East
West	—	0.08	0.07	0.06	0.03
North	0.09	—	0.05	0.06	0.05
Central	0.05	0.05	—	0.07	0.05
South	0.06	0.05	0.06	—	0.04
East	0.06	0.05	0.05	0.05	—

the largest wildlife refuge in the contiguous United States and the adjacent Nevada Test Site (3500 km^2). On average, nearly six times more harvest occurs in the East population (2.78 lions killed/1000 km^2) compared with the South population (0.47 lions killed/1000 km^2; Table 5). The South source population, with over 9000 km^2 of mountain lion refugia, and the East, North and Central populations all occur in similar Montane habitats typical of the Great Basin. In contrast, the Sierras where mountain lions are protected differ conspicuously in floristics, extent and ultimately habitat quality, from Great Basin ranges. Disparities in habitat quality and geographic extent may contribute to lower movement rates of mountain lions from the Sierras into the Great Basin, resulting in the West population being identified in our analyses as a relative sink. Although this hard defined ecotone may present itself as a partial barrier for lions occupying the Sierra Nevada, it may be attractive for lions residing in the Great Basin, particularly if the Sierra Nevada range is not saturated with resident lions. It is possible for instance that the West population, particularly the Sierra Nevada range, has higher mortality rates from causes that are not documented here. For example, the density of paved roads is greater in the Sierras than Great Basin mountain ranges, and vehicle collisions with mountain lions are not uncommon. Such undocumented mortality may keep lions in the Sierra Nevada range below carrying capacity. Alternately, mountain lion numbers may be

more effectively regulated in un-manipulated populations, where dominance relationships can maintain greater population stability than in highly manipulated (i.e. hunted) populations with ephemeral dominance relationships and thus higher densities of animals. We do not suggest, however, that the West population containing the vast Sierra Nevada range is unable to sustain itself without immigration from surrounding Great Basin populations; only that it provides less immigrants to surrounding sampled populations than it receives despite the relatively low rates of removal. A careful study of lion demographics would be necessary to test this hypothesis; see also Kawecki (2004) for a discussion of 'absolute' and 'relative' sinks.

Although our sampling area is extensive, it is necessary to note that identification of sources and sinks can only be fully validated by sampling all surrounding populations. For instance, although we identified the West population as a *relative* sink for surrounding populations in Nevada, it could be a source for un-sampled populations to the north, south, or west. In addition, although the East population would appear to be a sink population if only the South, Central and East populations were considered, it is identified as a source when the North population is considered. Although it is exceedingly difficult to sample all surrounding populations for wide-ranging species that occur at low densities such as mountain lions, Loxterman (2011) also documented significant asymmetrical movement rates from a subpopulation in southern Idaho into northern Nevada with no movement occurring from Nevada back into the Idaho subpopulation; those results provide further evidence that the North population in Nevada represents a sink.

We observed larger net gene movement out of the Southern source population compared with movement out of populations that have higher rates of harvest. This pattern of a population with relatively low rates of harvest pressure contributing to surrounding populations that have higher rates of removal is simi-

Population	Average number lions killed/year	Area of mountainous habitat (km^2)	Average harvest per 1000 km^2	Relative source/sink
Central	20	18 830	1.06	Source
West†	82	*c.* 100 480	0.82	Sink
North	38	25 575	1.49	Sink
South	13	27 388	0.47	Source
East	45	16 179	2.78	Source

†Data on number of mountain lions killed in California are only for those killed with depredation permits and obtained from http://www.dfg.ca.gov/news/issues/lion/dep-lions-killed.html. Depredation numbers were averaged across 2004–2009 for the counties of: Alpine, Amador, Butte, Calaveras, El Dorado, Fresno, Lassen, Madera, Mariposa, Modoc, Mono, Nevada, Placer, Plumas, Shasta, Sierra, Siskiyou, Tehama, Tulare, Tuolumne and Yuba. Number of mountain lions killed on the Nevada side of the Sierra population were added to those from California. As we do not have geographic coordinates of all lions killed in California, we included all individuals killed in counties that overlap the entire Sierra Nevada range.

Table 5 Average number of mountain lions killed (harvest, road kill, depredation and other sources of mortality) in five geographically delineated populations from 2004 to 2010, total mountainous habitat (calculated roughly as the total area of mountain ranges estimated to be contained in each population), the estimated average number of mountain lions killed per 1000 km^2 mountainous habitat for each population, and whether the population was identified as a relative source or sink population

lar to the 'vacuum effect' reported in demographic studies at smaller spatial scales; in which removal of adult male mountain lions create vacancies that attract dispersing males into unoccupied territories (Logan *et al.* 1986; Logan & Sweanor 2001; Stoner *et al.* 2006; Robinson *et al.* 2008; Cooley *et al.* 2009b). For this type of a system to persist, in which the sink is attractive to dispersers and there is relatively little migration back into the source, the source population must be able to sustain the drain of individuals imposed by emigration (Kawecki 2004). Whether the South population, which shows evidence of a recent reduction in effective population size, can sustain the demands of emigration imposed by surrounding sink populations that are under relatively high hunting pressure is uncertain. This question needs further study.

