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Streams over mountains: influence of riparian connectivity on gene flow in the Pacific jumping mouse (*Zapus trinotatus*)

SACHA N. VIGNIERI
Burke Museum and Department of Biology, University of Washington, Seattle, Washington 98195, USA

Abstract

In species affiliated with heterogeneous habitat, we expect gene flow to be restricted due to constraints placed on individual movement by habitat boundaries. This is likely to impact both individual dispersal and connectivity between populations. In this study, a GIS-based landscape genetics approach was used, in combination with fine-scale spatial autocorrelation analysis and the estimation of recent intersubpopulation migration rates, to infer patterns of dispersal and migration in the riparian-affiliated Pacific jumping mouse (*Zapus trinotatus*). A total of 228 individuals were sampled from nine subpopulations across a system of three rivers and genotyped at eight microsatellite loci. Significant spatial autocorrelation among individuals revealed a pattern of fine-scale spatial genetic structure indicative of limited dispersal. Geographical distances between pairwise subpopulations were defined following four criteria: (i) Euclidean distance, and three landscape-specific distances, (ii) river distance (distance travelled along the river only), (iii) overland distance (similar to Euclidean, but includes elevation), and (iv) habitat-path distance (a least-cost path distance that models movement along habitat pathways). Pairwise Mantel tests were used to test for a correlation between genetic distance and each of the geographical distances. Significant correlations were found between genetic distance and both the overland and habitat-path distances; however, the correlation with habitat-path distance was stronger. Lastly, estimates of recent migration rates revealed that migration occurs not only within drainages but also across large topographic barriers. These results suggest that patterns of dispersal and migration in Pacific jumping mice are largely determined by habitat connectivity.

Keywords: connectivity, gene flow, habitat heterogeneity, landscape genetics, limited dispersal, *Zapus trinotatus*

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Introduction

Habitat heterogeneity is a natural component of landscapes that can also result from anthropogenic habitat fragmentation. Both natural and anthropogenic habitat heterogeneity result in the geographical and demographic subdivision of populations. When population subdivision occurs, particularly in natural systems, patterns of connectivity between subpopulations are directed by topography and the distribution of suitable habitat, in that these factors affect the number and location of patches that actually exchange migrants (Wiens 1997). The specifics of these intersubpopulation pathways are not necessarily obvious but are important because they have a direct effect on the evolutionary trajectory of the species. Understanding these migration patterns can increase our knowledge of the biogeographical history of a species and provide valuable insight regarding the potential impact of landscape changes on species persistence.

In environments where suitable habitat is limited, due to factors such as heterogeneity or fragmentation, individual dispersal is likely to be constrained by habitat boundaries

Correspondence: S. N. Vignieri, Biology Department, Box 351800, University of Washington, Seattle, WA 98195 USA; Fax: 206-543-3041; E-mail: sachav@u.washington.edu

(Dieckmann *et al*. 1999; Wiens 2001). It is difficult to reveal the effects of habitat on dispersing individuals using direct mark–recapture methods, however, due to the large number of individuals that must be captured and monitored. An alternative approach is to infer patterns of dispersal from genetic data (Waser & Strobeck 1998). Limited dispersal will result in increased mating among neighbours. When repeated over generations, this will increase the relatedness of proximal individuals and result in striking patterns of spatial genetic structure (Wright 1943; Malecot 1948; Turner *et al*. 1982; Epperson 1995). The ability to detect these patterns of relatedness between individuals at very small scales allows one to draw conclusions regarding the effects of individual movement on the spatial patterning of similar genotypes. Specifically, it can increase our understanding of how dispersal contributes to the formation of genetic structure within a species (Slatkin 1994). Spatial autocorrelation analysis is one method that has successfully been used to reveal the role of such dispersal effects, in particular population clines (Cassens *et al*. 2000; Hardy *et al*. 2000; Tighe *et al*. 2003), limited dispersal (Arnaud *et al*. 2001; Peakall *et al*. 2003; Volis *et al*. 2004), and differential dispersal between males and females (Ehrich & Stenseth 2001; Richardson *et al*. 2002; Peakall *et al*. 2003).

In these contexts, dispersal generally refers to the movement of juvenile individuals away from their natal sites. These individual movements when averaged over many generations, however, lead to the patterns of gene flow and gene exchange we generally describe as migration. By incorporating landscape features, such as geographical barriers and habitat distribution, into our examination of spatial genetic structure, we can understand how environmental constraints placed on dispersers eventually impact larger-scale patterns of migration. The relationship between patterns of spatial genetic variation and landscape features can be explored using landscape genetic methods. Landscape genetics is an analytical approach that allows for the investigation of the relationship between landscape features, such as the location of suitable habitat, or geographical barriers and patterns of genetic variation (Manel *et al*. 2003). It has been used to demonstrate the importance of habitat as a structuring force among both individuals and populations in numerous studies. For example, patterns of genetic divergence have been observed to correlate with various barriers present in the landscape, such as roads (Keller & Largiader 2003) and agricultural fields (Vos *et al*. 2001), or the availability of habitat, such as patches of woodland (Keyghobadi *et al*. 1999; Coulon *et al*. 2004).

When describing patterns of connectivity in relationship to the landscape it is important to consider the impact of animal movement, habitat availability, and geographical barriers at multiple spatial scales. One should first test for the presence of significant subpopulation structure, the existence of which indicates the presence of structuring forces, such as limited dispersal or barriers to migration (Slatkin 1987). Information regarding the structuring effects of local dispersal can be gained through the use of measures that can reveal fine-scale spatial structure (Queller & Goodnight 1989; Bohonak 1999; Smouse & Peakall 1999). In addition, by testing for the existence of correlations between genetic distance and geographical distances that incorporate various landscape components, we can begin to reveal the environmental impact on the movement of individuals across the landscape (Arter 1990; Gerlach & Musolf 2000; Pfenninger 2002). Finally, the estimation of migration rates between subpopulations will allow us to further characterize the prevailing patterns of connectivity by revealing the level of gene flow that occurs between specific subpopulations (Wilson & Rannala 2003; Paetkau *et al*. 2004).

