Dispersal, disturbance, and distance: the connection between ecological processes and spatial genetic patterns in the Pacific jumping mouse (*Zapus trinotatus*)

Sacha N. Vignieri

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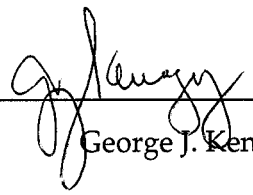

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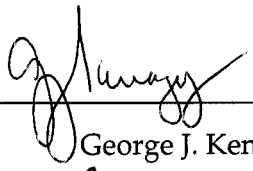

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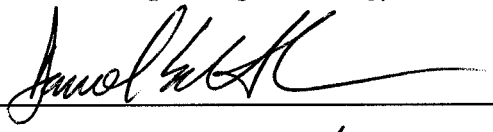

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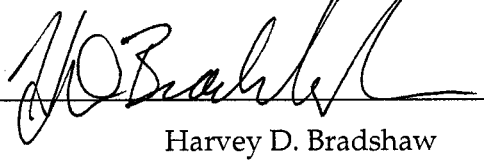

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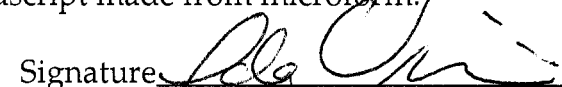
Signature 

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Abstract

Dispersal, disturbance, and distance: the connection between ecological processes and spatial genetic patterns in the Pacific jumping mouse (*Zapus trinotatus*)

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Professor G. James Kenagy
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Ecological mechanisms, such as dispersal, mating system, disturbance, and habitat affiliation can have profound impacts on genetic structure within a population, and on gene flow between populations. In this study, I isolated eight microsatellite loci from the Pacific jumping mouse (*Zapus trinotatus*) and used these to explore three components of the relationship between ecological processes and genetic structure. First, the genetic data were combined with field collected data on animal activity to reveal patterns of natal dispersal, mate choice, and reproductive success, and to infer the impacts of these on genetic structure in a small, semi-isolated population of Pacific jumping mice on the Dosewallips River in Washington State. I found a direct connection between patterns of dispersal and mating system, and the standing spatial genetic structure present in the population. Females were philopatric and mated with multiple neighboring

males. Dispersal was male biased, but interestingly was motivated by paternal avoidance. Consistent with these patterns, females were related and spatially structured, with proximal females more closely related than distant females, whereas these patterns were not present in males. The occurrence of a 25-year flood between the second and third year of this study allowed for the description of the impacts of the resulting bottleneck on this population. The spatial structuring found in the first component of the study in combination with the spatially explicit nature of the flood lead to spatially oriented survival and strong founder effects in the post-flood population; a rapid increase in relatedness, reduction in heterozygosity, and population divergence within a single generation. Finally, a GIS-based landscape genetics approach was used, in combination with fine scale spatial autocorrelation analysis and the estimation of recent inter-subpopulation migration rates, to infer patterns of dispersal and migration among nine populations across the larger three river system that includes the Dosewallips, Duckabush, and Hamma Hamma rivers. Dispersal was found to be limited in distance and movement of Pacific jumping mice across the landscape was directed along riparian pathways. These results indicate that patterns of dispersal and migration in Pacific jumping mice are largely determined by riparian habitat connectivity.

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To all of you, and to those I forgot

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DEDICATION

To the all of the creatures that have taught me what it is to be alive.

Your wordless expression of intelligence, emotion, and understanding consistently inspires me to explore the world around me and better understand its non-human inhabitants.

CHAPTER 1: ECOLOGICAL PROCESSES GENERATE GENETIC PATTERNS: NATAL DISPERSAL, MATING SYSTEM, AND FINE-SCALE STRUCTURE IN THE PACIFIC JUMPING MOUSE

INTRODUCTION

Dispersal has been described as the link between ethology, ecology, evolution, and population genetics (Stenseth and Lidicker 1992). In this context, dispersal refers to the movement of individuals from their natal site to their site of breeding (Howard 1960; Greenwood 1980) and thus describes the movement of an individual and its genes away from its kin to populations of less related individuals. Inherent in this definition of dispersal are four components, 1) the behavioral initiation of dispersal, 2) the ecological importance of dispersal as a generator of gender biased patterns in movement, home range, and mate selection, 3) the impact of dispersal on gender specific patterns of relatedness and therefore on allelic distributions within the population, and 4) the movement, by long distance dispersers, of genes from one population to another. Clearly, patterns of dispersal within a species have substantial impacts at both ecological and evolutionary levels, thus understanding such patterns can provide profound insight into the fundamental generation of mating system

(Greenwood 1980; Pusey 1987; Clobert *et al.* 2001), spatial genetic structure (Peakall *et al.* 2003; Double *et al.* 2005), and gene flow (Slatkin 1987; Johnson and Gaines 1990).

While known to be of extraordinary importance (Stenseth and Lidicker 1992; Dieckmann *et al.* 1999), dispersal has long been considered difficult to measure in the field (Koenig *et al.* 1996; Dieckmann *et al.* 1999). The task of marking pre-dispersal offspring and monitoring individuals during and after dispersal is generally prohibitive, and when undertaken may result in only a small number of identified dispersers. The relatively recent incorporation of molecular markers into studies of dispersal has greatly improved our ability to reveal dispersal patterns (Waser and Strobeck 1998; Peakall *et al.* 2003; Winters and Waser 2003; Double *et al.* 2005). Many studies incorporating genetic data have inferred patterns of dispersal between distinct populations through the use of F_{st} (Ennos 1994; Neigel 1997) and, more recently, assignment tests (Paetkau *et al.* 1995; Paetkau *et al.* 1998; Mossman and Waser 1999). While essential for understanding patterns of connectivity between populations, these population level approaches require the existence of allele frequency differences between focal populations and thus measure long term patterns of dispersal, *i.e.*, migration in the population genetic sense. More recently, individual level approaches, such as spatial autocorrelation and Mantel

tests designed to reveal patterns of local spatial genetic structure, have been employed within a single population (Peakall *et al.* 2003; Double *et al.* 2005). These methods reveal the patterns created by locally limited dispersal through the exploration of spatial patterning of genotypes. In addition, the use of genetically determined analysis of parent-offspring relationships has improved our ability to measure the movement of juveniles away from their parents in an indirect but quantitative way, as has been demonstrated in recent studies (Winters and Waser 2003; Proctor *et al.* 2004).

In this study I extend these individual based approaches by combining field and genetic methods in order to explore the connection between observed dispersal patterns, mating system, relatedness, spatial genetic structure, and gene flow in a patchily distributed small mammal species, the Pacific jumping mouse (*Zapus trinotatus*). The Pacific jumping mouse is a small rodent affiliated with riparian, meadow, and marsh habitat throughout its range from southern British Columbia to northern California (Maser et al. 1981). This affiliation results in Pacific jumping mice distributed as discontinuous subpopulations within semi-isolated patches of appropriate habitat. Activity in jumping mice is limited to approximately four months a year, from late April to late September (Edson 1932; Bailey 1936; Flahaut 1939) and they spend the remainder of the year in hibernation. Perhaps due to this brief annual period of activity, *Z. trinotatus*

(and *Zapus* species in general) display many life history traits unusual for small rodents. In particular, *Z. trinotatus* and its better studied congener *Z. princeps*, are relatively long lived, perhaps to seven years of age, and are thought to have high adolescent survival (Maser *et al.* 1981; Falk and Millar 1987). Females spend approximately half their active period producing a single litter of four to eight offspring per year (Bailey 1936), with approximately 18 to 23 days spent in gestation and a month or more in lactation (Maser *et al.* 1981). Both males and females become sexually mature in the summer following their birth (Maser *et al.* 1981), however, Falk and Millar (1986) found that 59% of juvenile female *Z. princeps* yearlings did not breed in their first year and that 30% of females aged 2 to 6 did not breed in a given year.

An estimate of neighborhood distance in *Z. trinotatus*, made using a spatial autocorrelation approach, indicates that dispersal is limited in this species (Vignieri 2005), however little else is known about its dispersal patterns and mating system. The unusual life history traits of the Pacific jumping mouse and its strong affiliation with patchily distributed habitats make it an ideal species in which to explore the connection between intrapopulation natal dispersal, mating system, spatial genetic structure, and gene flow. In order to explore this connection, genetic data from eight variable microsatellite markers were used to assign parentage to sampled

juveniles and to investigate patterns of relatedness and spatial genetic structure in a semi-isolated population of Pacific jumping mice on the Dosewallips River, in Washington State (Fig. 1.1a). These results were combined with mark-recapture data collected in the field in order to estimate dispersal distances and home range, and to determine movement patterns and locations of breeding individuals. In addition, the influence of long distance dispersers, or migrants, was examined through the detection of first generation migrants within the population. This combination of genetic data with detailed field data revealed intriguing patterns of dispersal, and the results of this study demonstrate empirically the powerful influence of ecological forces such as dispersal and mating system on genetic structure.

MATERIALS AND METHODS

Study site and population sampling

A 25,600m^2 trapping grid was constructed in June 2000 on a section of riparian habitat created by a meander in the Dosewallips River on the Olympic Peninsula in Washington State (Fig. 1.1A-C). This patch of riparian habitat contains a small population of Pacific jumping mice that is semi-isolated on three sides by the river meander and on the fourth by a steep slope beneath a road. A total of 245 (2000 and 2001) or 253 (2002) permanent

trap stations were placed in rows along a compass heading of 220° at 10m intervals to cover the area (Fig. 1.1c). The difference in number of traps in 2002 is due to the loss of four trap stations along the western edge of the grid, and the gain of 12 along the north-eastern edge, as a result of a 25 year flood event that occurred during the winter between the 2001 and 2002 seasons. The specifics of the flood and the substantial impacts of this flood on the population have been described in detail elsewhere (see chapter 2) and will not be repeated here. It is important to point out, however, that the population did experience a demographic and genetic bottleneck and that the impacts of the bottleneck were spatially explicit, with high survival centralized away from the river.

Nine sampling sessions occurred during the initial year, 2000, from June through September, totaling 2205 trap nights. In 2001 and 2002 trap sessions occurred every fourth week from the end of April through the end of September for 4 to 5 consecutive nights, for a total of 6125 (in 2001) and 7105 (in 2002) trap nights. Trapping was performed using Sherman traps (model #LFA) baited with heat-treated sunflower seeds. On their first capture event, all individuals were given a unique ear tag, weighed, aged, sexed, sampled for tail-tip tissue and released. On all recaptures animals were weighed, assessed for reproductive status, and released. Trap location was recorded for each capture. Except in analyses combined across years,

all individuals caught within a year were considered part of that year's population, even if first caught in a previous year. Age was recorded in the field, and a more precise identification, which included date of first lactation, weight of known adults, and last recorded capture date of a known adult, was made at the end of the study. See chapter 2 for a detailed description of this classification process.

Genetic Sampling and Analyses

Upon collection in the field, tissue samples were immediately placed in 95% ethanol and these were then stored in the laboratory at -80°C until the time of extraction. Each individual was genotyped at eight microsatellite loci, isolated from *Z. trinotatus,* (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 conditions, and genotyping of individuals were as described in Vignieri (2003), see Appendix A for details. Per-locus genetic variation in the form of expected heterozygosities (Table 1) was assessed across all years using the method of Nei (1987) as implemented in the program FSTAT (Goudet 2001). Significant per-locus deviation from Hardy-Weinberg equilibrium was

determined using the global exact test of Guo and Thompson (1992) as implemented in GENEPOP v3.4 (Raymond and Rousset 1995)

Parentage assignment

Because all individuals were captured after weaning, molecular genetic analysis of parentage was required. Candidate parents in each year consisted of all adults captured in that year. The likelihood based approach implemented in the program CERVUS (Marshall *et al.* 1998) was used sequentially to assign mothers and fathers for all young of the year in each year. In this method a log-likelihood ratio score, the LOD, is obtained for each candidate parent as the logarithm of the ratio of the likelihood that the parent is the true parent to the likelihood that it is not the true parent. A delta (Δ) score is next calculated as the difference between the two most likely candidates and confidence of the parent assignment is determined by comparison of the delta score to a delta distribution generated through a parentage simulation based on the observed allele frequencies. Due to the potential for amplification error in the genotyping process, this method allows for the identification of parent-offspring dyads with some number of mismatching loci. In order to minimize parentage misassignments a low typing error rate of 0.001 was invoked which decreased the likelihood of a parent-offspring match with multiple mismatching loci. Further, only

parent-offspring assignments made with 95% confidence and a maximum of one mismatch per parent were used in further analyses.

Annual reproductive success was determined as the number of offspring assigned to each individual parent, averaged across all adults identified as breeders, in each year. Individual reproductive success was determined as the absolute number of offspring each potential parent was assigned throughout the study. The age at first capture was determined for each individual assigned as a parent in order to investigate gender differences in post-juvenile breeding.

Patterns of genetic similarity

Average relatedness, *R*, among adult males and females and among males and females identified as breeders was calculated using the method of Queller and Goodnight (1989), using their program Relatedness, for each year. In these analyses, background allele frequencies used for each year were those present only in that year and significance was determined using a t-test to compare R values with standard errors calculated through bootstrap resampling across loci. Pairwise relatedness, *pR*, was calculated, also using Relatedness, between all identified mated pairs in each year to determine average *pR* of mates. In order to determine if mate selection was random with regard to relatedness, a Monte Carlo resampling approach

with 10000 iterations was used, within the program PopTools version 2.6 (Hood 2000), to sample all possible adult pairings in each year. In each iteration, *pR* values were selected randomly from a matrix containing all adult males and females in each year. The number of simulated pairs drawn in each iteration was equal to the number of mated pairs observed and the mean *pR* was calculated for each iteration to estimate the 95% confidence limits of possible relatedness between mated pairs.

To explore patterns of spatial genetic structure in males and females, a Mantel test, within the program GENALEX version 6 (Peakall and Smouse 2005) was used, with 9999 permutations, to test for a correlation between pairwise genetic distance and pairwise linear geographic distance. The X,Y location for each individual was determined as the centroid of each individual's calculated home range (see below) in each year, except in cases of single captures for which the single capture point was used. Genetic distance was calculated as described in Smouse and Peakall (1999); briefly, as the squared distance between two individuals at each locus, averaged across loci, with individuals sharing both alleles having a value of zero, individuals sharing one allele having a value of one, and individuals sharing neither allele having a value of two.

Presence of first generation migrants

In order to investigate the influence of migrants from adjacent populations, first generation migrants were identified using the likelihood based method of Paetkau et al (2004) and the frequency based assignment criteria of Paetkau et al (1995) within the program GENECLASS 2 (Piry *et al.* 2004). Using this method, the likelihood, L_h, that the alleles carried within an individual would have been drawn from the allele frequency distribution present in the focal population and two source populations, averaged across loci, was calculated. A delta value was then determined for each individual as the division of the likelihood that it was born in the sampled population by its maximum likelihood in any population. A delta distribution for rejection of the null hypothesis (that an individual was born in the focal population) was created using the Paetkau et al (2004) Monte Carlo sampling method with 10000 iterations and a Type I error rate of 0.005. This process creates simulated individuals by drawing multilocus gametes, with replacement, from candidate source populations. The employed Type I error rate resulted in the possibility of 0.480, 0.475, and 0.435 individuals misidentified as migrants in each year, respectively (determined as *N*0.005* in each year). Although the more appropriate measure to use in cases where not all source populations are represented, L_h has less power to identify migrants than estimators that assume that all source populations are included, *i.e.* Λ (Paetkau *et al.* 2004). Power of L_h

equal to that observed in Λ can be produced when the Type I error is increased by 5 times (Paetkau *et al.* 2004), however in the present study such an increase resulted in an unacceptable error rate of 2.2 to 2.4 individuals potentially misidentified as migrants per year. Based on these two factors, an error rate of 0.005 was chosen as an acceptable compromise between power and Type I error. In order to identify migrants from areas outside the study area, genetic data from two other populations within the Dosewallips river drainage were used as potential source populations. Size, population structure, and genetic characteristics of these two populations, located at either ends of the current study population in the mouth and center of the Dosewallips River, have been previously described (Vignieri 2005), see chapter 3. It will be useful to point out here, however, that significant allele frequency differences exist within these two source populations and that the sample sizes were similar in each, at n=31 in the Dosewallips center and n=26 in the Dosewallips mouth.