Loxterman (2011) observed that the southern part of her study area, including the North population of Nevada, had significantly reduced allelic richness and a slight reduction in heterozygosity compared with mountain lion populations north of the Snake River floodplain in Idaho. In addition, these populations with greater allelic richness in northern Idaho where habitat quality is greater and more contiguous incur substantially more harvest (4.4 lions/1000 km^2; Loxterman 2011). Allelic richness in the subpopulations of Nevada's Great Basin is also reduced compared with the West population which includes the Sierra Nevada Mountain range where habitat quality is high, but where mountain lions are protected. As allelic diversity is expected to decrease faster than heterozygosity, those results may suggest that harvest pressure has a more negative effect on genetic diversity of mountain lion populations that occupy areas where habitat is of lower quality and is less contiguous. Alternatively, lower genetic diversity in the Great Basin populations

may be a result of historically lower population sizes as Loxterman (2011) also proposes. This question also deserves further study. Although we observed evidence of a population bottleneck in the South population, high levels of migration can affect results of analyses used to examine genetic bottlenecks because those analyses assume no immigration (Cornuet & Luikart 1996). In addition, heterozygote excess is detectable for approximately 0.2–4 N_e, where N_e is the bottleneck effective size (Luikart & Cornuet 1998). This wide interval makes it difficult to estimate when the bottleneck occurred without additional demographic information. Nonetheless, the ratio test we implemented is likely to detect bottlenecks that are more recent and less severe than other methods commonly used (Williamson-Natesan 2005).

This analysis represents one of the first attempts to identify source-sink dynamics for a wide-ranging mammal using genetic techniques. Despite limitations on movement imposed by natural barriers that can contribute to the formation of genetic subpopulations, significant effective movement occurred between populations that we estimated using Bayesian analysis of multilocus genotypes. Although most 95% HDPIs from BIMR were overlapping, which may suggest that the data were less informative than is ideal (Faubet *et al.* 2007), we have provided evidence that migration rates among subpopulations were significantly asymmetrical such that sources and sinks could be identified. Nonetheless, we suggest that it would be premature to translate our findings into management practice at this time; our results should be considered hypotheses to motivate future research, potentially including an even greater portion of the geographic range of mountain lions. In addition, although migration rates estimated by BIMR indicate the proportion of the population that has

immigrated in the last generation, pooling of samples over multiple generations (as we have done out of necessity) likely leads to an overestimate of absolute migration rates by BIMR while the overall patterns of migration including identification of source and sink populations should remain stable (O. Gaggiotti, personal communication). We suspect that with a greater number of polymorphic loci or larger annual sample sizes and larger geographic sample, source-sink dynamics could be inferred with greater precision and confidence in estimated migration rates.

Source-sink dynamics for mountain lions appear to occur at a landscape scale and may be influenced by harvest pressure as demographic studies have demonstrated at smaller spatial scales (Sweanor *et al.* 2000; Logan & Sweanor 2001; Stoner *et al.* 2006; Robinson *et al.* 2008; Cooley *et al.* 2009a,b). Habitat quality for mountain lions in Nevada, indexed by densities of mule deer and precipitation, is far greater in the neighbouring East population, compared with the Southern source population (NDOW 2007). The South population identified as the largest net provider of dispersing individuals is comprised of refuges where harvest of mountain lions was non-existent or reduced in comparison to surrounding populations. This result supports demographic studies that have suggested that unequal harvest across the landscape can result in source-sink dynamics (Sweanor *et al.* 2000; Logan & Sweanor 2001; Stoner *et al.* 2006; Robinson *et al.* 2008; Cooley *et al.* 2009a,b). Moreover, it suggests that the 'vacuum effect' reported at smaller spatial scales may operate at larger spatial scales as well. Although this relationship is striking where refugia are present and there is a large degree of variation in harvest pressure, harvest pressure does not correlate perfectly with source and sink designations across the entire landscape. Our unexpected result that the West population is a relative sink, for instance, may suggest that a combination of habitat quality and hunting pressure is important for determining source-sink dynamics and direction of movement at the landscape scale, particularly where there is a large degree of variation among habitat types.

These results highlight the large spatial scale at which source-sink dynamics may operate for mountain lions throughout Nevada and the Great Basin, and the utility of genetic techniques to address conservation and management of large mammals at a landscape scale. Failure to recognize such population structure, especially in harvested populations, can have negative results if a constant level of harvest is assumed to be sustainable across the landscape without considering the role of immigration in sustaining populations, or if connectivity is not maintained between interacting populations (Cougar Management Guidelines Working Group 2005). Sink populations may maintain large population sizes if immigration is high (Van Horne 1983; Pulliam 1988; Robinson *et al.* 2008), however social stability and overall productivity of sink populations has been shown to decline as age and sex structure shift towards young, dispersal-age males (Logan & Sweanor 2001; Robinson *et al.* 2008; Cooley *et al.* 2009b). Surrounding source populations may be negatively affected by an excessive drain of individuals if immigration is not well reciprocated (Novaro *et al.* 2005; Kawecki 2008; Robinson *et al.* 2008). Management schemes identifying areas occupied by source and sink populations including designated refugia have been proposed (Logan & Sweanor 2001; Laundré & Clark 2003) and could be designed to allow traditional hunting levels to be maintained while ensuring the long-term viability of mountain lion populations (Laundré & Clark 2003). Additional research on the scale at which source-sink dynamics occur, environmental characteristics influencing movement and the size of refugia needed to sustain sink populations, particularly for large vagile mammals such as mountain lions, under different scenarios should be undertaken.

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Data accessibility

Microsatellite genotype data and sampling locations used for analyses for 739 Puma: DRYAD entry doi:10.5061/dryad.mj74q.