In this study, I have investigated the factors that contribute to the spatial genetic structure present within the riparian-associated Pacific jumping mouse (*Zapus trinotatus*). In order to conduct these investigations, eight highly variable microsatellite loci (Vignieri 2003) were isolated and described in 228 individuals across a system of three rivers in the Olympic Mountains of Washington State. A multitiered approach was then used to reveal the relationship between dispersal, landscape features, and spatial genetic structure. First, the genetic structure among nine sample 'subpopulations' was characterized across the three river drainages. Next, the impact of dispersal on fine-scale spatial genetic structure was explored by testing for the presence of genetic spatial autocorrelation among individuals (Smouse & Peakall 1999; Peakall *et al*. 2003). A landscape-based genetic distance approach was incorporated to determine how the Pacific jumping mouse's affiliation with particular habitat types influences patterns of connectivity between subpopulations. Finally, migration rates between subpopulations were estimated, using a Bayesian method (Wilson & Rannala 2003), to determine whether the observed relationship between landscape features and spatial genetic structure is reflected by recent migration patterns.

Materials and methods

*The Pacific jumping mouse (*Zapus trinotatus*)*

The Pacific jumping mouse is a small rodent that is distributed from southern British Columbia to northern California (Hall 1981). Individuals are only active in spring and summer, from late April through September, and they hibernate for the remainder of the year. Due to this reduced yearly active period they are relatively long lived, perhaps reaching as many as five or more years of age, and they produce only a single litter of four to eight young per

year (Bailey 1936). While hibernation has not been studied in *Zapus trinotatus*, the closely related *Zapus princeps* and *Zapus hudsonius* have been described as hibernating either singly or in pairs (Cranford 1983). Research on the ecologically similar *Z. princeps* indicates small and distinct home ranges, with the average size varying over a 3-year study from 0.17 to 0.61 ha (Cranford 1983). Cranford also found population densities to be stable due to adult longevity and facultative emergence from hibernation. Despite relatively stable population composition, population abundance of *Zapus* species varies considerably from site to site, and *Z. trinotatus* in particular are often found in pockets of unusual abundance (Howell 1923).

Zapus trinotatus is distributed in association with discontinuous and patchily distributed habitat. On the Olympic Peninsula in Washington State, Svihla & Svihla (1933) found them to be distributed in association with alpine and moist meadows, marshy thickets, and the edges of woodlands and thick forests. Maser *et al*. (1981) described them as inhabiting primarily riparian alder/salmonberry (*Alnus-Rubus spectabilis*), riparian alder (*Alnus*), and skunkcabbage (*Veratrum*) marsh ecosystems within Douglas fir forest. Despite this somewhat more general description of habitat used, they appear to be considerably more abundant in, and likely tied to, mesic habitat types. Gomez & Anthony (1998) found significantly more *Z. trinotatus* in riparian habitats than in upslope habitats of all types. Additionally, Jones (1981) indicated that their abundance increases along a precipitation gradient and suggested that they may be restricted to areas that receive > 30 cm of precipitation annually. Other much better-studied members of the genus *Zapus* also display an affiliation with riparian and mesic habitats. Clark (1971) stated that *Z. princeps* is generally not found more than 100 m from water and *Z. hudsonius* has been called partly aquatic (Quimby 1951), *Z. trinotatus* is ecologically similar to these species and likely shares these traits.

The Dosewallips, Duckabush, and Hamma Hamma river systems

This study was conducted within a system of three river drainages that exists on the eastern side of the Olympic Peninsula in Washington State and covers an area of approximately 945 km^2 (Fig. 1). The rivers (from north to south, the Dosewallips, Duckabush, and Hamma Hamma) lie adjacent to each other and flow east from the Olympic Mountains into the Hood Canal area of the Puget Sound.

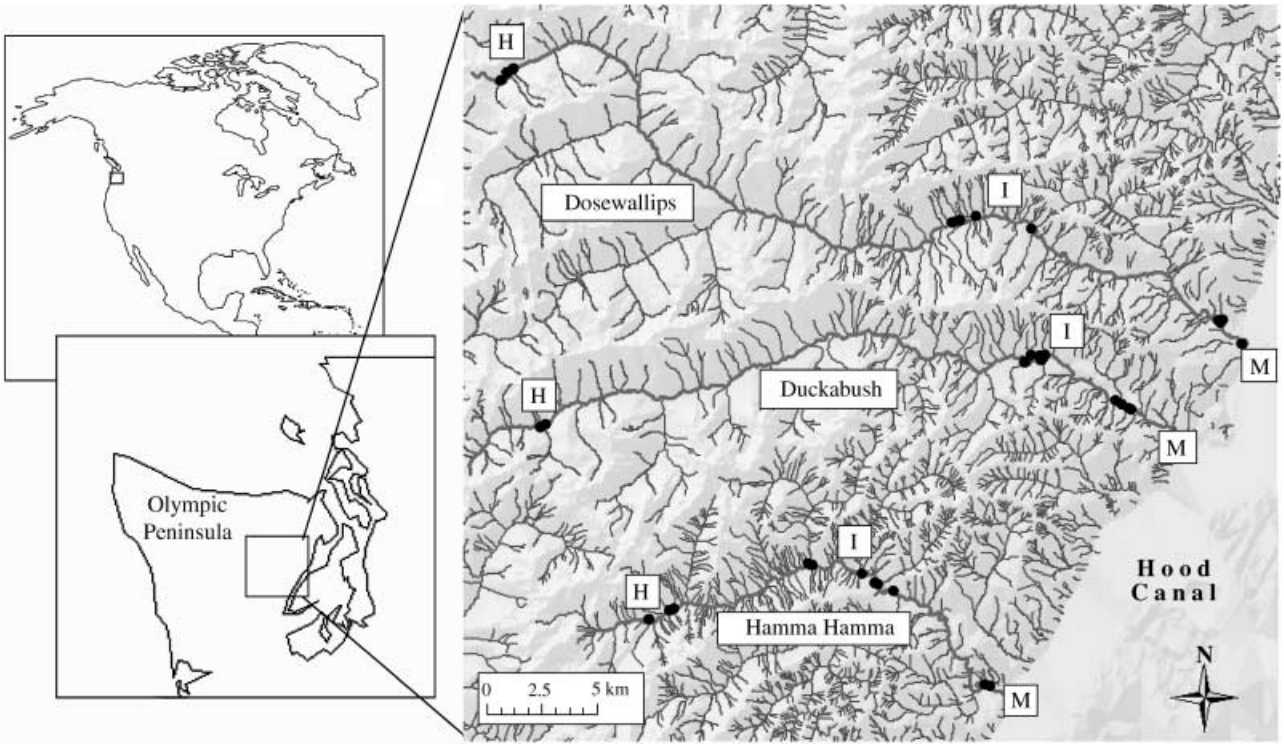

Fig. 1 Sample locations (black dots) for 228 *Zapus trinotatus* within a system of three adjacent river drainages, the Dosewallips, Duckabush, and Hamma Hamma, on the eastern side of the Olympic Peninsula in Washington State. Sample zones are indicated as H, headwaters; I, interior; and M, mouth. Samples from each of the nine zones were combined to form nine subpopulations.