Animal movement analyses

Home range

An annual home range was constructed for all individuals captured three or more times, using a 100% minimum convex polygon (MCP) in the program Biotas™ (Ecological Software Solutions). The centroid for each

individual home range was then calculated as the gravitational center of this area and this point was generally used in all pairwise comparisons requiring an X,Y location. The centroid for individuals captured only twice, or captured multiple times at only two locations, was determined as the halfway point between the two capture locations, and the X,Y point for individuals captured at only one point was equal to that single capture point. Consistency of individual home ranges across the three years of the study was estimated by measuring the area of overlap between an individual's home range across years and then determining the percentage of the home range in each year that area represented. In individuals for whom no overlap was observed, the distance between centroids in each year was measured. Additionally, across all individuals, the distance was measured between successive captures and the longest absolute distance moved was measured as the longest distance between two capture points.

Overlap between individuals identified as a mated pair was calculated in the same way as overlap for consistency of home range across years. In pairs for which no home range overlap was observed, distance between home ranges was measured in two ways: as the distance between each individual's home range centroid and as the closest distance between capture points for each individual.

Dispersal

Dispersal was measured as the distance between each juvenile's home range centroid and the centroid of both its mother and father (as identified through parentage analysis). These calculations were made in juveniles for whom both parents were identified. A two factor, mixed model ANOVA with repeated measures was used to test for significant differences in dispersal measured as distance from father and mother in males and females. Additionally, the distance between a juvenile's last capture point and the centroid of its mother's home range was calculated in order to determine if individuals moved farther from their natal sites as the season progressed. In the few cases where an individual initially captured as a juvenile was captured in subsequent years, the distance between its home range centroid in each year was measured and compared to the distribution of single year measures of dispersal.

RESULTS

A total of 225 Pacific jumping mice was marked and sampled over the three year study period. In 2000 and 2001, 96 and 95 individuals were captured, respectively. In 2002, following the flood, the number of individuals decreased slightly with a total of 87 individuals captured. Sex ratio was near unity across the three year study. In 2000 and 2001 the

number of adults was greater than the number of juveniles with 61 (n_M=24, n_F=37) and 74 (n_M=38, n_F=36) individuals identified as adults captured in each year respectively (with the number of juveniles at 25 and 20). In 2002, this pattern was reversed, with only 35 (n_M=15, n_F=20) adults captured as compared to 50 juveniles. As measured by over-winter survival and recapture, 35% of individuals survived from 2000 to 2001 (n=34; n_{juv}=6, n_{adult}=26, $n_{unknown}$=2) and juvenile survival was low. Increased mortality in the year of the flood decreased survival to 20% between 2001 and 2002 (n=19; n_{juv}=0, n_{adult}=19) and juvenile survival to zero. Estimated survival across the duration of the study was 9% with nine individuals surviving to be captured in all three years. Seven of the nine individuals to survive the duration of the study were first captured as adults, indicating a 7% survival rate to at least four years of age.

Home range and movement

Male home ranges were larger than female home ranges across all years (t-test, df=1, p=0.01, Fig 1.2a). Female home ranges were significantly smaller than those found in both adult and juvenile males and those in juvenile females (ANOVA, p=0.01, Table 2, Fig 1.2b). Post-hoc multiple comparisons in the form of least significant differences (LSD) revealed that there was no difference between juvenile and adult males (p>0.05).

Consistency of individual home range location was found throughout the study, with 60% of individual home ranges overlapping across years and with the amount of overlap varying from10% to 58%. This consistency is also reflected in the short distance between home range centroids across years ($d_{00\text{-}01}$=35.0m, SE=5.5m; $d_{01\text{-}02}$=45.3m, SE=7.4m; $d_{00\text{-}02}$=30.3m, SE=3.4m). The majority of movements (80%, 72%, and 73% in each year, respectively) made between any two captures within a year fell within the width of an average male home range in all three years, however a small proportion of movements made were considerably farther than the average (Fig. 1.3). The farthest distance moved differed between males (n=54) and females (n=54) with the mean longest distance between any two capture points significantly (t-test, df=1, p=0.008) longer in males (d=112.0m, SE=8.8m) than in females (d=83.1m, SE=5.9m). The farthest distance moved by juvenile males (n=30, d=107.5m, SE=12.5) was longer than the farthest distance moved by juvenile females (n=25, d=78.3, SE=9.0) (t-test; df=1, p=0.03). There was no significant difference between the farthest distance moved in adults and juveniles.

Patterns of relatedness and spatial genetic structure

Adult males (R=-0.0014 SE=0.012) were significantly (p=0.001) less related than adult females (R=0.0171 SE=0.008) across all years. There was

no significant difference between juvenile males (R=0.0005) and females (R=0.0012, p=0.8838). In analyses conducted by year, the above pattern in adult relatedness was observed in both 2001 and 2002 ($p_{00} \leq 0.001$, $p_{01} \leq 0.001$, Fig 1.4a). Interestingly, in the initial year of 2000, during which sampling was initiated later and was not conducted as regularly, this pattern was not observed (p=0.7089). The apparent difference in this year is largely due to increased relatedness observed among males, as little change in relatedness among females is present between 2000 and 2001. In 2002, the year following the flood, adult female relatedness increased significantly above that observed in previous years ($p_{00\text{-}02}=0.006$, $p_{01\text{-}02}=0.001$). This change was not observed for males (Fig. 1.4a)

Mantel tests revealed the presence of significant spatial structuring among adult females in 2001 (p=0.023, $R_{xy}=0.138$, Fig. 1.5a) and a similar pattern in 2002 (p=0.090, $R_{xy}=0.127$, Fig. 1.5b, years were not statistically independent since 22% of the individuals present in 2002 were also present in 2001). In each of these two years there was no correlation observed among adult males. As similarly observed for non-spatial relatedness, there was no difference between males and females in 2000 and no significant correlations were present (all $p \geq 0.05$, males $R_{xy}=0.082$, females $R_{xy}=-0.086$, not shown).

Parentage and mating system

Average numbers of alleles across loci of 8 to 21 resulted in a 99% power of parentage exclusion (Table 1). The majority of juveniles were assigned parents in each year with 80% confidence, however the stringent requirement of 95% confidence and only one mismatch per parent reduced the number to approximately 50% in each year (Table 3). These stringent requirements decreased the sample size of identified parent-offspring triads, but increased confidence in the patterns observed among triads. A varying proportion of adults were assigned as parents to the 95% confidence group of offspring, from a relatively low 17% of females in 2001 to a high of 45% of females in 2002 (Table 3). Multiple pairings were revealed through parentage analysis, with both males and females being matched with more than one mate in a single year (Table 3). Thus not only were males breeding with multiple females, but in some cases multiple males were fathering the offspring within the sole litter of a single female. Despite these observed patterns of multiple matings, average reproductive success was near one for both males and females in 2000 and 2001 (Fig. 1.6). This value increased for both males and females in 2002, where a few individuals were identified as the parents of multiple offspring. Individual reproductive success ranged from one to a maximum of seven, and averaged 2.1. All males identified as parents were first captured as adults.

This was not true for females, where 30% of females identified as mothers were first captured as juveniles in one of the previous years.

Average relatedness among female breeders was significantly higher than that observed among male breeders in both of the pre-flood years (t-test, df=1, p_{00}=0.001, p_{01}=0.05, Fig 1.4b). Observed means of relatedness between mated pairs did not fall outside of the Monte Carlo 95% confidence distribution of possible matings (Fig 1.7). Many breeding pairs (23%) overlapped in home range. Mean distance between the male and female in a breeding pair, as measured between centroids and between nearest points, was 80.3m (SE=8.9) and 60.4m (SE=11.0) respectively, indicating that when not overlapping, the majority of individuals chose mates from within a distance equivalent to two home ranges.

Dispersal

When measured in the traditional way, distance from natal or maternal home range, males (n=18, d=51.6m) did not disperse significantly (t-test, df=1, p=0.06, Fig. 1.8) farther than females (n=22, d=73.7m). Interestingly, however, males (d=104.3m) were found to disperse significantly farther than females (d=73.8m) when dispersal was measured as distance from paternal home range (t-test, df=1, p=0.03, Fig. 1.8). A two factor ANOVA revealed an interaction effect between offspring gender and

distance from parent (Table 4, $p=0.01$) and post-hoc multiple comparisons revealed that males dispersed significantly farther from their father than they did from their mother ($p<0.05$), and they dispersed significantly farther from their father than did females ($p<0.05$, Fig 1.8). There was no difference in the distance dispersed by females from their mother and father ($p>0.05$).

There was no difference between dispersal measured as the distance between maternal and offspring centroid and that measured as distance between maternal centroid and last offspring capture point in the season (males-$d_{central}$=51.6m SE=8.64m, d_{last}=48.0m SE=9.68m; females-$d_{central}$=73.7m SE=10.1m, d_{last}=75.5 SE=9.91m; t-test, df=1, $p=0.533$) indicating that dispersal distance did not increase as the season progressed. Distance between home range centroids across years of individuals first captured as juveniles could be measured in five individuals, four females and one male. These distances fell below and outside of the distribution of parent-offspring dispersal distances, however, well within the distribution of distances between home range centroids across years (data not shown) revealing that dispersal occurred during these individuals' first summer and not following their first hibernation.

Of the 225 jumping mice captured over the duration of the study, just two individuals were identified as long distance dispersers, or

migrants, from the two potential source populations. This number of identified migrant individuals indicates a measured migration rate of 0.67 per year. These individuals, #283 and #383, were both identified as migrants from the Dosewallips mouth population ($p \leq 0.01$), both were male, and both were first captured as adults. The first of these long distance dispersers, #283, was initially captured in 2000 and the second in 2001. No new migrants were identified in 2002. Male #283 was captured in both 2000 and 2001, but no offspring were assigned to him in either of those years. Male #383 was captured in both 2001 and 2002 and he was assigned as the father of one offspring in 2002.

DISCUSSION

There is a fundamental connection between genetic structure and gene-flow and the actions of individuals (Crow and Kimura 1970; Wright 1978; Lidicker and Patton 1987; Shields 1987). Although this is well understood (Koenig *et al.* 1996; Clobert *et al.* 2001), few studies have sought to address this connection directly (Sumner *et al.* 2001; Winters and Waser 2003). Through a comprehensive combination of field and genetic data, this study demonstrates the strong relationship between locally driven processes, such as dispersal and mating system, and fine scale genetic structuring within a population. Further, it reveals that patterns observed at

the genetic level are not always generated at the ecological level in the way we might assume.

Genetic structure

Patterns of relatedness and genetic structure in Pacific jumping mice were found to be gender specific. Adult females were significantly more related than adult males over the duration of the study and in each of the two years for which sampling was conducted throughout the entire active season. The failure to detect this pattern in the first year is likely a result of the incomplete sampling scheme used in that year, which resulted in incomplete spatial data and may have complicated age classification. Interestingly, in the year following spatially oriented flood survival, relatedness among females increased. These results demonstrate the persistence of female relatives within the breeding pool and suggest that the importation of novel genetic diversity is largely facilitated by males.

Similarly, despite the small scale of the study, a positive correlation between genetic distance and geographic distance was found in females demonstrating that neighboring females are closely related. There was no correlation observed between genetic and geographic distance in males indicating increased mixing of male genotypes relative to space over this small scale. Fine scale spatial genetic structure indicative of limited

dispersal (Wright 1943; Malecot 1946; Peakall *et al.* 2003) has been previously detected in this species (Vignieri 2005), using spatial autocorrelation analysis over a larger geographic scale. The detection of gender specific patterns of relatedness and spatial genetic structure in this study confirms this previously observed pattern of limited dispersal in Pacific jumping mice and further suggests that patterns of dispersal are different for males and females (Chesser 1991, 1991; Peakall *et al.* 2003).

Mating system

The informative microsatellite loci used in this study provided reasonable power to detect parent-offspring relationships, however stringent requirements limited absolute matching success to approximately 50%. Despite the reduced sample size, parent-offspring triads that were identified were done so with high confidence. In addition, the inability to assign parents to a number of offspring was likely not due to their being the offspring of unsampled individuals, for a number of reasons. The majority of offspring were assigned to resident parents with 80% confidence in each of the two pre-flood years 2000 and 2001. Fewer offspring were assigned to resident parents in 2002, however, in this year the relatedness of both adults and juveniles increased, as will be discussed in chapter 2. Contrary to this observed pattern, had the flood precipitated a punctuated influx of

migrants, we might expect relatedness among individuals within the population to decrease. Further, high relatedness among potential parents will increase the number of offspring not assigned parents due to small differences in likelihood scores between potential, related parents (Marshall *et al.* 1998). Given the relatedness results obtained in this study, this may have contributed to the lower parentage assignment success throughout the duration of the study, as well.

Mated pairs often had home ranges that overlapped; when not overlapping, mates generally lived within two home ranges of each other. Male home ranges were larger than female home ranges allowing for overlap of a single male home range with that of multiple females. This observation was complemented by the finding that males are polygynous in this species, as might be expected, and tend to mate with multiple neighboring females. Interestingly, however, in two of the years females were found to have multiple mates for the production of a single litter, indicating that females are also breeding with multiple nearby males. Polyandry in females has been hypothesized to increase fitness in multiply mating females through a variety of mechanisms; from 1) the acquisition of direct benefit through avoidance of male harassment, to 2) improving on previous mates through pre-copulatory choice, 3) using post-copulatory mechanisms to bias paternity toward the "best" male, 4) production of

genetically varied offspring in order to "bet-hedge" regarding their adaptability to changing environments, and 5) overall reduction in relatedness among offspring (Jennions and Petrie 2000). Given the production of a single litter per year in Pacific jumping mice, the dynamic nature of riparian habitat, and the spatial genetic structure present among females, it is possible that many of these mechanisms are acting in this species. Although it is beyond the scope of the present study, future studies may reveal the action of these mechanisms.

In polygynous mating systems, males are expected to accept the increased risk associated with greater movement in exchange for the higher reproductive success acquired by breeding with multiple females (Clutton-Brock 1989). Interestingly, were one to investigate jumping mice only in terms of home range size and presumed male behavior, they would likely conclude that a purely polygynous system is acting in this species. The incorporation of parentage analysis in this study, however, revealed a pattern slightly different from that that might be assumed. In Pacific jumping mice multiple matings occurred in both males and females. This pattern of both polygynous males and polyandrous females is consistent with a promiscuous, facultative mating system wherein both males and females may breed with multiple neighboring individuals (Clutton-Brock 1989). Despite these patterns of multiple matings in both males and

females, average reproductive success was near one in both genders in the two pre-flood years of the study. This pattern of low and equal reproductive success is atypical in a polygynous/promiscuous mating system and is more commonly found in long lived, monogamous species (Clutton-Brock 1988). However, the unusual life history traits exhibited by *Zapus* species, such as multiple year longevity and small annual litter size, are somewhat consistent with expectations of low annual reproductive success.

In the year following flood-induced high mortality, reproductive success increased overall and was higher in males than in females, a change likely resulting from reduced mate competition and increased survival in young of the year. This post-flood increase is particularly interesting due to the affiliation of jumping mice with dynamic, flood prone, riparian habitats. The advantage afforded to multiply breeding males and females in years following occasional flood events may prevent the evolution of smaller male home ranges and a less promiscuous mating system in this relatively long-lived small mammal, despite the low and equal reproductive success observed in non-flood years.

An examination of the observed mating system in jumping mice in light of the other components of this study provides insight into its role as a structuring force. Individuals tend to breed with neighbors thus creating

the potential for the development of strong spatial genetic structure. Additionally, patterns of breeding and reproductive success impact relatedness in the population. In average years, low reproductive success and polyandry of females with likely unrelated males results in lower levels of relatedness within the population, as observed in 2000 and 2001. In contrast, in unusual years where average reproductive success is high and a few surviving individuals produce the majority of offspring through multiple pairings, offspring on the whole will be more closely related, as observed in this population following the flood in 2002 (see chapter 2). Given the propensity for individuals to breed with neighbors and the influence mating system has on relatedness, dispersal can be expected to play a large role in facilitating gene-exchange within the population.

Dispersal

Natal dispersal, the movement of individuals away from their natal site, is an important ecological and evolutionary process (Wright 1943; Koenig *et al.* 1996; Dieckmann *et al.* 1999; Clobert *et al.* 2001). In mammals, this process has been found to be strongly gender biased with primarily males, in most species, propelled to move away from their natal, or maternal, home range (Greenwood 1980; Dobson 1982; Greenwood 1983). Following the strict definition of dispersal as movement from maternal

range, there was no difference found between dispersal in males and females in this study, with the maternal distance in both males and females approximately two home ranges in distance, or less. In fact, although the difference was not significant, the average distance moved by females from their maternal site was larger than that observed in males. Clearly, however, there is strong evidence for increased movement and dispersal among males. Relatedness is significantly lower in males than in females and they display no pattern of relatedness based on location, whereas spatial genetic structure is present in females. Additionally, both male home ranges and the longest distance moved between any two captures were larger in males than in females, indicating a greater propensity for males to make longer daily and long-distance movements.

Following only the strict definition of natal dispersal as maternal distance would have revealed no gender differences and resulted in a contradiction between the behavioral pattern and the genetic pattern in this species, as has been observed previously for other species (Waser and Elliott 1991). In this study, however, the identification of father-offspring pairs, in conjunction with mark-recapture data and home range construction, allowed for movement away from paternal site to be revealed as an important component of natal dispersal. Such paternally influenced juvenile dispersal will have impacts similar to maternally influenced

dispersal, i.e. the separation of related littermates and the integration of their genotypes into areas outside of the pool of locally generated offspring. However, the distance moved by an individual prompted to disperse due to avoidance of his father may be larger because of the larger home ranges in males. While the behavioral motivation of father avoidance was not determined in this study, aggressive interactions and scent cues are likely possibilities (Wilson 1975; Brandt 1992).

A pattern of male biased dispersal is apparent in first generation migrants as well. Only two migrants were identified over the three year study, indicating that migration into this population is relatively low. These two migrants were both male and at least one of them reproduced within a year of arrival. Although the small number of migrants prohibits any conclusions, the fact that both were male is consistent with other patterns observed; male-biased dispersal, longer movements, and lower relatedness among males. Additionally, no male first captured as a juvenile was assigned to any of the 95% confidence offspring, whereas 30% of females assigned as mothers were first captured as juveniles. This pattern suggests both that yearling male dispersers are more successful (or more available) than native yearlings, and that reproductive success of males may increase with age.

Conclusion

The interaction between ecological processes, such as dispersal and mating system, and evolutionary patterns such as population structure and gene-flow has long been predicted (Greenwood 1980; Greenwood 1983; Slatkin 1987; Chesser *et al.* 1993), but until recently has rarely been examined empirically (Sumner *et al.* 2001; Winters and Waser 2003; Double *et al.* 2005). In this study, ecological mechanisms in the Pacific jumping mouse were described within a small population and related directly to the genetic patterns observed within that population. Gender-specific patterns of genetic structure were found to be generated by a combination of gender-specific dispersal and the selection of nearby individuals as mates. Surprisingly, although dispersal was male biased, patterns of male dispersal were generated by movement of juvenile males away from their father's home range, rather than their mother's. Paternally influenced natal dispersal has rarely been observed (Gerlach 1996), however the results of this study indicate that this alternative behavioral motivator may be an important component of the dispersal process. In addition, mating system was found to be facultative polygyny/polyandry rather than purely polygynous. This pattern had direct effects on gender based reproductive success, and influenced patterns of relatedness, particularly following a natural disturbance.

These local ecological processes clearly impact evolutionarily important genetic patterns. The specifics of each of these mechanisms, however, would likely have been missed in a purely genetic study of dispersal or genetic structure. While the application of genetic techniques to studies of dispersal has vastly improved our ability to detect patterns of dispersal, the results of this study indicate that they should not be used singly to infer the specifics of the ecological processes generating these patterns. Thus, the sole collection of genetic data should not be substituted for field-collected data and exploration. Rather, this study demonstrates that the combination of powerful genetic methods with detailed, field-based inquiry and data collection can result in a previously unequaled ability to reveal the connection between complicated ecological mechanisms and evolutionarily important patterns at very fine scales.

Table 1.1 Genetic diversity and exclusionary power of eight Pacific jumping mouse (*Zapus trinotatus*) microsatellite loci within a small population of jumping mice over three years, expressed as (A) the average number of alleles and observed (H_o) and expected (H_e) heterozygosities observed per locus during the study, and the probability of excluding an incorrect parent when (P_E-1st) no parents are known, and (P_E-2nd) after one parent has been identified for each locus, and when all loci are combined, in each year. Deviation from Hardy-Weinberg equilibrium in a single locus indicated by *$p \leq 0.05$, ***$p \leq 0.001$

				2000		2001		2002	
Locus	A	H_o	H_e	P_E-1st	P_E-2nd	P_E-1st	P_E-2nd	P_E-1st	P_E-2nd
Ztri2	17.00	***0.755	0.895	0.635	0.777	0.655	0.792	0.627	0.771
Ztri24	10.33	*0.842	0.863	0.544	0.707	0.568	0.727	0.554	0.715
Ztri3s	10.00	0.736	0.771	0.382	0.563	0.432	0.610	0.368	0.550
Ztri17	12.00	0.823	0.850	0.558	0.719	0.532	0.697	0.509	0.678
Ztri18	21.00	0.930	0.923	0.699	0.823	0.726	0.841	0.727	0.841
Ztri4	8.00	0.777	0.804	0.429	0.607	0.435	0.613	0.431	0.608
Ztri19	8.67	0.875	0.807	0.455	0.631	0.463	0.638	0.419	0.597
Ztri19+	9.33	0.757	0.755	0.432	0.610	0.378	0.558	0.320	0.500
Total probability of exclusion				0.998	0.999	0.998	0.999	0.997	0.999

Table 1.2. Mixed model ANOVA results for analysis of home range size in Pacific jumping mouse adult and juvenile males and females, with (*df*) degrees of freedom, (*MS*) mean squares, (*F*) F-score, and (*P*) significance.

	df	MS	F	P	Variables
Between groups	3	14510014	3.9338	0.0106	Juv-females
Within groups	103	3688502			Juv-males
Total	106	3994771			Adult-females
					Adult-males

Table 1.3. Pacific jumping mouse 95% confidence parent-offspring triads. Both individual identification numbers are indicated when both a mother (F) and a father (M) were identified. Percentage of all candidate adult males and females identified as parents is indicated.

2000			2001			2002		
Offspring	M	F	Offspring	M	F	Offspring	M	F
229	279	240	422	256	235	620		229
231	293	238	423	256	235	552	242	254
232	258	250	433	256	235	592	242	254
236	289	284	428	260	324	553	358	254
239	279	240	441	271	244	538	339	273
248	242	240	427	281	229	601	339	273
254	260	296	436	281	229	608	392	273
269	258	270	435	285	265	611	392	273
286	208	244	437	285		622	392	273
313	245	238	432	378		605		273
316	245	255	426	383	268	540	399	341
323	260	261	431	400		543	399	341
336	280	235		21%	17%	603	358	398
338	280	246				544	392	404
	33%	30%				548	392	404
						550	358	421
						545		533
						549		533
						551	339	535
						589	339	535
						602	358	535
						609	358	535
						610	358	535
						614	358	535
							33%	45%

Table 1.4. Two factor ANOVA results for analysis of dispersal distance from mother and father (distance from parent) in juvenile male and female (gender) Pacific jumping mice, with (*SS*) sum of squares, (*df*) degrees of freedom, (*MS*) mean squares, (*F*) F-score, and (*P*) significance.

Source	SS	df	MS	F	P
Between genders	95368.19	39			
Gender	543.64	1	543.64	0.22	0.64
Subjects within gender	94824.55	38	2495.38		
Within gender	105882.50	40			
Distance from parent	10237.81	1	10237.81	4.81	0.03
Gender X Parent distance	14768.21	1	14768.21	6.94	0.01
Distance from parent X Subjects within gender	80876.48	38	2128.33		
Total	201250.69	79			

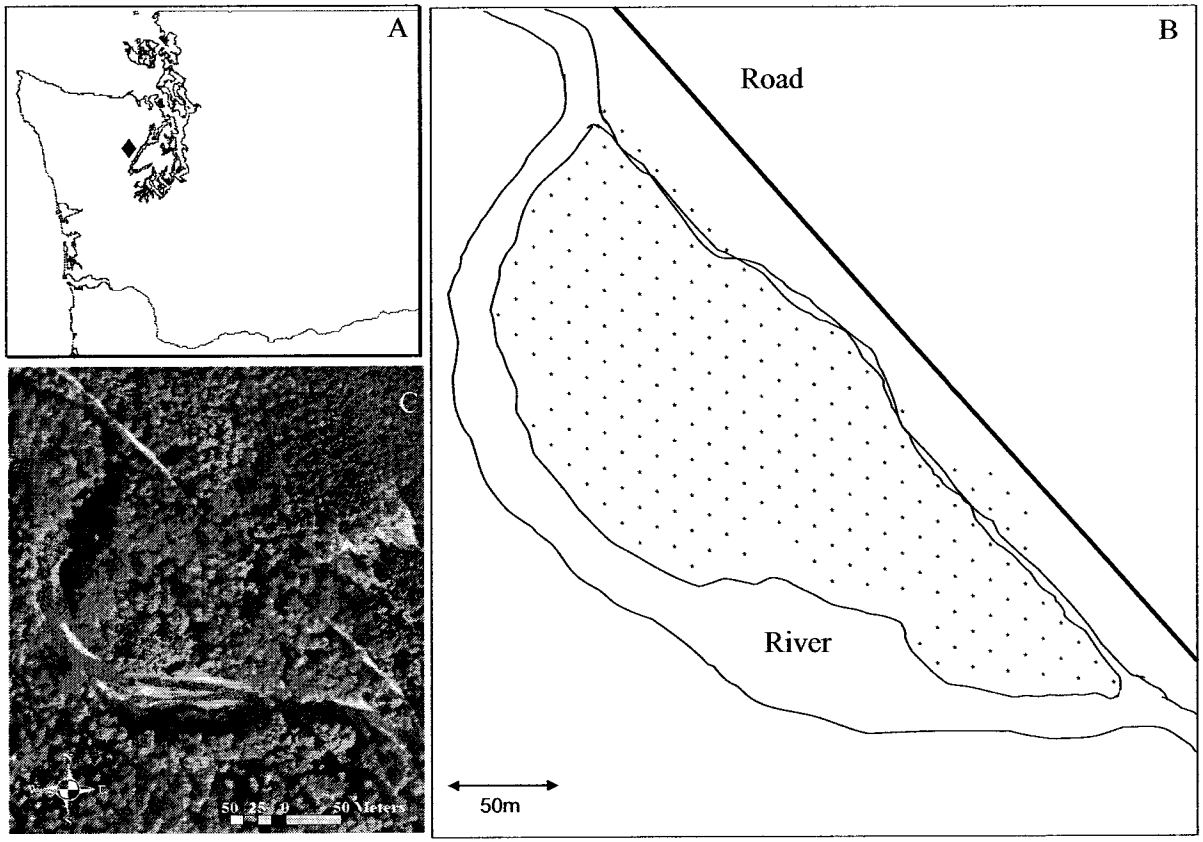

Fig. 1.1 (A) Location of Pacific jumping mouse population subject to study on the Dosewallips River on the Olympic Peninsula in Washington State. (B) Aerial photograph of the patch of riparian habitat, created by a river meander and semi-isolated by the river and a road, within which the study population exists. (C) Map of the sample grid established within this area consisting of traps placed 10m apart along a 220°compass heading (trap locations indicated by dots).

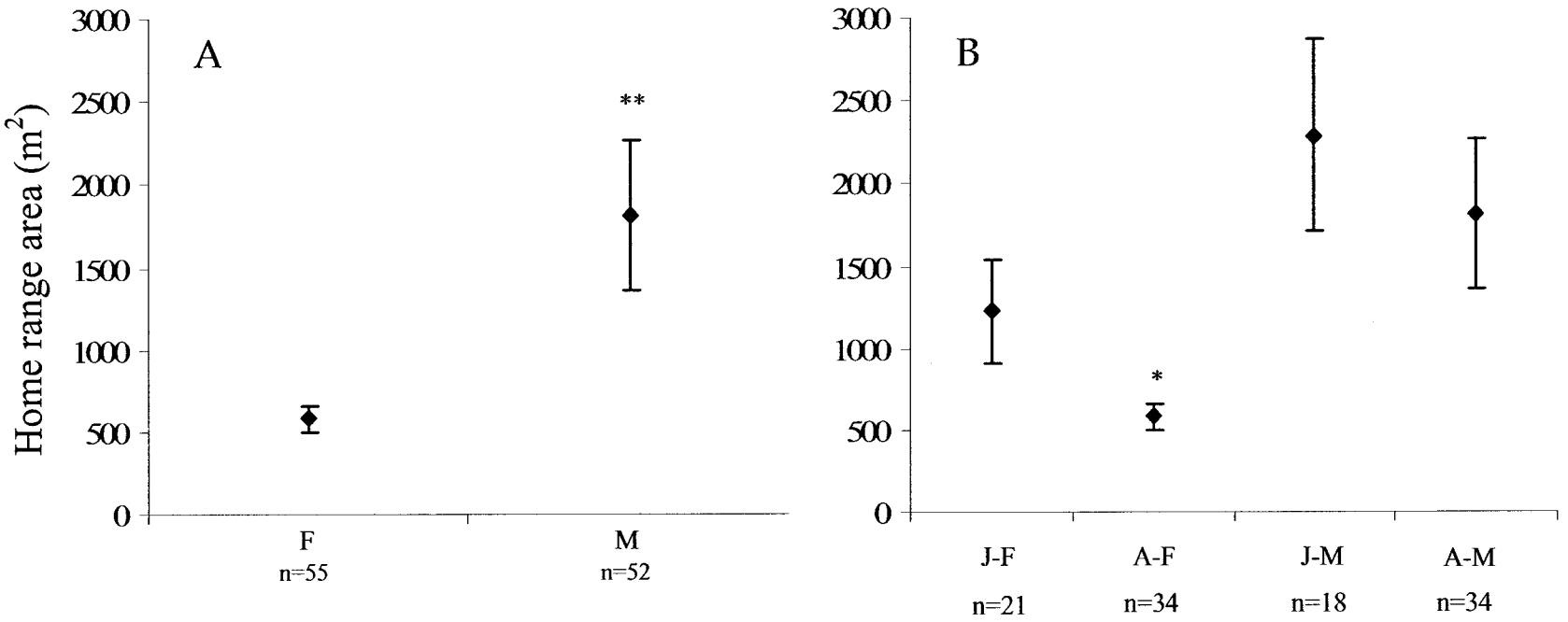

Fig. 1.2. (A) Home range size of male (M) and female (F) Pacific jumping mice averaged across the duration of the three year study with sample sizes indicated by "n" and significance **$p \leq 0.01$. (B) Average home range size in adult and juvenile males and females with significance of *$p \leq 0.05$ for a comparison made among all groups. Bars are standard errors.