Outside of the riparian zones, the area is largely covered by mixed coniferous forest (mostly Douglas fir *Pseudotsuga menziesii*, western red cedar *Thuja plicata*, and western hemlock *Tsuga heterophylla*), and alpine parkland at high elevations (Washington GAP Analysis Program). The area is mountainous, with the headwaters of each river lying at high elevations (1400 m, 820 m, and 520 m, respectively). In addition, the terrain between each of the rivers is rugged with average elevations of 1263 m between the Dosewallips and the Duckabush, and of 1093 m between the Duckabush and the Hamma Hamma.

Sample collection and genotyping

Tissue samples were collected from tail tips of *Z. trinotatus* across the study site over 3 years, 2000–2002. In order to investigate the influence of landscape features across this mountainous region, individuals were sampled from three main areas within each river, the headwaters (H), interior (I), and mouth (M) (Fig. 1). Actual sampling localities were dictated by the presence of suitable habitat and river access, both of which were variable. Samples were collected from numerous sites within each of these three main areas and then lumped to form three successive zonal 'subpopulation' groups per drainage. The distance within which all samples were assumed to be from the same subpopulation varied due to accessibility and habitat continuity, and ranged from 266 m, at the mouth of the Hamma Hamma River, to 4229 m in the interior of the Hamma Hamma. A total of 228 individuals (130 females, 98 males) were sampled across all nine subpopulations (sample sizes in Table 1). Upon collection in the field, tissue samples were immediately placed into 95% ethanol. Each animal was given a unique ear tag to prevent resampling, sexed, weighed, and immediately released. Using a Garmin 'GPS 12' unit, geographical coordinates were assigned for each sampled animal at the capture point. Upon return from the field, tail tips were stored in ethanol at –80 °C until the time of DNA extraction. Each individual was genotyped at all eight loci (Table 1) on a MegaBACE 1000™ (Molecular Dynamics) automated sequencer. Genomic DNA extraction, isolation of microsatellite loci, determination of linkage disequilibrium for loci, polymerase chain reaction (PCR) conditions, and genotyping of individuals were as described in Vignieri (2003).

Genetic structure analyses

In order to gauge overall levels of genetic diversity within the system, F_{IS} (Wright 1978) and levels of heterozygosity were calculated for each subpopulation and all loci, and allelic richness (El Mousadik & Petit 1996) for all subpopulations, using the program TFPGA version 1.3 (Miller 1997). The exact test of Guo & Thompson (1992), as implemented by GENEPOP version 3.4 (Raymond & Rousset 1995), was used to test for deviation from Hardy–Weinberg equilibrium at each locus and within each subpopulation. Per-locus differences in allele frequencies between subpopulations were determined using Fisher exact tests (Raymond & Rousset 1995) and Fisher combined probability tests (Sokal & Rohlf 1995) were used to determine overall significance across loci, both in the program TFPGA version 1.3. In order to investigate the degree and pattern of differentiation between specific subpopulations, pairwise values of subpopulation F_{ST} were estimated using the method of Weir & Cockerham (1984) within the program ARLEQUIN version 2.000 (Schneider *et al*. 2000).

Spatial autocorrelation analysis

To determine if dispersal and gene flow are limited, spatial autocorrelation analysis (SA) was used as implemented in GENALEX version 5.1 (Peakall & Smouse 2001). This method is unlike traditional SA (Sokal & Oden 1978; Peakall & Beattie 1995), which has generally been executed one allele at a time, in that it is inherently multivariate. Using pairwise geographical and individual–individual genetic distance matrices, it generates an autocorrelation coefficient, *r*, which is similar to Moran's *I*, and provides information regarding the presence of a correlation between the relatedness of individual genotypes and space (Smouse & Peakall 1999). A positive correlation is predicted in cases of restricted dispersal (Peakall *et al*. 2003), when individuals within a given distance class are more closely related than would be expected by chance. Significance is determined through comparison to the 95% confidence interval around the null hypothesis of 'no relationship', generated through 999 random permutations of the genotype data. In addition, a one-tailed test for positive spatial structure is conducted by comparing the observed *r* values to the permuted *r* values in order to estimate the probability of achieving a value greater than, or equal to, the observed *r*. If the probability is less than 0.05, the alternative hypothesis, that positive spatial structure exists, is accepted.

In this study, the distance between individuals was calculated as the linear distance between two individuals based on their *X Y* capture coordinates. Patterns of SA were investigated at two spatial scales. First, an analysis was conducted at the local scale to test for the effects of limited individual dispersal, this test only included comparisons between individuals within the same subpopulation. In order to increase the number of individual comparisons included in the estimation of *r* for a given distance class, and thereby increase the power of the test, this analysis was conducted using the multiple population option within GENALEX version 5.1. This computes *r* as summed over the combined set of subpopulations, producing the estimate across subpopulations as *rc*. This is done by

Table 1 Genetic diversity across eight microsatellite loci for nine subpopulations of Pacific jumping mice from three river drainages on the Olympic Peninsula