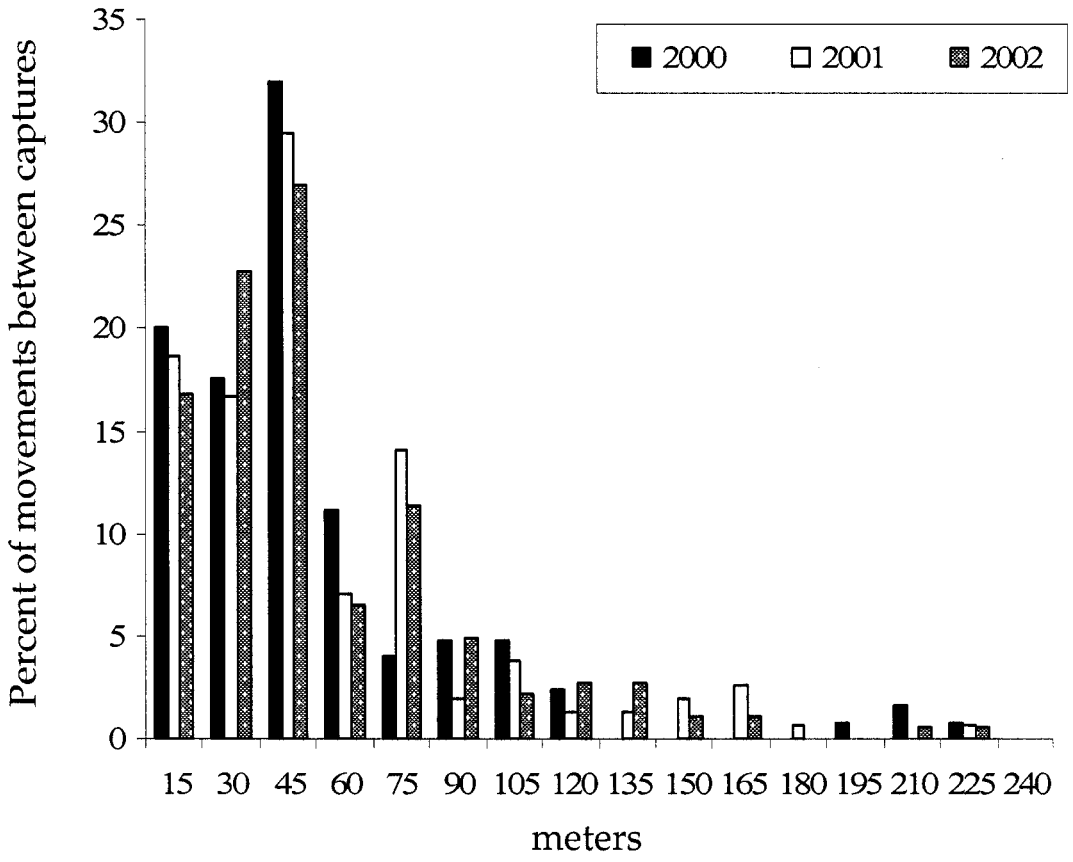

Fig. 1.3. Distribution of distances moved by Pacific jumping mice between two successive capture events, for each of the three years of the study, 2000, 2001 and 2002.

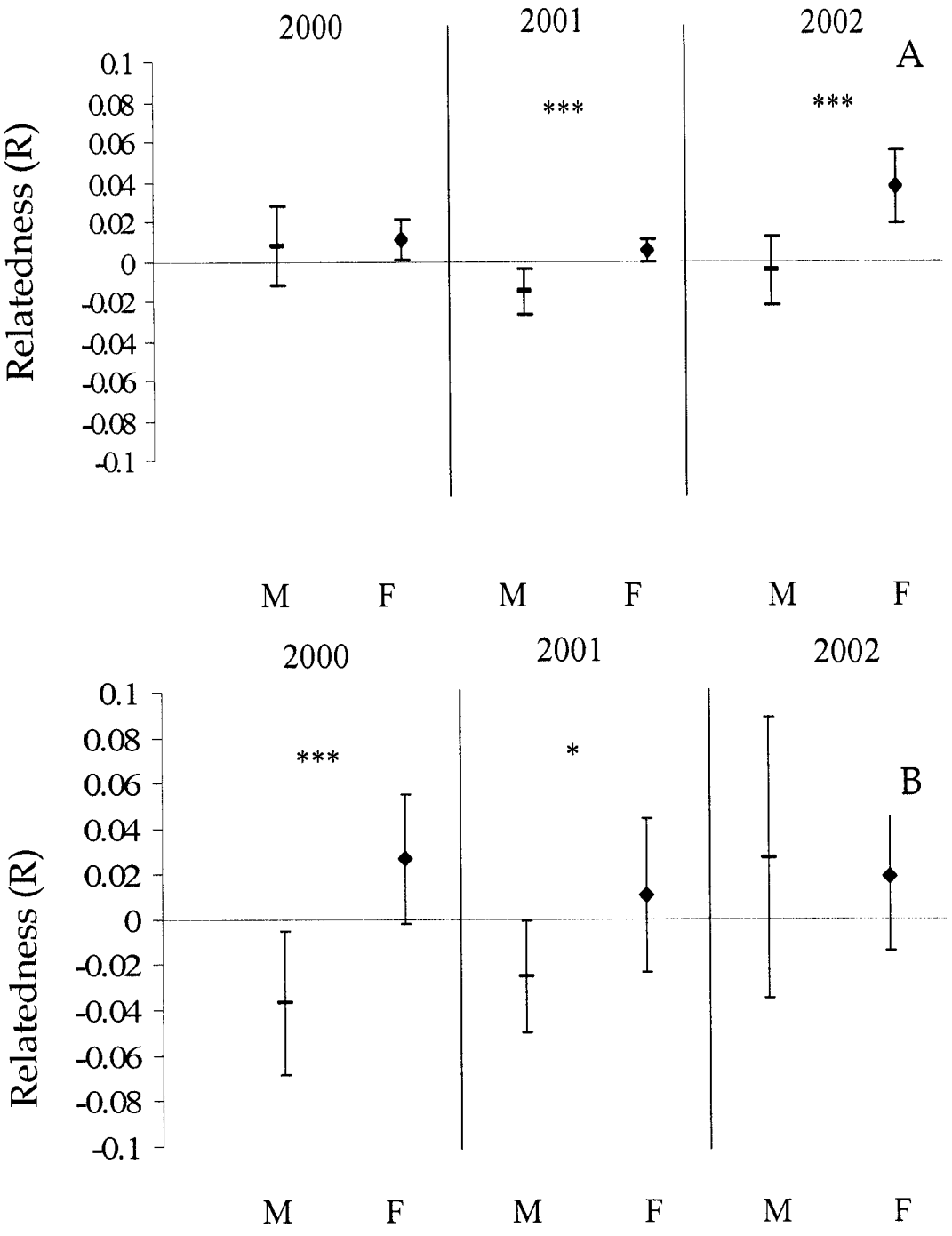

Fig. 1.4. Average relatedness among (A) all adult males (M) and females (F) within the study population of Pacific jumping mice and (B) among only those adults identified as parents, for each of the three years of the study. Significance indicated as *$p \leq 0.05$, ***$p \leq 0.001$. Bars are standard errors around mean relatedness estimates.

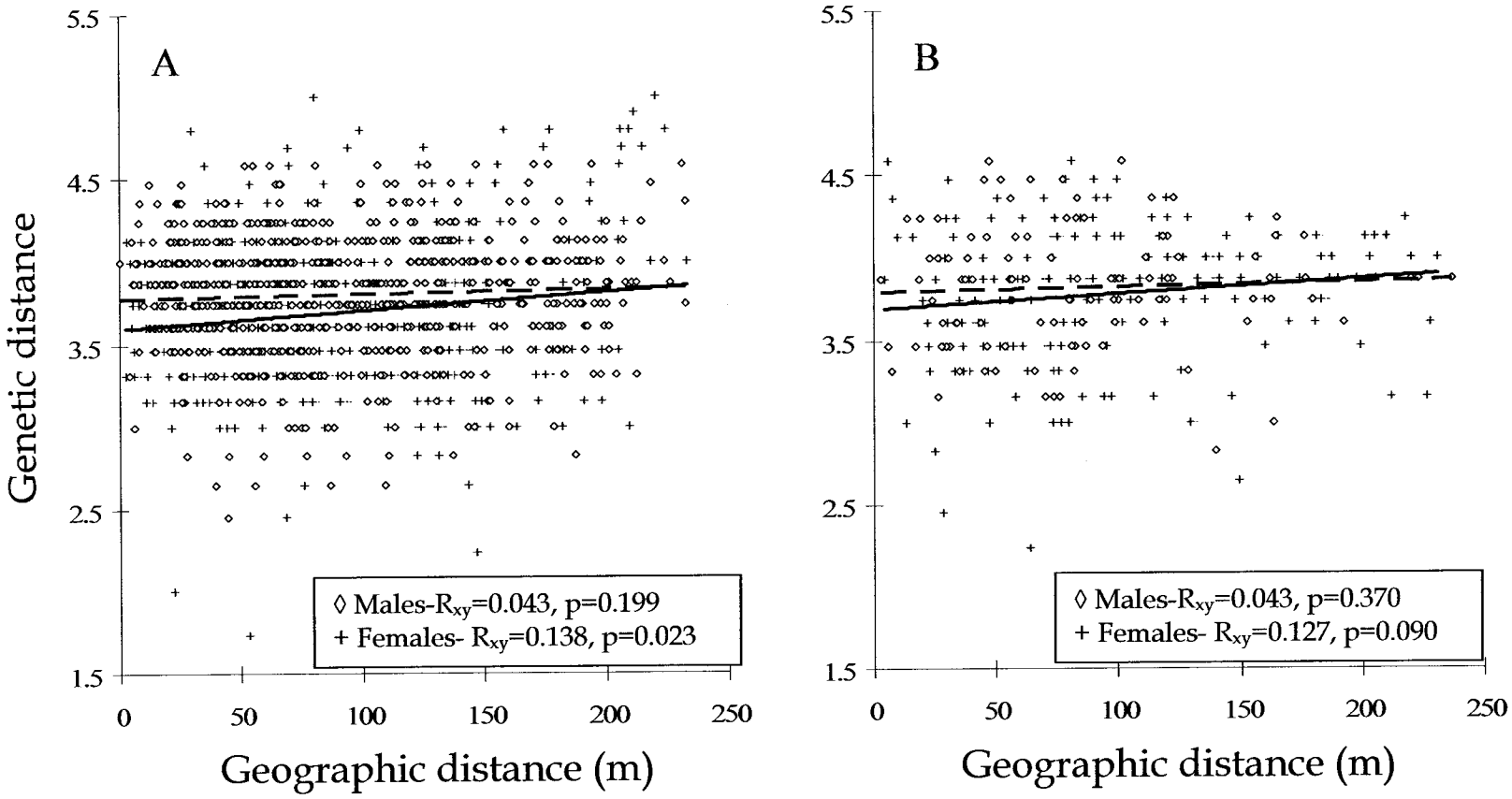

Fig. 1.5. Plots indicating spatial genetic structure as an isolation by distance correlation, *Rxy*, between genetic distance and geographic distance in male and female Pacific jumping mice over the two years for which sampling was conducted over the entire active season, (A) 2001 and (B) 2002. Significance of the correlation in each year, as determined through a Mantel test with 9999 permutations is indicated, *p*, and the trend is represented as dashed lines for males and solid lines for females.

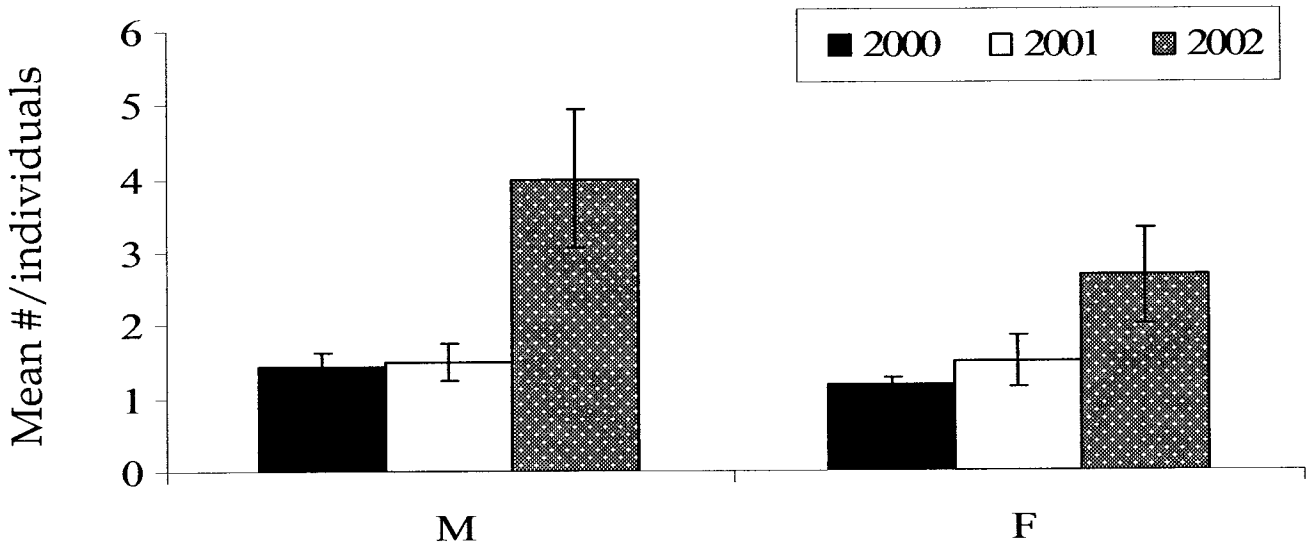

Fig. 1.6. Average reproductive success for male (M) and female (F) Pacific jumping mice identified as breeders over the duration of the three year study. Bars are standard errors around the means.

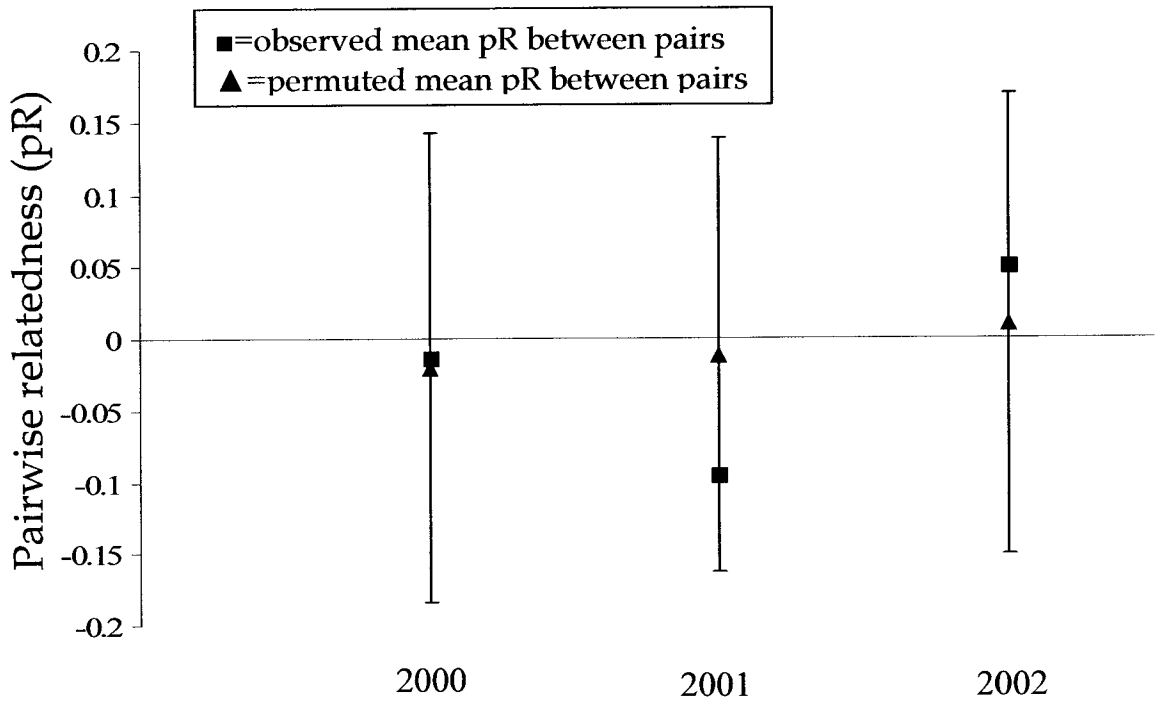

Fig. 1.7. Pairwise relatedness observed between mated pairs of Pacific jumping mice relative to the distribution of possible pairwise relatedness values between all adults, produced through a Monte Carlo resampling regime with 10000 iterations (see text for details), in each of the three years of the study. Bars are the 95% confidence distribution of permuted pairwise relatedness values.