	Dosewallips Mouth (N = 26)						Dosewallips Interior (N = 31)						Dosewallips Head (N = 45)					
Locus	HWE	F_{IS}	N_a	A_R	H_E	H_O	HWE	F_{IS}	N_a	A_R	H_E	H_O	HWE	F_{IS}	N_a	A_R	H_E	H_O
Ztri2	0.69	0.01	16.0	11.48	0.93	0.92	*0.03	0.10	17.0	11.72	0.93	0.84	0.75	−0.03	18.0	11.36	0.93	0.96
Ztri24	*0.01	0.26	8.00	6.85	0.83	0.61	0.37	0.03	10.0	8.25	0.87	0.90	0.99	0.01	9.00	7.30	0.85	0.84
Ztri3s	0.49	0.07	7.00	5.08	0.70	0.65	*0.01	0.11	10.0	7.45	0.80	0.71	0.40	−0.02	10.0	7.13	0.81	0.82
Ztri17	0.40	0.04	11.0	8.73	0.89	0.92	*0.04	0.05	11.0	8.31	0.89	0.94	0.46	−0.05	11.0	7.79	0.85	0.89
Ztri18	0.16	0.04	16.0	9.86	0.88	0.85	0.59	0.02	13.0	8.81	0.86	0.87	0.84	−0.04	20.0	11.34	0.92	0.96
Ztri4	0.94	0.18	6.00	5.48	0.75	0.88	0.67	0.04	7.00	6.27	0.84	0.87	0.11	−0.04	7.00	5.85	0.79	0.82
Ztri19	0.50	0.03	7.00	5.51	0.67	0.69	0.22	0.09	8.00	5.78	0.77	0.84	*0.04	0.24	6.00	4.79	0.72	0.56
Ztri19+	0.54	0.08	5.00	4.24	0.66	0.61	0.35	0.10	7.00	5.09	0.72	0.65	0.10	0.12	8.00	5.51	0.76	0.67
Overall	0.17	0.03	9.50	7.16	0.79	0.77	*0.01	0.01	10.4	7.71	0.83	0.83	0.24	0.02	11.1	7.63	0.83	0.81
	Duckabush Mouth (N = 15)						Duckabush Interior (N = 32)						Duckabush Head (N = 10)					
Locus	HWE	F_{IS}	N_a	A_R	H_E	H_O	HWE	F_{IS}	N_a	A_R	H_E	H_O	HWE	F_{IS}	N_a	A_R	H_E	H_O
Ztri2	*0.04	0.08	15.0	12.04	0.94	0.87	0.27	0.08	17.0	10.63	0.92	0.84	0.19	0.15	13.0	13.00	0.93	0.80
Ztri24	0.08	0.00	9.00	8.01	0.87	0.87	*0.00	0.14	11.0	9.06	0.90	0.78	0.93	−0.01	8.00	8.00	0.89	0.90
Ztri3s	*0.01	−0.10	7.00	6.35	0.79	0.87	0.98	−0.07	10.0	7.79	0.85	0.91	0.79	−0.09	10.0	10.00	0.92	1.00
Ztri17	0.10	−0.02	10.0	9.30	0.91	0.93	0.94	−0.01	13.0	8.94	0.90	0.91	0.90	−0.05	8.00	8.00	0.86	0.90
Ztri18	*0.03	0.20	13.0	10.43	0.91	0.73	0.83	−0.03	15.0	10.13	0.91	0.94	1.00	−0.08	11.0	11.00	0.93	1.00
Ztri4	0.32	−0.14	7.00	6.29	0.82	0.93	0.71	−0.05	7.00	5.72	0.80	0.84	0.79	0.05	8.00	8.00	0.84	0.80
Ztri19	0.59	0.11	6.00	5.23	0.75	0.67	0.16	0.08	8.00	5.68	0.75	0.69	0.22	0.13	5.00	5.00	0.57	0.50
Ztri19+	0.50	−0.18	5.00	4.49	0.66	0.77	0.12	0.12	8.00	5.16	0.68	0.60	0.62	0.11	6.00	6.00	0.78	0.70
Overall	*0.00	0.00	9.00	7.77	0.83	0.83	0.12	0.03	11.1	7.89	0.84	0.81	0.93	0.02	8.62	8.62	0.84	0.82
	Hamma Hamma Mouth (N = 10)						Hamma Hamma Interior (N = 32)						Hamma Hamma Head (N = 27)					
Locus	HWE	F_{IS}	N_a	A_R	H_E	H_O	HWE	F_{IS}	N_a	A_R	H_E	H_O	HWE	F_{IS}	N_a	A_R	H_E	H_O
Ztri2	0.44	0.02	9.00	9.00	0.92	0.90	*0.00	0.20	16.0	11.33	0.93	0.75	*0.02	0.10	15.0	10.08	0.86	0.78
Ztri24	0.24	0.17	6.00	6.00	0.83	0.70	0.67	0.08	9.00	6.96	0.84	0.78	0.10	0.15	10.0	7.81	0.87	0.74
Ztri3s	0.75	−0.03	8.00	8.00	0.87	0.90	0.31	−0.15	12.0	8.22	0.87	1.00	0.91	−0.09	9.00	7.22	0.81	0.89
Ztri17	0.71	−0.19	7.00	7.00	0.85	1.00	0.45	−0.06	12.0	8.82	0.88	0.94	0.86	0.02	12.0	8.48	0.87	0.85
Ztri18	1.00	−0.10	9.00	9.00	0.92	1.00	0.44	−0.04	17.0	9.64	0.87	0.91	0.16	0.02	19.0	12.77	0.95	0.93
Ztri4	0.32	−0.08	5.00	5.00	0.74	0.80	0.86	0.08	8.00	5.86	0.81	0.75	0.72	−0.06	7.00	5.86	0.80	0.85
Ztri19	0.90	−0.20	5.00	5.00	0.76	0.90	0.37	−0.12	8.00	5.99	0.78	0.87	0.91	−0.07	7.00	5.80	0.80	0.85
Ztri19+	1.00	−0.24	5.00	5.00	0.65	0.80	0.91	0.00	8.00	6.37	0.81	0.81	0.44	−0.02	9.0	6.73	0.80	0.82
Overall	0.94	−0.07	6.75	6.75	0.82	0.87	*0.04	0.00	11.2	7.90	0.85	0.85	0.25	0.01	11.0	8.09	0.84	0.84

Estimates for each subpopulation, per locus and over all loci, for (HWE), significant deviation from Hardy–Weinberg equilibrium (significance indicated by *); (F_{IS}), Wright's inbreeding coefficient; (N_a), number of alleles; (A_R), allelic richness based on a sample size of 10 (El Mousadik & Petit 1996); and (H_E), expected and (H_O), observed heterozygosities.

summing the individual components of the numerator and denominator of r at a given distance class across subpopulations and then producing the estimate at that distance class as the division of the total numerator and denominator (see Smouse & Peakall 1999, equation 15). In addition to tests conducted at the local scale, the pattern of SA that exists across the entire study area was examined. Comparisons made at this level included both those made within a single subpopulation and those made across much larger distances between individuals from different subpopulations. Distance classes at the local scale were selected using a method, implemented in GENALEX version 5.1, which equalizes the number of comparisons at each distance class. This method is particularly useful for reducing variance in confidence intervals due to unequal sampling. Distance classes at the larger scale were in increments of 1500 m.

Landscape genetic analyses

Genetic distance. Genetic distance between subpopulations was calculated as D_{LR}, the genotype likelihood ratio distance of Paetkau *et al*. (1997), using the DOH assignment test calculator (Brzustowski 2002). This distance measure calculates the likelihood that a given genotype originated in its sample subpopulation relative to other subpopulations. It performs extremely well at fine scales where drift and migration are the most likely drivers of genetic distance (Paetkau *et al*. 1997).

Landscape distances. Individual capture locations were plotted in a geographical information system, or 'GIS' (ARCGIS™ version 8.3). Polygons were created around each group of subpopulation samples and the centre of each of these was considered the subpopulation 'location' for geographical distance analyses. Subpopulation locations were layered with a 10 m digital elevation model (DEM) of the study area and a comprehensive stream map of the Olympic Peninsula (both from the United States Geological Survey). Four pairwise distances were then obtained between all nine subpopulations; three inherent distances (Euclidean distance, river distance, and overland distance) and a least-cost 'habitat-path' distance. The Euclidean distance was simply the shortest straight-line distance on a map between subpopulations, not including elevation (Fig. 2a). The river distance was measured as the distance

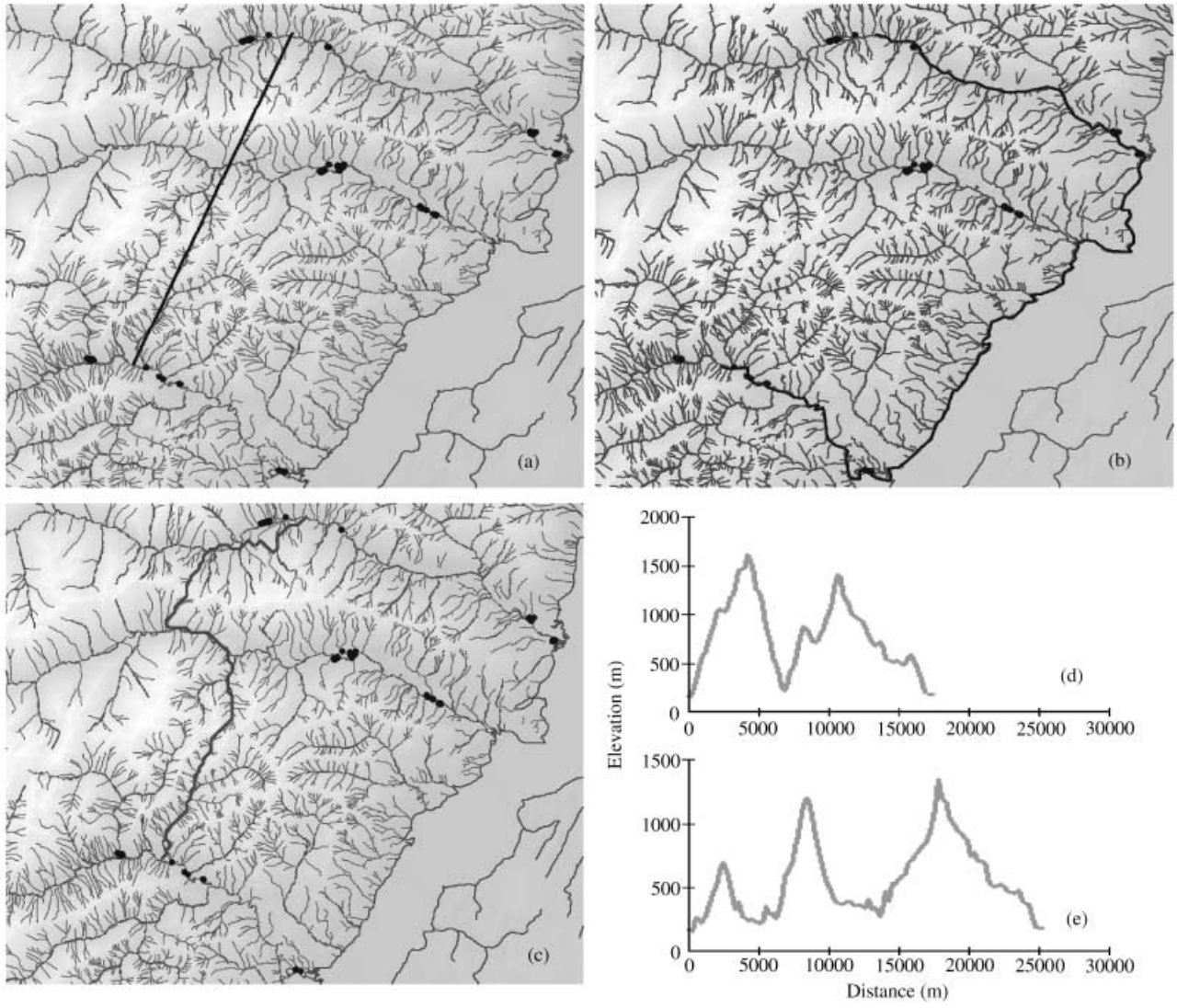

Fig. 2 Geographic distance measures, and elevation profile graphs, as estimated between the subpopulations DWI and HHI. (a) Euclidean distance, the shortest line between the subpopulations. (b) River distance, distance when travel is restricted to rivers and shoreline only. (c) Habitat-path distance, the least-cost path calculated using the habitat-path model of animal movement (see text for details). (d) The profile graph for Euclidean distance, used to estimate overland distance. (e) The profile graph for the habitat-path distance.

travelled along the river between two subpopulations, not allowing for travel across land except at the shoreline (Fig. 2b). The overland distance was measured along the shortest straight line between two subpopulations, including elevation. Specifically, a line was drawn between two subpopulations (as for Euclidean distance), an elevational profile graph was then created along this straight-line path and the overland distance was then determined by measuring the total distance including that created due to elevational rise (Fig. 2d).

The least-cost habitat-path distance was based on the ecological expectation that the Pacific jumping mouse, due to its riparian habitat association, would be most likely to move across land along riparian habitat pathways. Additionally, in cases of movement across mountains jumping mice should be expected to follow stream paths or mountain passes. In order to model this type of directed movement between subpopulations, a cost surface was created that assigned low cost values to landscape cells that contained streams or lower elevations. All possible paths were then calculated based on the cost of travelling across each type of landscape cell. The 'least-cost' path between all subpopulation pairs was then determined within the program ARCGIS™ version 8.3 as the lowest value path between two subpopulations (Fig. 2c). Distance along these paths was measured as it was for the overland paths (through the creation of an elevational profile graph following the least-cost path) and accounts for elevation (Fig. 2e).