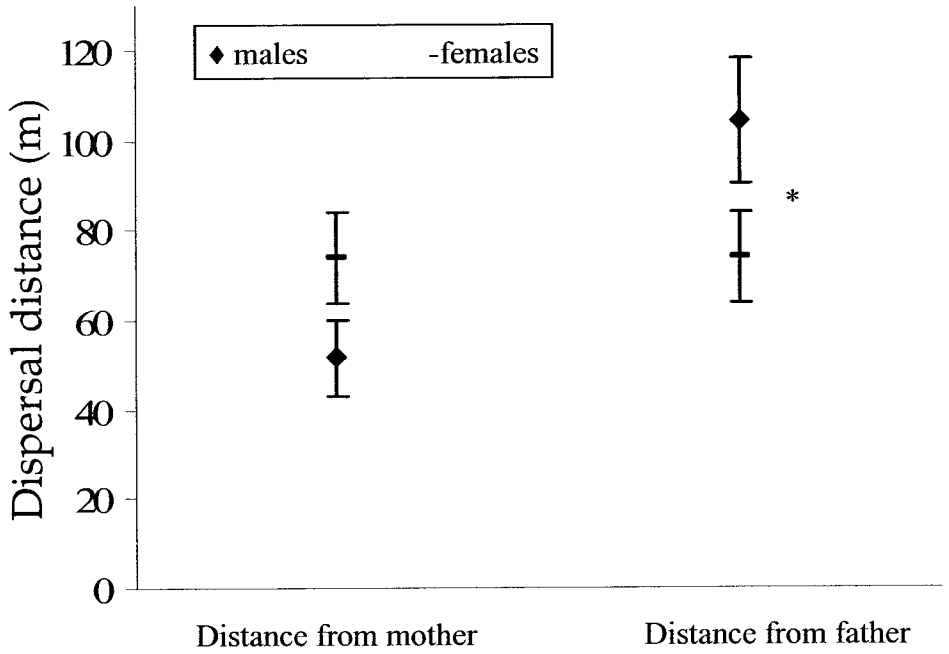

Fig. 1.8. Average dispersal distances in juvenile male and female Pacific jumping mice as measured as distance from identified mother and father. Bars around estimates are standard errors and significance between genders is indicated as *$p \leq 0.05$.

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CHAPTER 2: IMPACTS OF A 25 YEAR FLOOD AND EFFECTS OF VARIATION IN FLOOD REGIME ON A RIPARIAN POPULATION OF PACIFIC JUMPING MICE

INTRODUCTION

Disturbance is a natural part of many ecosystems. Events such as fire and flooding occur with regularity in nature and ecosystems affected by these events tend to be adapted to their occurrence (Folke *et al.* 2004). Human activities such as fire suppression and flood control have drastically changed the nature of disturbance in many managed forest and riparian systems by reducing the frequency of fires and floods, and increasing the intensity of these events when they do occur (Vitousek *et al.* 1997; Folke *et al.* 2004). This direct anthropogenic control of disturbance has thus far largely been exerted in managed areas, allowing for more natural regimes in remote and unmanaged regions. Climate studies have revealed, however, that human activities are having a global impact on temperature and precipitation (Hennessy *et al.* 1997; Groisman *et al.* 1999; McCarthy *et al.* 2001) demonstrating that anthropogenic impacts are cosmopolitan. Anthropogenically induced climate change is predicted to precipitate large increases in both the frequency and severity of disturbance events such as

fire and flooding within the next 100 years (Fowler and Hennessy 1995; Hennessy *et al.* 1997; McCarthy *et al.* 2001; Williams *et al.* 2001; de Groot *et al.* 2003; Brown *et al.* 2004). Such rapid and large changes in disturbance regimes could have considerable impacts in disturbance-influenced habitats and species affiliated with these habitats.

Natural disturbance in dynamic habitats likely facilitates frequent population bottlenecks in affiliated species. In these species, regular bottleneck events will precipitate repeated founding of recovery populations from a small number of pre-bottleneck population members. This reduced number of founders is expected to result in the presence of strong founder effects (Mayr 1963) such as allele frequency divergence, loss of allelic diversity and heterozygosity, and increased inbreeding in post-bottleneck populations (Nei *et al.* 1975; Chakraborty and Nei 1977). Such reductions in genetic divergence and increases in inbreeding have been shown to result in reduced fitness (Reed and Frankham 2003) and evolutionary potential (Frankham *et al.* 1999; England *et al.* 2003). Reduced evolutionary potential is expected to reduce adaptability to environmental changes, potentially resulting in population decline or extinction. Despite this expectation, many species persist in these naturally dynamic habitats indicating the presence of a relationship between disturbance and recovery in these environments.

The regular occurrence of natural disturbance in disturbance-influenced systems will increase the importance of these events as drivers of genetic diversity in affiliated species. In these species, the cycle of population bottleneck, founder event, population growth, and population bottleneck would be expected to have a large impact on allele frequencies and genetic variation in affected populations (Nei *et al.* 1975; Maruyama and Fuerst 1985). Since the impact of a bottleneck on genetic diversity is directly related to its severity and persistence (England *et al.* 2003), response and recovery in populations impacted by natural disturbance may exist in a balance with the frequency and severity of these bottleneck-inducing events. Given this balance, expected rapid climate-change induced variation in the frequency and intensity of natural disturbances could have an impact on genetic diversity and evolutionary potential within species existing with current levels of disturbance.

While the impacts and importance of large scale bottlenecks have been explored (Glenn *et al.* 1999; Hoelzel 1999; Leonard *et al.* 2005), and several studies have investigated past bottleneck events through the use of museum specimens (Bouzat *et al.* 1998; Whitehouse and Harley 2001) or comparison of newly founded populations with ancestral populations (Fleischer *et al.* 1991; Gullberg *et al.* 1998), much less is known empirically about the direct and immediate impacts of natural, disturbance-induced

bottlenecks in action (Keller *et al.* 1994; 2001; Eldridge *et al.* 2004)). Because natural disturbances are unpredictable, the detailed characterization of a population both immediately before and after a disturbance-induced bottleneck has, to my knowledge, been previously described only once in the literature (Keller *et al.* 1994; 2001) in a population of song sparrows subjected to an unusually harsh winter storm. In the present study, the occurrence of a 25-year flood between the second and third year of a three-year mark-recapture study of a riparian rodent, the Pacific jumping mouse (*Zapus trinotatus*), provided the opportunity to explore the impacts of a disturbance induced bottleneck in a species subject to regular disturbance. Further, the data acquired in this study allowed for exploration of the potential impacts predicted changes in flood regime might have in riparian populations of this largely riparian affiliated species.

In order to conduct these investigations, mark-recapture data were used to reveal demographic and spatial patterns of survival following the flood. Patterns of genetic diversity and relatedness, among eight highly variable microsatellite markers, were then determined both before and after the flood to ascertain whether it precipitated a genetic bottleneck. Lastly, the impacts on this population of a potential increase in flood severity and frequency predicted to occur in response to global climate change was explored through simulations.

Materials and Methods

The Pacific jumping mouse (Zapus trinotatus)

The Pacific jumping mouse is a small North American rodent in the family Dipodidae that is distributed from southern British Columbia to northern California. The species is largely affiliated with mesic and heterogeneously distributed habitat types. Maser (1981) described these as primarily riparian alder /salmonberry (*Alnus-Rubus spectabilis)* and skunkcabbage (*Veratrum*) marsh ecosystems within Douglas fir forest. These mice are also found in alpine meadows, marshy thickets, and the edges of thick forest (Svihla and Svihla 1933). They are significantly more abundant, however, in riparian areas than in upslope habitats of all types (Gomez and Anthony 1998) and they exhibit inter-population migration largely directed along riparian pathways (Vignieri 2005)

Individuals are active only from late April through September and hibernate for the remainder of the year. Over the active period individuals emerge in spring, reproduce in early to mid-summer, and then re-enter hibernation (adults prior to juveniles) in late summer after acquiring sufficient fat stores (Quimby 1951; Cranford 1983). Perhaps due to their reduced yearly active period, jumping mice are relatively long lived, often reaching as many as five or more years of age. They mature at one year and

produce only a single litter of 4-8 young per year (Bailey 1936). Research on the ecologically similar *Zapus princeps* indicates small and distinct home ranges, with average size over three years varying from 0.17-0.61 ha (Cranford 1983). Cranford also found stable population densities due to adult longevity and facultative emergence from hibernation. Preliminary analyses from other components of the present study indicate patterns of home range size in *Zapus trinotatus* that are consistent with those observed in *Z. princeps*.

Study site

Population study

A 25,600m^2 trapping grid was constructed in June 2000 on a section of riparian habitat created by a meander in the Dosewallips River on the Olympic Peninsula in Washington State (Fig. 2.1). This patch of riparian habitat contains a small population of Pacific jumping mice that is semi-isolated on three sides by the river meander and on the fourth by a steep slope beneath a road. A total of 245 (2000 and 2001) or 253 (2002) permanent trap stations were placed in rows along a compass heading of 220° at 10m intervals to cover the area. The difference in number of traps in 2002 is due to the loss of four trap stations along the western edge of the grid, and the gain of 12 along the north-eastern edge, as a result of the flood. Nine

sampling sessions occurred during the initial year, 2000, from June through September, totaling 2205 trap nights. In 2001 and 2002 trap sessions occurred every fourth week from the end of April through the end of September for 4 to 5 consecutive nights, for a total of 6125 (in 2001) and 7105 (in 2002) trap nights. Trapping was performed using Sherman traps (model #LFA) baited with heat-treated sunflower seeds. On their first capture event, all individuals were given a unique ear tag, weighed, aged, sexed, sampled for tail-tip tissue and released. On all subsequent captures animals were weighed, assessed for reproductive status, and released. Trap location was recorded for each capture. Except in analyses combined across years, all individuals caught within a year were considered part of that year's population, even if first caught in a previous year.

Although age was recorded in the field, a more precise identification of age class was made at the end of the study due to a variation in size of adults across the active season. In each year, the date of first lactation was recorded and all individuals captured prior to that date were assumed to be adults. Similarly, the last observation of a known adult was recorded and all individuals caught after that date were assumed to be juveniles. Finally, the lowest weight observed for a known adult in each year was determined and any individual whose initial capture in that year fell between the two other cut-off dates was assigned to adult or juvenile status based on weight.

These classifications were compared to the field based classifications and individuals for whom the discrepancy was large were not included in analyses based on age class.

The 2002 flood

On January 6 and 7, 2002 a winter storm increased the flow of the Dosewallips River to 260m^3/sec, as estimated by the observed flow on the closest gauged river, the Duckabush, using a drainage area adjustment equation (Cenderelli 2003). Such a flow is estimated to have a recurrence rate of 25 years, or a probability of occurrence in any one year of 4%. The overbank discharge in this flood event resulted in an estimated cross-sectional average flow width of 71.54m and an estimated average cross-sectional flow area of 121.02m^2. For comparison, a more common bank-full discharge with a recurrence rate of 1.5 years and a flow rate of 90 m^3/sec produced estimates of only 56.86m and 56.53m^2 for these same measures respectively (Cenderelli 2003). The large overbank flow washed over the habitat patch and trapping grid, scouring vegetation, washing away approximately 10m^2 of river bank on the northeastern edge of the meander, and re-routing secondary channels running throughout the grid.

Genetic Sampling and analyses

Upon collection in the field, tissue samples were immediately placed in 95% ethanol and these were then stored in the laboratory at -80°C until the time of extraction. Each individual was genotyped at eight microsatellite loci, isolated from *Z. trinotatus*, (Table 2.1) on a MegaBACE 1000™(Molecular Dynamics) automated sequencer. Genomic DNA extraction, isolation of microsatellite loci, determination of linkage disequilibrium for loci, polymerase chain reaction conditions, and genotyping of individuals were as described in Vignieri (2003), see Appendix A. Per-locus genetic variation in the form of observed and expected heterozygosities (Table 2.1) was assessed across all years using the method of (Nei 1987) as implemented in the program FSTAT (Goudet 2001). Significant per-locus deviation from Hardy-Weinberg equilibrium was determined using the global exact test of Guo and Thompson (1992) as implemented in GENEPOP v3.4 (Raymond and Rousset 1995)

Spatially explicit flood impacts

Survival in this study refers to individuals that survived and were recaptured and is therefore likely a portion of the total number of individuals to actually survive between any two years rather than a precise count of the total number of individuals to survive. Spatial patterns of over-winter survival in each of the two winter seasons were investigated and

compared. The last capture location from the previous year was plotted for each animal to survive and be recaptured between both of the over-winter seasons, 2000-01 and 2001-02. A 99% minimum convex polygon (MCP) was constructed around these points in order to create a "survivor range" for each of the over-winter seasons, within the program Biotas™ (Ecological Software Solutions). A MCP utilization area curve was constructed for each year to determine area differences with equal sample sizes. A X^2 poisson test for complete spatial randomness was conducted, also in Biotas™, to determine whether survival patterns varied from random in each of the over-winter seasons (Greig-Smith 1964). Finally, comparisons were made between the area inside the 2001-02 survivor range and the area outside that range for both over-winter seasons to determine whether the flood event spatially impacted the number of captures and surviving individuals across the entire trapping grid. Comparisons made include the total proportion of individuals captured within each area (TC), the total proportion of survivors caught within each area (TS), and the proportion of individuals within each area to survive (S).

Population comparisons before and after the flood

A Wilcoxon signed rank test under the two-phase mutation model (with 70% TPM) following the method of Cornuet and Luikart (1996) was

used within their program Bottleneck to test for a bottleneck-induced deficit of heterozygosity in both pre and post-flood populations. In addition, several measures of genetic diversity were estimated both before and after the flood to look for evidence of a flood-induced bottleneck and subsequent post-bottleneck founder effects. To determine if the relatedness of individuals within the population had increased, relatedness, *R*, among all individuals, adults, juveniles, and between adults and juveniles was determined in each year using the estimator of Queller and Goodnight (1989) within their program Relatedness. Additionally, F_{is} (Wright 1978) was estimated, using the program FSTAT (Goudet 2001), in each of the years to determine whether there was an overall increase in the level of inbreeding within the population following the flood. In addition, each year was tested for conformity to Hardy-Weinberg equilibrium using the exact test of Guo and Thompson (1992) as implemented in GENEPOP v3.4 (Raymond and Rousset 1995). To test for an overall reduction in genetic diversity, the number of observed alleles and the levels of observed and expected heterozygosity across all loci in each year were determined using the program TFPGA v1.3 (Miller 1997). Differences between pre- and post-flood levels of heterozygosity were tested for significance using a Wilcoxon paired sign rank test (Zar 1999) with comparisons made between years for each locus.

In order to investigate whether the flood event precipitated post-bottleneck genetic divergence, allele frequency distributions were compared between years using Fisher's exact test (Raymond and Rousset 1995) and Fisher's combined probability test (Sokal and Rohlf 1995) was used to determine the overall significance across loci in TFPGA v1.3. In addition, to investigate the level of post-bottleneck divergence, pairwise values of F_{st} between years were estimated using the method of Weir & Cockerham (1984) within the program Arlequin v2 (Schneider *et al.* 2000).

Simulated effects of changes in flood frequency and severity

The potential impacts of increases in flood frequency and severity were explored using the method of Kuo and Janzen (2003) within their simulation program BOTTLESIM. This method allows for specification of longevity, age at maturation, and percent of overlap among generations and thus allows for a relatively realistic representation of jumping mouse life-history. Within this simulation framework genetic diversity, as the average number of observed alleles and observed heterozygosity, after one hundred years was determined for four different flood frequency and severity scenarios (Table 2.2). In addition, fixation probability was determined for each of the scenarios as the proportion of iterations for which a locus became fixed at a single allele, averaged across loci. Flood

scenarios were designed to approximate 1) current conditions (25 year flood recurrence rate and proportionally high survival), 2) an increase in flood-induced mortality with no increase in flood frequency (25 year recurrence rate and low survival), 3) an increase in flood frequency without an increase in mortality (12 year recurrence rate and high survival), and 4) an increase in both flood frequency and flood-induced mortality (12 year recurrence rate and low survival) (Table 2.2). Genotypic data from the pre-flood population (in 2001) was used to determine allele frequencies in the first year of each of the simulations and populations were simulated for 100 years and 10,000 iterations. In each of the simulations post-bottleneck recovery to previous population sizes occurred within a year. Simulated life history parameters were derived from known life history traits in jumping mice and were consistent across the different flood scenarios, 1) longevity equal to 5 years, 2) age at maturity equal to 1 year, 3) one hundred percent overlap in generations, 4) random mating, and 5)a one to one sex ratio.

Because migration and mutation are not implemented in this method, a gradual loss of genetic diversity would be expected to occur in this small population, even at constant population size. To determine the impact of potential changes in flood regime above and beyond those due to isolation of the simulated population, a baseline simulation was conducted for which the population size was maintained at 100 individuals

throughout the duration of the simulation (Table 2.2). Effects of each of the subsequent flood regime scenarios were then determined in the 100th year as the percent change from the baseline simulation results in the 100th year. Significance of these differences, for both observed alleles and heterozygosity, was determined using a Wilcoxon paired signed-rank test across all loci (Zar 1999).

RESULTS

Demographic flood impacts

A total of 225 Pacific jumping mice was marked and sampled over the three year study period. In the pre-flood years, 2000 and 2001, 96 and 95 individuals were captured, respectively. In 2002, following the flood, the number of individuals decreased slightly with a total of 87 individuals captured (Fig. 2.2). Sex ratio was near one across the three year study and was not impacted by the flood. Unlike sex ratio, age structure in the population was impacted by the flood. In both pre-flood years the number of adults was greater than the number of juveniles with 61 and 74 individuals identified as adults captured in each year respectively (with the number of juveniles at 25 and 20). Following the flood, this pattern was reversed, with only 35 adults captured as compared to 50 juveniles, double the number captured in pre-flood years (Fig. 2.2). As measured by over-

winter survival, the flood increased mortality by 44% with 34 individuals marked in 2000 recaptured in 2001, as compared to 19 marked in 2001 and recaptured in 2002. Nine individuals were captured in all three years.

Spatial flood impacts

The post-flood survivor range area was 9,000m^2 as compared to 15,850m^2 for that over the non-flood winter season (Fig. 2.3a). The utilization area curve (not shown) reveals that the pre-flood survivor range was larger than the post-flood survivor range at all sample sizes above 7 by a minimum of 800m^2. X^2 tests revealed that capture points within the post-flood survival range were distributed in a significantly non-random way ($p=0.01$, $X^2=6.28$). This was not true for the pre-flood survivor range where the null hypothesis of random distribution was not rejected ($p=0.16$, $X^2=2.01$).

The proportion of individuals captured inside the post-flood survivor range did not change as a result of the flood. However, patterns of survival outside the range were strikingly different before and after the event (Figs. 2.3a and 2.3b). About two-thirds of all individuals captured in both the immediately pre- and post-flood populations were captured inside the area defined as the 2001-02 survivor range. In the pre-flood population, the proportion of individuals surviving inside and outside of this area

mirrored the number captured, at 66% within the survivor range and 33% outside the range (Fig. 2.3a). Additionally, before the flood the total proportion of over-winter survivors was equal inside (37%) and outside (36%) the 2001-02 survivor range. Following the flood, the total proportion of individuals within the 2001-02 survivor range to survive was similar to that of the previous season (30%); however, the proportion of individuals surviving outside the range dropped by an order of magnitude, to 3% (Fig. 2.3b). As expected given that the 2001-02 survivor range area was defined by individuals surviving over the 2001-02 season, 95% of all survivors in the post-flood season were last captured in the previous year within the post-flood survivor range (Fig 2.3b). Because the post-flood survivor range was defined by the post-flood survivors, this value alone is not meaningful. However, when compared to the proportion of survivors found in the same area in the previous year, which was considerably lower at 66%, it demonstrates a change in survival patterns following the flood (Fig.2.3a).

Bottleneck and founder effects

In populations that have experienced a bottleneck, the expected number of alleles is predicted to decrease more rapidly than the gene diversity (Nei *et al.* 1975; Maruyama and Fuerst 1985; Fuerst and Maruyama 1986). This results in a scenario in which the actual gene diversity is higher

than the expected equilibrium gene diversity thus creating an excess of heterozygosity (Luikart *et al.* 1998). Wilcoxon signed rank tests revealed a significant excess of heterozygosity, not only in the post-flood year, but in all three years (Table 2.3). Average relatedness among all comparisons did not change between the first two years (not shown), but nearly tripled following the flood event (Fig. 2.4). Similarly, F_{is} values in the two pre-flood years were not different or significant, but F_{is} in the year following the flood was double that observed in the previous years and indicated a significant deficit of heterozygotes (Table 2.3). Expected heterozygosities were similar in all three years (0.84, 0.84 and 0.82) as were the observed number of alleles (Table 2.1, Table 2.3). Observed heterozygosities were similar in the first two years and not different from expectation (0.83 and 0.83, $p_{00-01}>>0.05$). However, observed heterozygosity in the post-flood population was significantly lower than that of the previous years (0.79, $p_{00-02}=0.01$ and $p_{01-02}=0.05$) and different from that expected under Hardy-Weinberg proportions (Table 2.3). As expected based on the heterozygosity patterns, the post-flood population was significantly out of Hardy-Weinberg equilibrium but this was not the case for the two pre-flood years (Table 2.3).

The post-flood population was significantly diverged genetically from the pre-flood population in both years, as revealed through significant allele frequency differences ($p_{00-02}<0.001$, $p_{01-02}=0.03$, Table 2.4). Allele

distributions did not differ between the two pre-flood years ($p_{00\text{-}01}$= 0.21). Similarly, a low, but significant F_{st} value (F_{st}=0.003, p=0.049) was found between 2000 and 2002 and a marginally significant F_{st} value was found between 2001 and 2002 (F_{st}=0.002, p=0.054) whereas F_{st} between the pre-flood years of 2000 and 2001 was three times lower and not significantly different from zero (F_{st}=0.0009, p=0.23, Table 2.4)

Simulations

All patterns are reported as percent change from the pattern observed in the baseline simulations (those for which population size was kept constant). Patterns for observed allele number and observed heterozygosity were similar across flood scenarios, although the magnitude of change in allele number was always larger than that in heterozygosity. Interestingly, genetic diversity was significantly higher in simulations representing the current flood regime (high survival and 25-year flood intervals) than in the baseline simulations (Fig. 2.5). Increased flood-induced mortality had the largest impact on genetic diversity, with both a decrease in survival in the current flood regime, and a decrease in survival concomitant with an increase in flood frequency, precipitating decreases in allele number and heterozygosity (Fig. 2.5). An increase in both flood-induced mortality and flood frequency had the largest impact on genetic

diversity, decreasing allele number by 38% and heterozygosity by 11% below baseline simulations. High bottleneck survival was shown to be capable of preventing a loss of genetic diversity due to the impacts of an increase in flood frequency, as demonstrated by the results of simulations with increased flood frequency but high survival. However, an increase in flood frequency largely prevented the increase in genetic diversity observed in populations simulated under the current flood regime (Fig. 2.5). Allele fixation probabilities reflected observed patterns in genetic diversity, however, fixation probability was less sensitive to flood frequency with simulations at both flood frequency levels near zero. Low survival had a large impact on allele fixation, however, with simulations subject to increased flood frequency and flood-induced mortality having a 44% probability of allele fixation after 100 years (Fig. 2.5).

Discussion

This study describes in detail the impacts of a flood on a population of riparian Pacific jumping mice by revealing patterns of post-flood survival and characterizing the founder effects caused by a flood-induced bottleneck in the post-flood population. In addition, the impact that predicted climate-induced changes in frequency and severity of flooding

might have on this riparian population was investigated and found to be substantial.

Impact of flood event

The impacts of the 2002 Dosewallips flood were spatially explicit. As might be expected for a riverine flood, survival of individuals was concentrated near the upslope area of the trapping grid and away from the rivers edge. Although spatial patterns of capture did not change across the trapping grid before and after the flood event, survival drastically decreased in areas close to the river in response to the flood. This pattern of higher survival in areas further from the river leads to the conclusion that more intense flooding with larger overbank flows would decrease flood survival. Although an estimate of the size of the bottleneck in terms of population number was not possible, the number of survivors across each of the two over-winter periods (34 from 2000-01 and 19 from 2001-02) indicates that survival decreased by approximately 44% in the flood year. If we additionally examine the proportion of individuals surviving both inside and outside of the flood-survivor range in the non-flood year, we can see that it was the same in both areas, approximately 35%. A weighted average of the two areas in the flood year indicates that the total post-flood survival was approximately 20% (with 30% inside the survivor range and

3% outside the range). Using these simple proportional approximations we can estimate that depending on location, the flood event decreased survival in the population to 3% to 44%. Overall, the impact on the population of the observed bottleneck was mild to moderate.

Population size (number of individuals captured) following the flood was lower than in previous years (despite the larger number of trap nights), although only slightly (87 in 2002 vs. 96 and 95 in each of the previous years). This presumably rapid recovery to near pre-flood population size following a flood-induced increase in mortality is interesting in a species with only a single bout of reproduction per year and a relatively small litter size. However, the doubling of the number of juveniles captured in the post-flood year may indicate a numerical response to the change in conditions, such as an increase in the availability of resources, following the flood. This response could be modulated by increased juvenile survival due to decreased intra-specific competition or by increased reproductive output in females in the form of increased litter size. It is impossible to differentiate between these possibilities at this point, but further analyses, including parentage and reproductive success, may provide insight regarding the importance of each of these factors to the increase in juvenile recruitment.

Bottleneck impacts and founder effects

The post-flood population in this study displayed a series of traits expected in a recently bottlenecked population. Interestingly, excess heterozygosity was present in all three years, not only the post-flood population. Bottleneck induced heterozygosity is transitory but is detectable for 0.2-4 N_e generations (Luikart *et al.* 1998). Estimates of N_e made in each of the three years using the linkage disequilibrium method of Hill (1981) within the program Nestimator (Peel *et al.* 2004) indicate a 95% confidence range of N_e=46-132. Given this number, and assuming a generation time of one year, a bottleneck within this population would be detectable for 9.2 to 528 years. While floods as severe as the one observed in this study are relatively infrequent, they do have a 4% probability of occurring in any given year. Given the regularity of these events and the amount of time required for the transitory signal of excess heterozygosity to dissipate, a test for heterozygosity excess is not capable of differentiating the immediate bottleneck from those that occurred due to prior flood events. Instead, this test has detected the influence of past bottleneck events and in doing so provides evidence of regular flood induced bottlenecks in this population.

Although the direct test for bottleneck effects could not differentiate the effects of the current bottleneck from those of presumed past

bottlenecks, comparison of the pre- and post-flood populations provides substantial evidence of a flood-induced bottleneck and subsequent founder effects. The relatedness among individuals in all comparisons nearly tripled within only one generation following the flood. These increased levels of relatedness provide support for the conclusion that a limited number of survivors founded the post-flood population. The increased relatedness among individuals within the population also provides evidence that the increase in the number of juveniles following the flood was not due to immigration. In addition, the high relatedness observed among adults and juveniles indicates potential relatedness among founders. High relatedness among adult founders in the post-flood population will mean that the offspring of a set of parents will not only exhibit high relatedness with their parents, but also with their parents' relatives.

The post-flood increase in relatedness among adults led to an increase in overall levels of inbreeding (as measured by F_{is}), after a single bout of reproduction, and a significant deficit of heterozygotes in the post-flood population. These increased inbreeding and relatedness levels, in combination with general bottleneck induced drift, led to deviation from Hardy-Weinberg equilibrium in the post-flood population. Although other factors such as selection, increased gene-flow, or Wahlund effects can cause a population to deviate from Hardy Weinberg proportions (Frankham *et al.*

2002), these factors are considerably less likely in this case. Importantly, were the deviation due to an increase in migrants from other populations in response to the bottleneck, we would not expect to see high levels of relatedness in the subsequent population. This observation indicates that the increase in population size following the bottleneck was not due to a post-flood influx of migrants.

In addition to the general increase in relatedness and inbreeding observed following the flood, a significant overall reduction in genetic diversity was observed. Surprisingly, and contrary to the pattern predicted to follow a bottleneck (that the number of alleles will be reduced more rapidly than heterozygosity (Nei *et al.* 1975; Maruyama and Fuerst 1985; Leberg 1992; Luikart *et al.* 1998), the number of observed alleles did not change. However, an immediate decrease in the observed heterozygosity was detected following the flood. It is difficult to ascertain for certain the exact cause of this pattern, however it may be due to the high relatedness observed among founding adults increasing the presence of more common alleles. In this case, heterozygosity may have decreased due to increased relatedness among breeders while allele number was not significantly reduced due to the relatively high bottleneck survival.

The founder effects observed following the flood induced-bottleneck include not only increases in inbreeding and relatedness and decreases in

genetic diversity, but also significant genetic divergence of the post-flood population from previous year's populations. This was true both in allele frequencies and, more surprisingly, as detected by a low, but non-zero, F_{st}. This pattern of increasing F_{st} following founder events is expected, as demonstrated by Austerlitz et al. (1997) in simulations, and has been observed in captive populations (Schonhuth *et al.* 2003). Despite this expectation, such rapid, significant post-bottleneck divergence in F_{st} has not, to my knowledge, previously been observed in nature. This could be due to the rarity with which genetic diversity within a population has been characterized immediately before and after a bottleneck, since the increase in F_{st}. between years is expected to quickly dissipate (Austerlitz *et al.* 1997). Its presence here demonstrates the rapid impact a disturbance can have on allele composition within a population.

Expected influence of variation in flood regime and severity

Mutation and migration are not implemented in these simulations and it is important to briefly discuss these forces. Mutation would be expected to increase genetic diversity. Given the one hundred year time frame of these simulations, however, mutation is unlikely to have a large impact, with estimated microsatellite mutation rates of $5x10^{-3}$-$5x10^{-5}$ (Estoup and Angers 1998). Migration will similarly increase genetic diversity within

simulated populations and is much more likely to play an important role in doing so over the time frame of the simulations. While migration into this population certainly occurs, the genetic results demonstrate that it did not increase following the flood and is therefore likely to occur at a rate independent of flooding. Given this conclusion, we would expect migration into this population to increase genetic diversity somewhat in each of the scenarios. Measuring flood scenario effects as differences from the baseline, non-bottlenecked population, minimizes the impact of the absence of migration in the simulation, since its effects would be expected to be similar across flood scenarios. Thus the approach used in this study focuses more on the direct changes to genetic diversity caused by changes in flood frequency and severity and less on precise levels of genetic diversity.

Simulation results indicate that the frequency and severity of disturbance-induced bottlenecks have important impacts on genetic diversity. Interestingly, simulations designed to emulate current levels of flood frequency and bottleneck severity increased genetic diversity above levels observed in a non-bottlenecked population. This increase is likely due to the divergence produced in allele frequencies and the increased production of juveniles following a bottleneck. Given this result, we can hypothesize that current levels of flood-induced disturbance may be an important component of population genetic processes in this population.

Increases in frequency and severity of flood events, however, were shown to increase the risk of allele fixation and to have a large negative impact on neutral diversity levels. In simulations with increased flood frequency but high survival, genetic diversity was not lost, however, the increase in genetic diversity observed to occur at current disturbance levels was not present. Although these results were obtained for neutral loci, they can inform our understanding of the overall influence of the drift inducing impacts of disturbance on genetic diversity across the genome. Further, based on the results obtained for nuclear loci in this study we can speculate about the impacts of increases in flood severity and frequency on loci under selection for improved flood survival. At current rates of disturbance, strong selection during flood years may function to increase the frequency of "flood-survival alleles" and thus increase relatedness among survivors. However, during the period between floods we would expect drift and selection for other traits to have a more powerful influence. Increased flood frequency and severity would increase the strength of selection for flood survival traits and in combination with stronger drift induced by repeated bottlenecks could decrease the overall evolutionary potential held within impacted populations. Future studies that examine the impacts of increases in disturbance on loci under selection could greatly improve our

understanding of the interaction between drift and selection in response to rapid environmental change.

This study focused on the impact of changes in disturbance regime within a single, semi-isolated population. Clearly, in nature such a population would be part of a larger metapopulation. Intensive flooding, however, would be expected to impact the majority of riparian populations similarly within a single drainage, thus simultaneously reducing population sizes and likely decreasing the number of potential post-flood migrants. This would be especially true in cases of high flood frequency and low flood survival where smaller more isolated populations may suffer extinction and lower probabilities of recolonization. Given these conditions, the results of this study are likely to be indicative of the larger pattern throughout the drainage metapopulation. Nonetheless, simulations that investigate the impacts of changes in disturbance regime within the framework of a metapopulation model will be especially important for exploring the larger scale applicability of the results of this more localized study.