Geographic and genetic correlations. The presence of an isolation-by-distance relationship between the genetic distance matrix and each of the four geographical distance matrices was tested for using pairwise Mantel tests (Mantel 1967) as implemented by the program 'ZT' (Bonnet & Van de Peer 2002). Pearson's correlation coefficients (generally referred to as *r*, but here called *pr* to avoid confusion with the autocorrelation coefficient, *r*) and significance of each of the correlations were determined through 100 000 randomizations of the data.

Migration rate estimates

Estimates of recent migration rates between subpopulations were made using the Bayesian multilocus method of Wilson & Rannala (2003) as implemented in their program BAYESASS version 1.2. This method allows for the simultaneous inference of recent asymmetric migration rates, allele frequencies, inbreeding coefficients, and individual migrant ancestries and does not require genotypes within subpopulations to be in Hardy–Weinberg equilibrium. In order to estimate the posterior probability distribution for the migration rates between subpopulations, the program was run using a Markov chain Monte Carlo (MCMC) length of 3×10^6 with three separate sets of initial input parameters (Δp = allele frequency, Δm = migration, and ΔF = inbreeding coefficient, all equal to 0.05, 0.10, or 0.20). Variation of the starting parameters provides information regarding the consistency of the resulting posterior distributions. Further, a X^2 likelihood-ratio test was conducted on each subpopulation, as implemented in BAYESASS, in order to determine whether the posterior probability distributions for migration rate were significantly different from the prior distributions. A nonsignificant result indicates that the data do not contain enough information to allow for estimates of migration rate to be made. In each of the runs, the first 10^6 iterations were discarded as burn-in. This allowed the chain to reach stationarity prior to sampling. Stationarity of the chain was determined by plotting the log-posterior probabilities against the iteration number. Samples were collected every 2000 iterations and used by the program to infer the posterior probability distribution of migrant proportions for each subpopulation.

Results

Population structure

Genetic diversity of jumping mice, as indicated by heterozygosity, number of alleles per locus, and allelic richness, was high across all nine subpopulations (Table 1). Single locus F_{IS} values varied from −0.24 to 0.24, but were generally close to zero for each subpopulation (Table 1). All subpopulations but three, the interior of the Dosewallips (DWI), the mouth of the Duckabush (DBM), and the interior of the Hamma Hamma (HHI), were in Hardy–Weinberg equilibrium over all loci (Table 1). In each of these three cases, heterozygote deficiencies in one (HHI) to three (DWI and DBM), loci appear to be driving the overall result. Differences in allele frequencies, as tested by Fisher exact tests, were significant at $P < 0.001$, after Bonferroni corrections, between all but the two most proximal subpopulations, the interior and mouth of the Duckabush (DBI and DBM). Similarly, levels of differentiation, as measured by F_{ST}, revealed low (0.02–0.08), but significant, divergence among all subpopulations except for the interior and mouth subpopulations in the Duckabush drainage (Table 2).

Spatial autocorrelation

The correlogram for the within-subpopulation analysis indicates a significant correlation at the first two distance classes, 51 m ($r_c = 0.024$, $P = 0.001$) and 103 m ($r_c = 0.006$, $P < 0.01$), with an *x*-intercept of 153 m (Fig. 3a). The correlogram produced for the entire study area reveals a significant correlation that persists up to *c*. 5000 m ($r = 0.015$, $P = 0.001$, Fig. 3b). At this point, *r* begins to decline, intercepting the *x*-axis at 7930 m and becoming significantly negative at

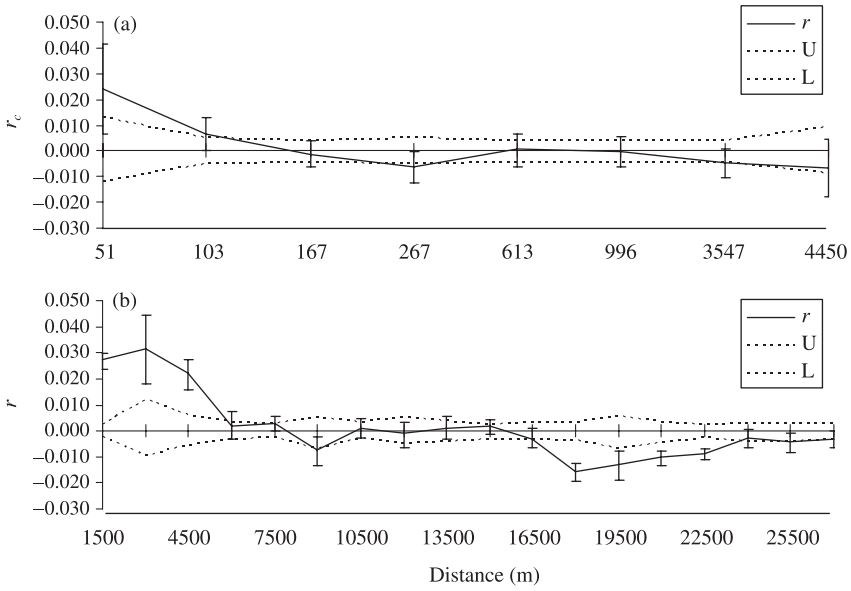

Fig. 3 Spatial autocorrelation correlograms indicating multilocus genetic correlation with distance in metres at two levels (a) only amongst individuals from within the same subpopulations, r_c, and (b) amongst individuals across all subpopulations, r. Dashed lines indicate 95% confidence intervals around the null hypothesis of no correlation between space and genotypes as determined by 999 permutations of genotypic data (U, upper limit; L, lower limit). Vertical bars represent 95% confidence intervals around estimates for r, determined by bootstrap resampling.