Conclusions

Population bottlenecks impact genetic diversity and levels of inbreeding (Wright 1931; Nei *et al.* 1975; Leberg 1992; Hoelzel 1999; Keller *et*

al. 2001). In this study, the effects of a flood induced-bottleneck on a riparian population of Pacific jumping mice were extremely rapid, with significant increases in relatedness, inbreeding, and genetic divergence within a single generation. Explorations of the impact of various levels of bottleneck frequency and strength caused by variation in flood regime indicated that current levels of disturbance actually increase neutral genetic diversity above that observed at constant population size. This result demonstrates that the increase in genetic mixing that follows an event precipitating strong selection and genetic drift may counter these diversity reducing mechanisms. Given the strong impacts of the observed bottleneck however, it becomes clear that the effects of repeated bottlenecks are highly dependent on the regularity and severity of bottleneck inducing events. Considerable increases in flood frequency and severity are expected to occur in response to human-induced climate change(Fowler and Hennessy 1995; Hennessy *et al.* 1997; Groisman *et al.* 1999). In this study, such changes were found to disrupt the balance between disturbance and recovery, precipitating considerable losses in neutral genetic diversity in the worst case. This finding indicates that even in areas far removed from direct human impacts, species affiliated with dynamic habitats may experience decreases in genetic diversity and adaptability in response to predicted changes in climate. Although in this study genetic diversity was measured

in neutral loci, extremely rapid changes in disturbance regime might also be expected to reduce adaptive diversity due to repeated selective sweeps and a subsequent reduction in adaptive potential for traits not related to disturbance survival. Such a loss of evolutionary potential at a time of rapid human-induced change in disturbance levels could have catastrophic effects on persistence in species affiliated with disturbance adapted habitats.

Table 2.1. Genetic diversity of eight Pacific jumping mouse (*Zapus trinotatus*) microsatellite loci within a small population of jumping mice over three years, expressed as observed (H_o) and expected (H_e) heterozygosities and the observed number of alleles found in each year, the last of which experienced a 25 year flood event. Deviation from Hardy-Weinberg equilibrium in a single locus indicated by *=p≤0.05, ***=p≤0.001

	Observed allele number						
Locus	2000	2001	2002	Mean/locus	Total	H_o	H_e
Ztri2	17	17	17	17.00	17	***0.755	0.895
Ztri24	11	10	10	10.33	11	*0.842	0.863
Ztri3s	10	11	9	10.00	11	0.736	0.771
Ztri17	13	12	11	12.00	13	0.823	0.850
Ztri18	19	22	22	21.00	22	0.930	0.923
Ztri4	8	8	8	8.00	8	0.777	0.804
Ztri19	8	9	9	8.67	10	0.875	0.807
Ztri19+	9	10	9	9.33	10	0.757	0.755
Total	95	99	95				

Table 2.2. Flood regimes imposed on simulated Pacific jumping mouse populations as determined through (N_P) population size at carrying capacity, (N_B) size of population during flood-induced bottlenecks, (F_F) frequency, in years, of bottleneck inducing floods, and, ($F_N/100$) the total number of flood-induced bottlenecks occurring during the 100 year simulation.

Flood regime	N_P	N_B	F_F	$F_N/100$
No disturbance	100	100	0	0
Current regime	100	50	25	4
Increase in severity	100	10	25	4
Increase in frequency	100	50	12	8
Increase in frequency and severity	100	10	12	8

Table 2.3. Pre (2000 and 2001) and post-flood (2002) measures of inbreeding (F_{is}), genetic diversity in the form of expected (H_e) and observed (H_o) heterozygosities, founder-induced deviation from Hardy Weinberg equilibrium (D_{HW}), and tests for heterozygosity excess (H_{ex}), the presence of which is indicative of a recent bottleneck, in a population of Pacific jumping mice subject to a 25 year flood event. D_{HW} and H_{ex} reported as p-values, significance in all cases indicated by *=p≤0.05, **=p≤0.01, ***=p≤0.001.

Year	F_{is}	H_e	H_o	D_{HW}	H_{ex}
2000	0.017	0.834	0.823	0.070	**0.004
2001	0.017	0.834	0.826	0.070	**0.009
2002	**0.043	0.822	**0.787	***0.000	*0.014

Table 2.4. Measures of divergence, in the form of F_{st} values (below the diagonal) and allele frequency differences as measured by Fisher's exact test (above the diagonal), between populations of Pacific jumping mice before and after a 25 year flood event. Significance indicated as *=p≤0.05, **=p≤0.01, ***p≤0.001, ns=non-significant.

	2000	2001	2002
2000	0	ns	***
2001	0.0009	0	**
2002	*0.0026	0.0025	0

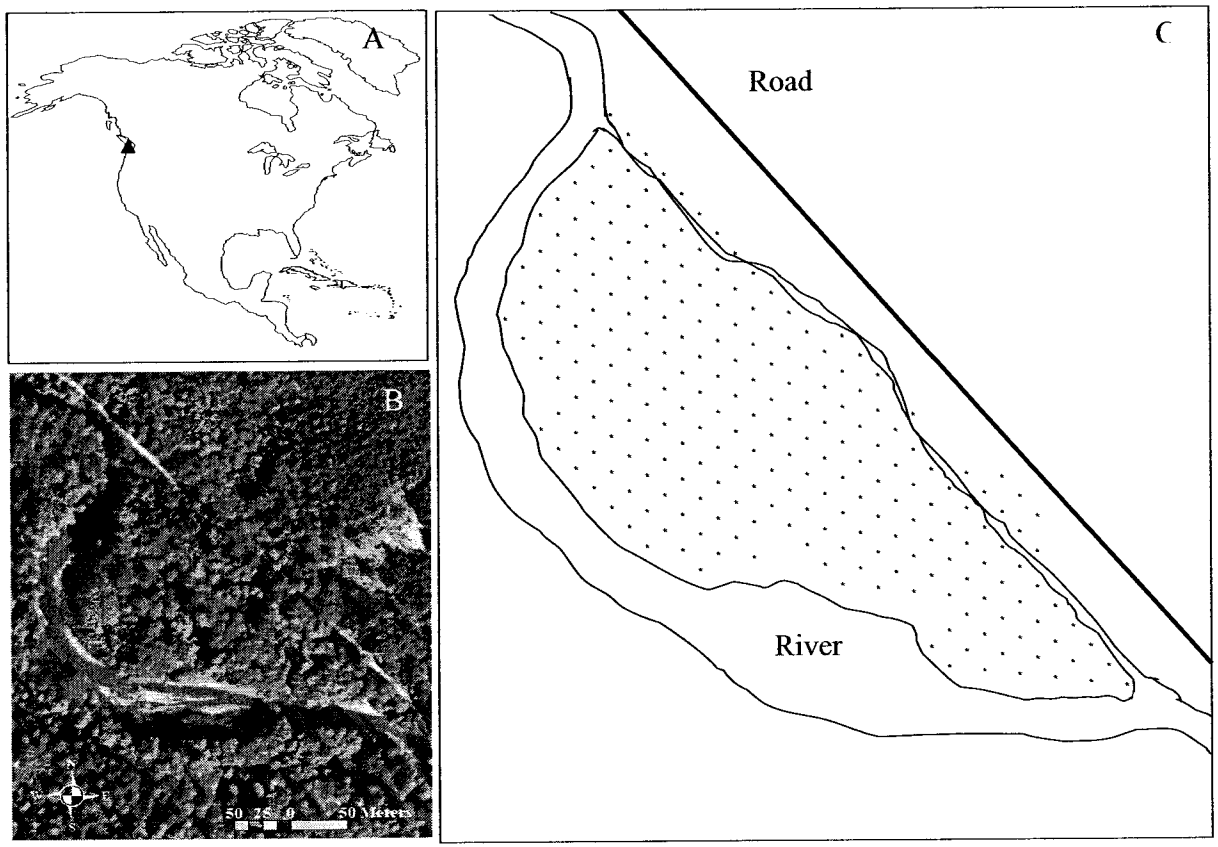

Fig. 2.1. (A) Map indicating location of Pacific jumping mouse population investigated before and after a 25 year flood on the Dosewallips River in Washington State. (B) Aerial photograph depicting the riparian habitat patch, semi-isolated by the river and a road, within which the population exists. (C) Diagram of the sample grid established within this area consisting of traps placed 10m apart along a 220°compass heading (trap locations indicated by dots).

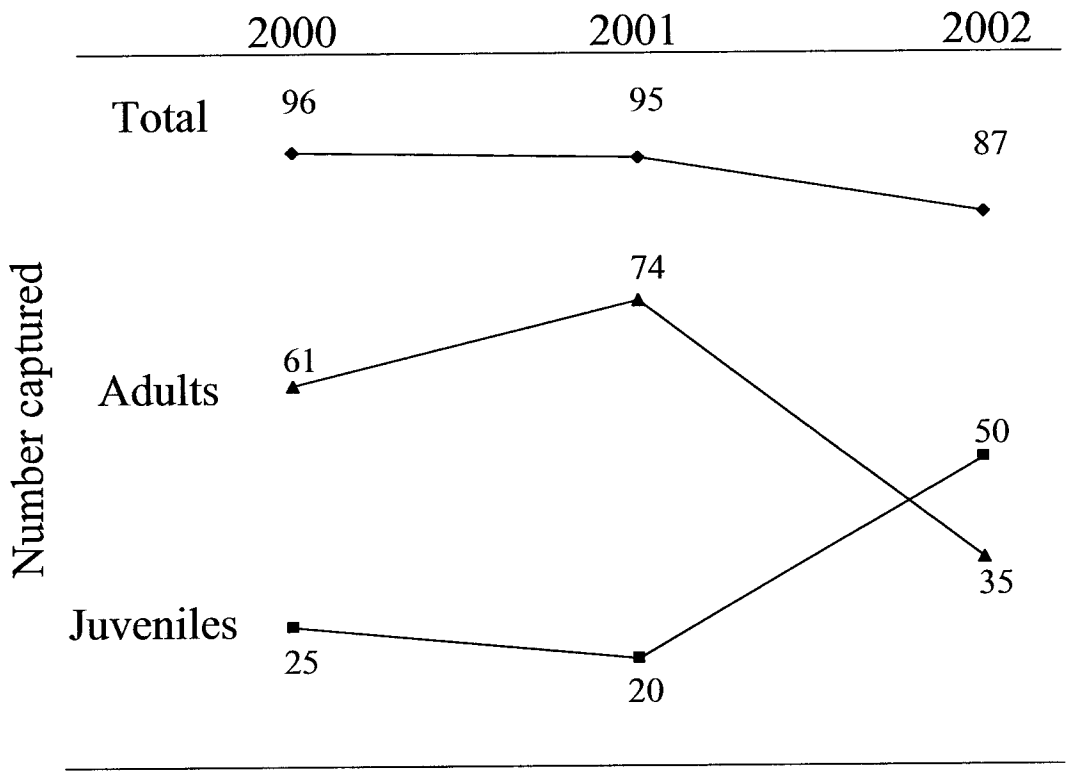

Fig. 2.2. Impact of a flood during the third year of a three year study on the number of Pacific jumping mice captured within the 2.5 ha sampling grid, including the total number of individuals, adults, and juveniles (N_i).

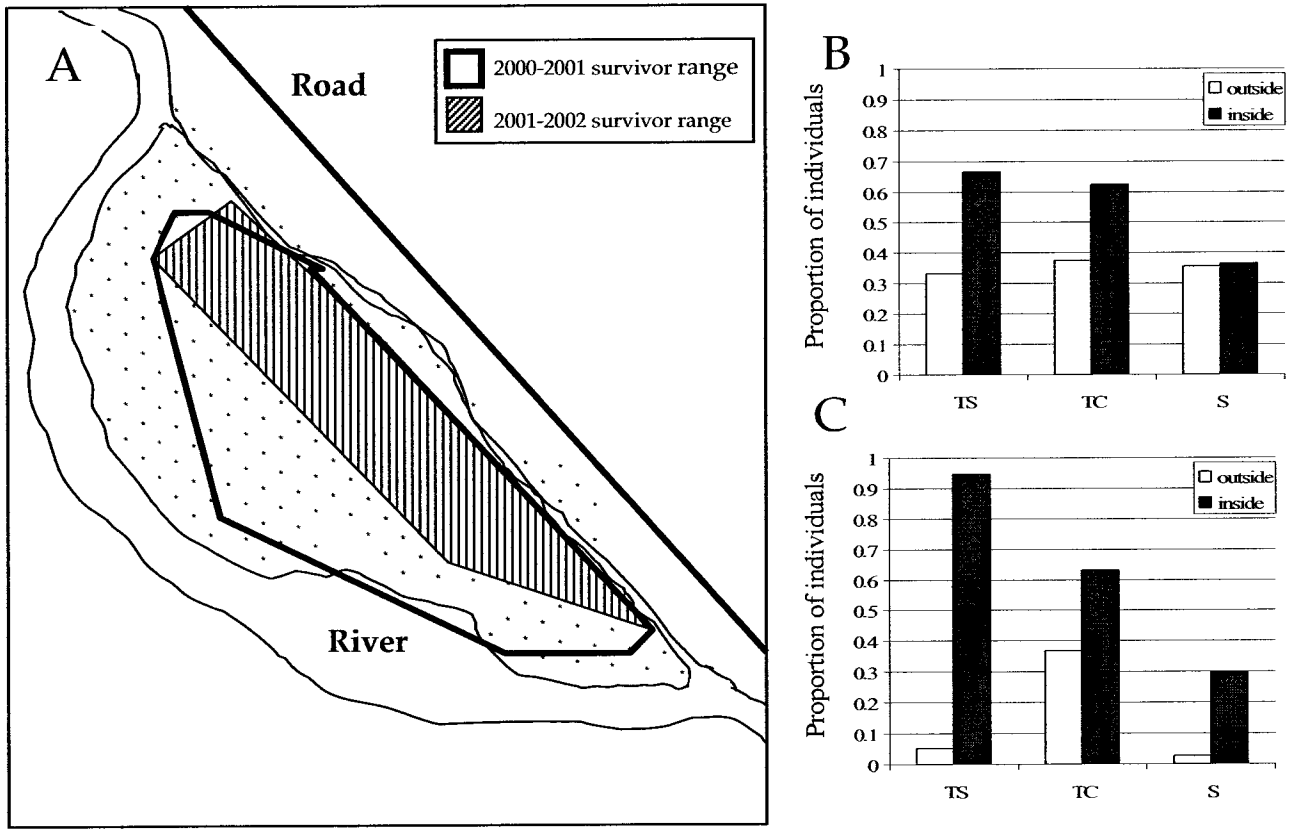

Fig. 2.3. Spatial patterns of capture and survival inside and outside of the (A) post-flood survivor range (B) before and (C) after the 25 year flood event. Patterns shown in graphs are, the proportion of the total number of individuals to be captured in each area (TC), the proportion of the total number of survivors to be captured in each area (TS), and the proportion of individuals captured within each area to survive (S).

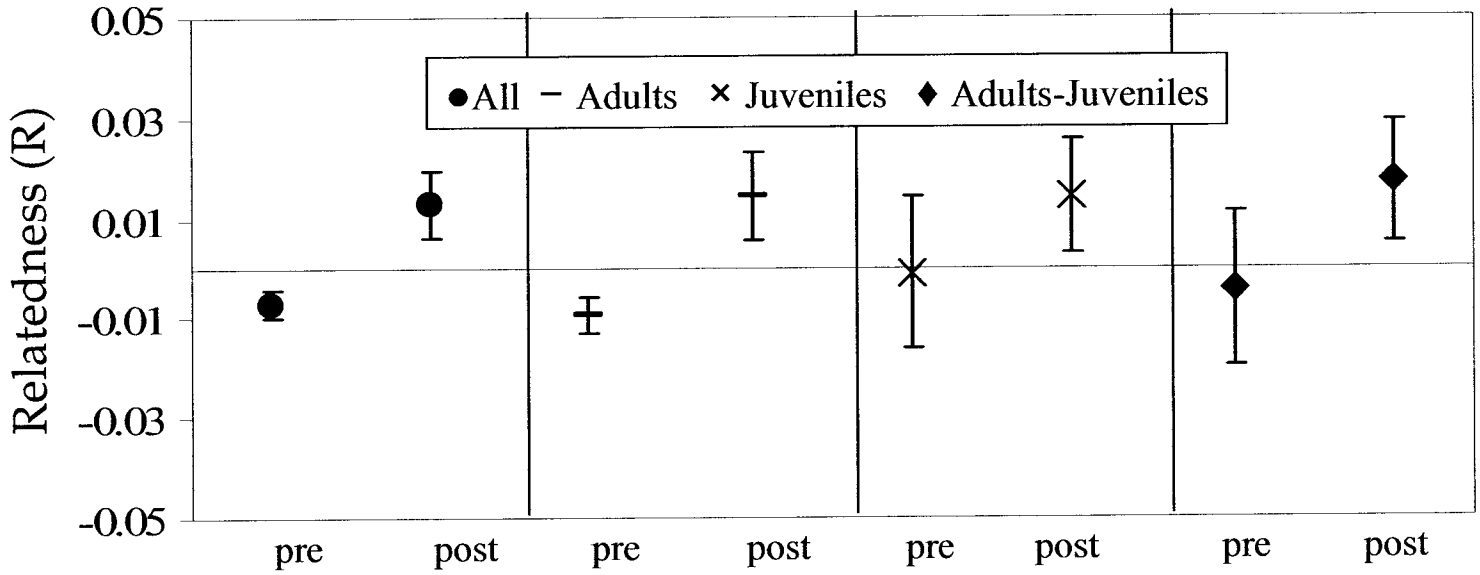

Fig. 2.4. Genetic relatedness, *R*, in a population of jumping mice as determined before (2000 and 2001 combined) and after (2002) the 25 year flood among all individuals, adults, juveniles, and between adults and juveniles. Bars around estimates are standard errors produced by jackknife resampling of loci. All comparisons are significant; among all individuals and among adults $p<0.0001$, among juveniles $p<0.05$, and among adults-juveniles $p<0.01$.