	DW-M	DW-I	DW-H	DB-M	DB-I	DB-H	HH-M	HH-I	HH-H
DW-M		***	***	***	***	***	***	***	***
DW-I	0.04		***	***	***	***	***	***	***
DW-H	0.04	0.03		***	***	***	***	***	***
DB-M	0.04	0.02	0.02		ns	***	***	***	***
DB-I	0.05	0.02	0.03	*0.00*		***	***	***	***
DB-H	0.06	0.06	0.04	0.03	0.05		***	***	***
HH-M	0.08	0.05	0.05	0.02	0.05	0.05		***	***
HH-I	0.07	0.05	0.03	0.02	0.03	0.03	0.04		***
HH-H	0.05	0.03	0.03	0.02	0.03	0.05	0.03	0.03	

Table 2 Pairwise F_{ST} and genotypic differentiation, as measured by Fisher exact tests, among nine zonal subpopulations of Pacific jumping mice (DW, Dosewallips; DB, Duckabush; and HH, Hamma Hamma, for all M, mouth; I, interior; and H, headwaters)

All F_{ST} values (below the diagonal) are significantly different from 0 except for the one that is italicized. Significance for Fisher exact tests (above the diagonal) reported after Bonferroni correction as $P < 0.001$, ***; not significant, ns.

16 500 m ($r = -0.003$, $P = 0.97$). No significant differences were found between correlations for males and females. However, male r values were always lower than female r values at smaller distance classes, a trend suggestive of male dispersal (data not shown).

Landscape genetic analyses

The results of the Mantel tests indicate a significant isolation-by-distance relationship between the genetic distance, D_{LR}, and both the overland and habitat-path distances, but not the river or Euclidean distances (Table 3). Although there was a correlation between genetic distance and both the overland and habitat-path distance measures, the correlation between the D_{LR} matrix and the habitat-path matrix was both greater and significant at a higher level ($pr = 0.42$, $P = 0.03$ for habitat-path distance vs. $pr = 0.37$, $P = 0.05$ for overland distance, Table 3). Significant correlations were present between the different landscape-specific geographical distance measures (river, overland, and habitat-path), but absent between these and the landscape nonspecific measure of Euclidean distance.

Migration rates

The X^2 likelihood ratio tests for all subpopulations were significant, indicating that the information contained in the data was sufficient for estimating migration rates. Stationarity of the chain for all three runs was reached by the 15 000th iteration. The three independent runs produced very similar results, indicating convergence of the MCMC algorithm, despite the different initial conditions. Only the results obtained with all starting parameters (Δp, Δm, and ΔF) equal to 0.10 are reported here (deviations from these

Table 3 Correlation between genetic distance, D_{LR}, and four different measures of geographical distances. Pearson's correlation coefficient, *pr*, as determined through Mantel tests and the significance of the correlation, *P*, determined through 100 000 randomizations of row and column labels for each matrix, * indicates significance at $P \leq 0.05$

Distance	*pr*	*P*
Euclidean	0.064	0.373
River	0.125	0.296
Overland	0.370	0.045*
Habitat Path	0.420	0.029*

results are indicated in Table 4). The mean posterior probabilities of the immigration rates among subpopulations are shown in Table 4. The majority of individuals were native to their sample subpopulations in all subpopulations (0.68–0.99), indicating relatively low rates of migration between subpopulations. Four pairs of subpopulations, however, did exchange a relatively high proportion of migrants, DBI and DWI ($m = 0.19$), DBM and DBI ($m = 0.21$), HHI and HHM ($m = 0.17$), and DBI and HHH ($m = 0.10$), in each case migration was asymmetric. In all pairs of subpopulations containing DBI, migrants between the subpopulations originated in that subpopulation.

Discussion

Population structure

Significant measures of divergence were observed among all subpopulations, other than the two most proximal (DBI and DBM). This indicates the presence of structuring forces within the system despite the relatively short distances between subpopulations. Interestingly, divergence between subpopulations was not only observed across drainages, but also within drainages, indicating movement between subpopulations may be restricted similarly without reference to topographic barriers. This observation is further supported by the F_{ST} results which indicate patterns of subpopulation similarity that do not coincide with those expected if divergence was driven solely by the presence of topographic barriers. Specifically, the most closely related subpopulations are not necessarily those that come from within the same drainage. These results indicate that while structuring forces are present within the system, they are not those we might predict based purely on the topography of the region. Rather, movement seems to be restricted regardless of the presence or absence of large perceived topographic barriers. This observation provides support for the hypothesis that restricted dispersal and habitat availability are the forces driving patterns of spatial genetic structure in this system.

Pattern of dispersal

Further support for the hypothesis that dispersal is restricted in this species is found in the SA results. It has been shown that limited dispersal will create patterns of spatial genetic structure detectable as SA between genotypes and distance (Sokal *et al*. 1989; Epperson 1995). In this study, tests for significance indicated that spatial genetic structure is present within subpopulations of Pacific jumping mice at the first two distance classes, 51 m and 103 m, and that the *x*-intercept occurs within a relatively short distance, 153 m. It is common in SA analyses to interpret the *x*-intercept as the patch size, a measure of the size of patches containing closely related individuals (Sokal 1979; Sokal & Wartenberg 1983; Epperson 1990b). The development of these high relatedness patches within a

Table 4 Migration rates between *Zapus trinotatus* subpopulations across three river drainages obtained using the program BAYESASS version 1.2 (Wilson & Rannala 2003) from initial conditions of Δp, Δm, and $\Delta F = 0.10$. Means of the posterior distributions for, *m*, the migration rate per generation, into each subpopulation are shown for each subpopulation pair. Migration rates are estimated as the proportion of individuals in column subpopulations that are derived from subpopulations in rows. Values along the diagonal are representative of the proportion of individuals within a subpopulation derived from that subpopulation. Estimates ≥ 0.10 are italicized. Results obtained with initial conditions of Δp, Δm, and $\Delta F = 0.05$ or 0.20 that deviated from these results by greater than 0.05 are indicated in parentheses

	DWM	DWI	DWH	DBM	DBI	DBH	HHM	HHI	HHH
DWM	*0.91*	0.05	0.00	0.01	0.01	0.03	0.01	0.01	0.02
DWI	0.00	*0.72*	0.00	0.01	0.01	0.02	0.01	0.01	0.02
DWH	0.01	0.01	*0.99*	0.03	0.01	0.04	0.02	0.01	0.06
DBM	0.00	0.01	0.00	*0.69*	0.00	0.02	0.01	0.00	0.01
DBI	0.06	*0.19*	0.00	*0.21*	*0.96*	0.05	0.05 (*0.11*)	0.02 (*0.10*)	*0.10*
DBH	0.00	0.01	0.00	0.01	0.00	*0.70*	0.01	0.00	0.01
HHM	0.00	0.01	0.00	0.02	0.01	0.07	*0.85* (*0.70*)	0.17 (*0.00*)	0.08
HHI	0.00	0.01	0.00	0.01	0.01	0.05	0.03	*0.78* (*0.86*)	0.03
HHH	0.00	0.01	0.00	0.01	0.00	0.02	0.01	0.01	*0.68*

species indicates low levels of dispersal (Epperson 1993) and small neighbourhood sizes (*sensu* Wright 1946). Both the small patch size and the significant fine-scale spatial structure found in Pacific jumping mice are consistent with SA patterns observed in other small mammals (Peakall *et al*. 2003), and are indicative of locally restricted individual dispersal.

When we broaden our examination of genetic spatial structure to the scale of the entire study area we can see that the relationship remains positive up to about 5 km and thereafter begins to decline, eventually becoming negative. Here, the *x*-intercept appears to occur at approximately the average distance between subpopulations. This is most likely an artefact of the clumped sampling regime and not the exact point at which the relatedness relationship begins to change. Additionally, the spatial scale at which the analysis is conducted can impact the overall pattern observed (Epperson 1990a). While at the local scale, we were able to make conclusions regarding the impact of individual dispersal, at this scale, the result indicates the existence of subpopulation structure and is more reflective of migration patterns between subpopulations (Epperson 1993). This is apparent in the presence of strong significant correlations between individuals that fall within the same sample subpopulation and significant negative correlations between individuals from distant subpopulations. Overall, the pattern observed across the entire study area reveals the existence of an interaction between limited dispersal at short distances (those within a subpopulation) and increasing genetic drift, due to limited migration, among increasingly distant subpopulations (Barbujani 1987).

Landscape correlations

The inclusion of landscape components in measures of geographical distance increased the correlation between genetic and geographical distance in this study. There was no relationship between the landscape nonspecific measure of Euclidean distance and the genetic distance. This is not surprising. Given the topographic relief of the area, the Euclidean distance is not representative of the actual travel distance between subpopulations, and therefore tells us little about the potential for connectivity between them. There was also no observed relationship between genetic distance and river distance. Although this measure incorporates aspects of the landscape, travel restricted purely to rivers is a relatively poor approximation of this species' likely dispersal repertoire. Despite the Pacific jumping mouse's demonstrated association with riparian habitat, they are clearly capable of traversing a variety of non-riparian habitat types and are not tied to river travel in the way that an obligate aquatic species would be.

Both overland and habitat-path distance are significantly correlated with genetic distance. This result allows us to conclude that attributes of the landscape are indeed impacting patterns of subpopulation connectivity, as has been observed using similar methods in other studies (e.g. daphnia *Daphnia ambigua*, Michels *et al*. 2001; kelp *Laminari digitata*, Billot *et al*. 2003; roe deer *Capreolus capreolus*, Coulon *et al*. 2004; damselflies *Coenagrion mercuriale*, Watts *et al*. 2004). The correlation observed between genetic distance and the habitat-path distance both explained more of the variation, and was significant at a higher level, than the correlation between genetic distance and overland distance. The presence of a significant correlation between these geographical distances complicates the interpretation of this result. However, although the correlation with habitat-path distance was only slightly greater, the improvement is notable considering the number of potential migration routes between populations. Each of these drainages is composed of hundreds of streams that drain from high elevations into the rivers. Given the extremely large number of potential habitat paths that fall within the hypothesized pattern of animal movement, and considering that many of these will also move in the same direction as the overland paths, an improvement of 5% when a specific model of animal movement is incorporated is substantial. The presence of this improvement indicates that the addition of this type of species-specific movement hypothesis will allow for a better estimation of reality than a pure shortest path hypothesis, even one that considers landscape features. Overall, the results of the landscape-based analyses provide strong support for the hypothesis that the riparian association of Pacific jumping mice facilitates dispersal along habitat pathways and that the presence and degree of connectivity of this type of habitat is contributing considerably to patterns of genetic structure.

Migration

Consistent with the patterns observed thus far, migration between subpopulations appears to be limited. Interestingly, the few subpopulations that were found to exchange a relatively large number of migrants were not necessarily within the same drainage (notably DBI & DWI and DBI & HHH). Although migration clearly was occurring to a large degree between DBI and DBM, as would be expected based on their proximity, it was occurring to a similar degree between DBI and DWI, across a large physical barrier. This cross-drainage pattern of migration would be unexpected under a model of animal movement largely directed by the presence or absence of topographic barriers. The combined results obtained for this species in the SA and landscape-based analyses, however, reveal that animal movement is restricted and appears to be directed by the location of riparian habitat. Given this observation, these cross-drainage patterns of migration are not surprising. Instead, they further support the hypothesis that, in this system, connectivity of

habitat plays a considerably larger role in limiting or facilitating dispersal and migration than does the presence of large topographic barriers.

Conclusion

In this study, a combination of methods was used to increase our understanding of the ways in which the interaction between dispersing Pacific jumping mice and their environment contributes to the creation of spatial genetic structure. Spatial autocorrelation analysis allowed for the identification of locally restricted dispersal. This may be due, at least in part, to the heterogeneity of riparian and mesic habitats and the limitations placed on dispersers by habitat boundaries. A landscape genetics approach revealed that both the inclusion of landscape features, and the inclusion of a species-specific model of animal movement, can greatly improve our understanding of the structuring forces that drive genetic distance and population divergence. The improved correlations found between genetic distance and increasingly landscape- and species-specific measures emphasize the importance of including both of these components in studies of population structure. The results of the landscape analysis support the habitat-directed model of Pacific jumping mouse dispersal and movement, although the presence of a very strong correlation between the two significant geographical distances is a complicating factor. Lastly, the investigation of current migration patterns between subpopulations allowed for an important final test of the hypotheses about this species. The limited number of migrants between subpopulations and the patterns of cross-drainage migration provide additional support for the presence of both restricted dispersal and habitat directed movement in Pacific jumping mice.

These results highlight the importance of exploring the relative role of habitat connectivity and topographic barriers in facilitating gene flow. Interacting subpopulations may not always be those we might presume based on topography, thus, the identification of these subpopulations requires more than basic topographic knowledge. Understanding this will be essential as we face the changes in habitat connectivity expected to come with increased anthropogenic fragmentation and climate change.

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Sacha Vignieri is a PhD candidate in the Department of Biology at the University of Washington. This study was completed as part of her dissertation research, which is focused on understanding the effects of habitat heterogeneity on the population genetics and ecology of the Pacific jumping mouse. She is interested in ecological, evolutionary, and conservation questions in mammalian populations.