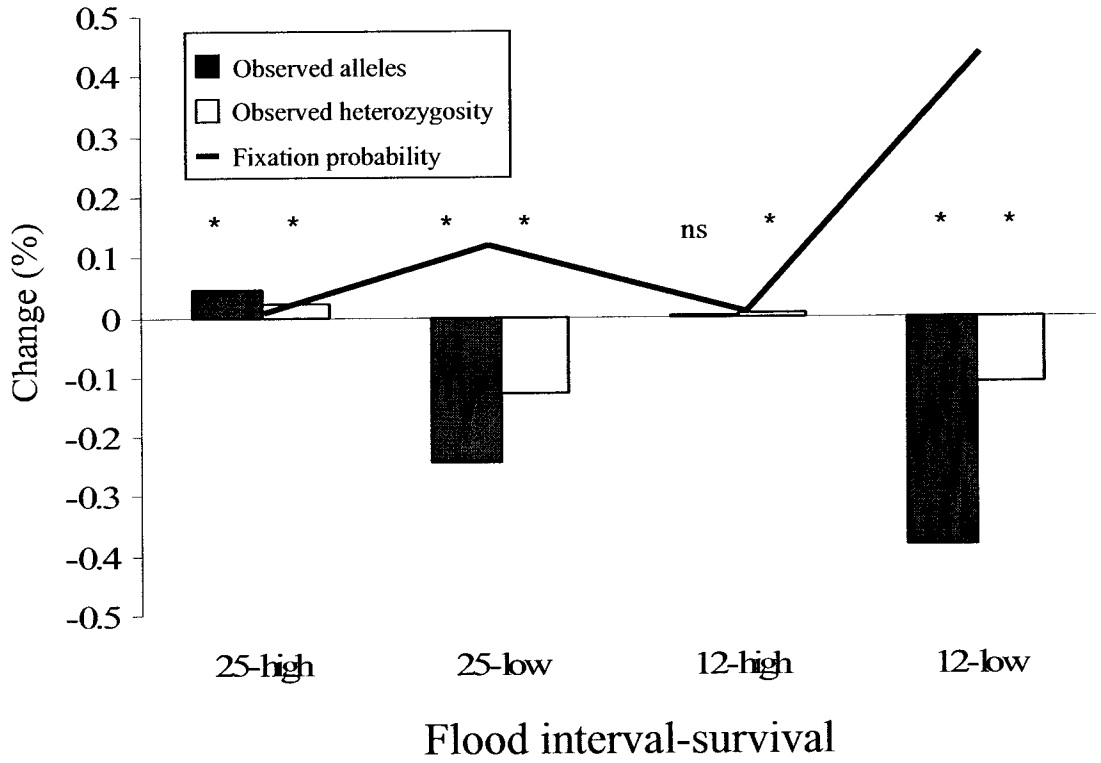

Fig. 2.5. Impact of climate induced changes in flood frequency and severity on allele fixation probability and genetic diversity, measured as observed allele number and heterozygosity, in a simulated population of Pacific jumping mice after 100 years. The impact of four different flood regimes, determined by flood frequency and bottleneck survival, are represented (see text for details). Changes to genetic diversity are measured as the percent difference from those observed in a baseline, non-bottlenecked, population after 100 years and significance of these differences is indicated as *p=0.008, ns=non-significant.

NOTES TO CHAPTER 2

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CHAPTER 3: STREAMS OVER MOUNTAINS: INFLUENCE OF RIPARIAN CONNECTIVITY ON GENE FLOW IN THE PACIFIC JUMPING MOUSE

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 geographic 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 inter-subpopulation 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 biogeographic 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 (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 and Strobeck 1998). Limited dispersal will result in increased mating among neighbors. 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 and 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 geographic 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 geographic 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 2001), or the availability of habitat, such as patches of woodland (Keygohbadi *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 geographic 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 and Goodnight 1989; Bohonak 1999; Smouse and Peakall 1999). In addition, by testing for the existence of correlations between genetic distance and geographic 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 and Musolf 2000; Pfenniger 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 and 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 multi-tiered 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 and 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 and 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 4-8 young per year (Bailey 1936). While hibernation has not been studied in *Z. trinotatus,* the closely related *Z. princeps* and *Z. hudsonius* have been described as hibernating either singly or in pairs (Cranford 1983). Research on the ecologically similar *Zapus princeps* indicates small and distinct home ranges, with the average size varying over a three year study from 0.17-0.61 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).

Z. trinotatus is distributed in association with discontinuous and patchily distributed habitat. On the Olympic peninsula in Washington State, Svihla and 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) describe 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 *et al.* (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 >30cm of precipitation annually. Other much better studied members of the genus *Zapus* also display an affiliation with riparian and mesic habitats. Clarke (1971) stated that *Z. princeps* is generally not found more than 100m 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 27 x 35 km square (Fig. 3.1). 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. 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 (1400m, 820m, and 520m respectively). In addition, the terrain between each of the rivers is rugged with average elevations of 1263m between the Dosewallips and the Duckabush, and of 1093m 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 three 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. 3.1). 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 266m, at the mouth of the Hamma Hamma River, to 4,229m 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 3.1). 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, geographic 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 3.1) on a MegaBACE 1000™ (Molecular Dynamics) automated sequencer. Genomic DNA extraction, isolation of microsatellite loci, determination of linkage disequilibrium for loci, polymerase chain reaction 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 and Petit 1996) for all subpopulations, using the program TFPGA (Miller 1997). The exact test of Guo and Thompson (1992), as implemented by GENEPOP v3.4 (Raymond and 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's exact test (Raymond and Rousset 1995) and Fisher's combined probability test (Sokal and Rohlf 1995) was used to determine overall significance across loci, both in the program TFPGA v1.3. 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 v2 (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 v5.1 (Peakall and Smouse 2001). This method is unlike traditional SA (Sokal and Oden 1978a; Peakall and Beattie 1995), which has generally been executed one allele at a time, in that it is inherently multivariate. Using pairwise geographic 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 and 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 v 5.1. This computes *r* as summed over the combined set of subpopulations, producing the estimate across subpopulations as *rc*. This is done by 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 and Peakall 1999, eq 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 v. 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 1,500m

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 geographic information system, or "GIS" (ArcGIS™ v. 8.3). Polygons were created around each group of subpopulation samples and the center of each of these was considered the subpopulation "location" for geographic distance analyses. Subpopulation locations were layered with a 10m 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. 3.2a). The river distance was measured as the distance traveled along the river between two subpopulations, not allowing for travel across land except at the shoreline (Fig. 3.2b). 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. 3.2d).

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 traveling across each type of landscape cell. The "least-cost" path between all subpopulation pairs was then determined within the program ArcGIS™ v. 8.3 as the lowest value path between two subpopulations (Fig. 3.2c). 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. 3.2e).

Geographic and genetic correlations

The presence of an isolation-by-distance relationship between the genetic distance matrix and each of the four geographic 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 and Rannala (2003) as implemented in their program BayesAss v1.2. 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 length of $3x10^6$ 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

by the program, in order to determine whether the posterior probability distributions for migration rate were significantly different from the prior distributions. A non-significant 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 2,000 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 3.1). Single locus F_{is} values varied from -0.24 to 0.24, but were generally close to zero for each subpopulation (Table 3.1). 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 3.1). 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's exact test, 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 3.2).

Spatial autocorrelation

The correlogram for the within-subpopulation analysis indicates a significant correlation at the first two distance classes, 51m (rc=0.024 P=0.001) and 103m (rc=0.006 $P<0.01$), with an x-intercept of 153m (Fig. 3.3a). The correlogram produced for the entire study area reveals a significant correlation that persists up to ~5,000m (r=0.015, P=0.001, Fig. 3.3b). At this point, r begins to decline, intercepting the x-axis at 7,930m and becoming significantly negative at 16,500m (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 3.3). 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 3.3). Significant correlations were present between the different landscape-specific geographic distance measures (river, overland, and habitat-path), but absent between these and the landscape non-specific 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 results are indicated in Table 3.4). The mean posterior probabilities of the immigration rates among subpopulations are shown in Table 3.4. 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, 51m and 103m, and that the x-intercept occurs within a relatively short distance, 153m. 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 and Wartenberg 1983; Epperson 1990b). The development of these high relatedness patches within a species indicates low levels of dispersal (Epperson 1993) and small neighborhood 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 5km 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 artifact 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 geographic distance increased the correlation between genetic and geographic distance in this study. There was no relationship between the landscape non-specific measure of Euclidean distance and the genetic distance. This is not surprising since, given the topographic relief of the area, the Euclidean distance is not representative of the actual travel distance between populations, 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 population 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 geographic 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. 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 dispersal is restricted and that animal movement 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. SA 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 geographic 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.

Table 3.1. Genetic diversity across eight microsatellite loci for 9 subpopulations of Pacific jumping mice from three river drainages, (A) Dosewallips, (B) Duckabush, and (C) Hamma Hamma, on the Olympic Peninsula. Estimates for each subpopulation, per locus and over all loci, for †significant deviation from Hardy Weinberg equilibrium (significance indicated by *), ‡Wright's inbreeding coefficient, ξnumber of alleles, ζallelic richness based on a sample size of 10 (El Mousadik and Petit 1996), and δexpected and φobserved heterozygosity.

A

	Dosewallips Mouth (N=26)						Dosewallips Interior (N=31)						Dosewallips Head (N=45)					
Locus	†HWE	‡F_{is}	ξN_A	ζA_R	δHz	φHo	†HWE	‡F_{is}	ξN_A	ζA_R	δHz	φHo	†HWE	‡F_{is}	ξN_A	ζA_R	δHz	φHo
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

Table 3.1 continued

B

Locus	Duckabush Mouth (N=15)						Duckabush Interior (N=32)						Duckabush Head (N=10)					
	†HWE	‡F_{is}	§N_A	ζA_R	δHz	φHo	†HWE	‡F_{is}	§N_A	ζA_R	δHz	φHo	†HWE	‡F_{is}	§N_A	ζA_R	δHz	φHo
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

C

Locus	Hamma Hamma Mouth (N=10)						Hamma Hamma Interior (N=32)						Hamma Hamma Head (N=27)					
	†HWE	‡F_{is}	§N_A	ζA_R	δHz	φHo	†HWE	‡F_{is}	§N_A	ζA_R	δHz	φHo	†HWE	‡F_{is}	§N_A	ζA_R	δHz	φHo
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

Table 3.2. Pairwise F_{st} and genotypic differentiation, as measured by Fisher's Exact test, 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 underlined. Significance for Fisher's exact test (above the diagonal) reported after Bonferroni correction as P<0.001=***, not significant=ns.

	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 3.3. Correlation between genetic distance, D_{LR}, and four different measures of geographic 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*

Table 3.4 Migration rates between *Z. trinotatus* subpopulations across three river drainages obtained using the program BayesAss v 1.2 from initial conditions of Δp, Δm, and ΔF =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 represent the proportion of individuals within a subpopulation derived from that subpopulation. Estimates $\geq$0.10 are italicized. Results obtained with initial conditions of Δp, Δm, and ΔF =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*

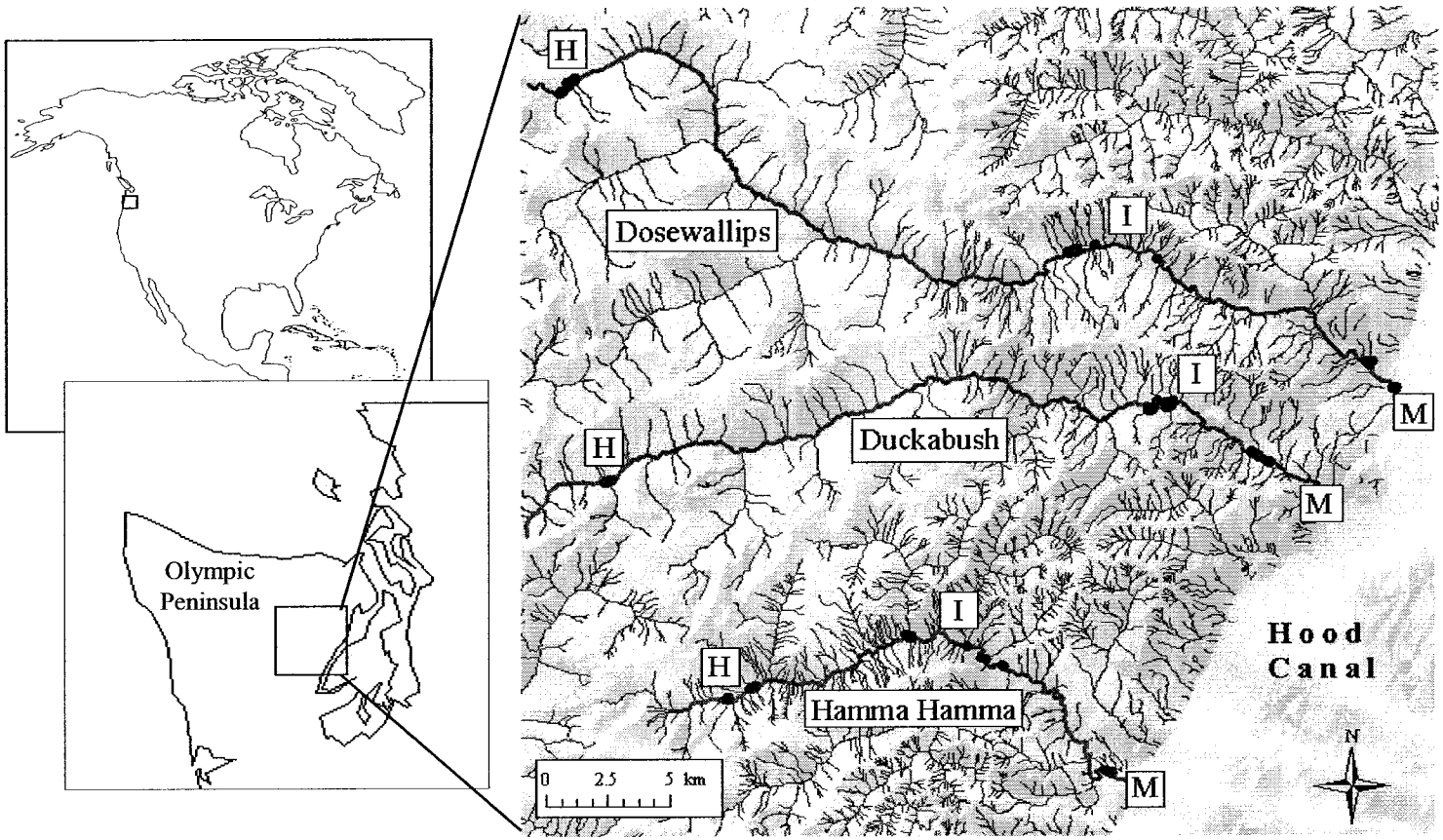

Fig. 3.1. Sample locations (black dots) for 228 *Zapus trinotatus* within a system of three adjacent river drainages, the Dosewallips, Duckabush, and Hamma Hamma, on the eastern side of the Olympic Peninsula in Washington state. Sample zones are indicated as H=headwaters, I=interior, and M=mouth. Samples from each of the nine zones were combined to form nine subpopulations.

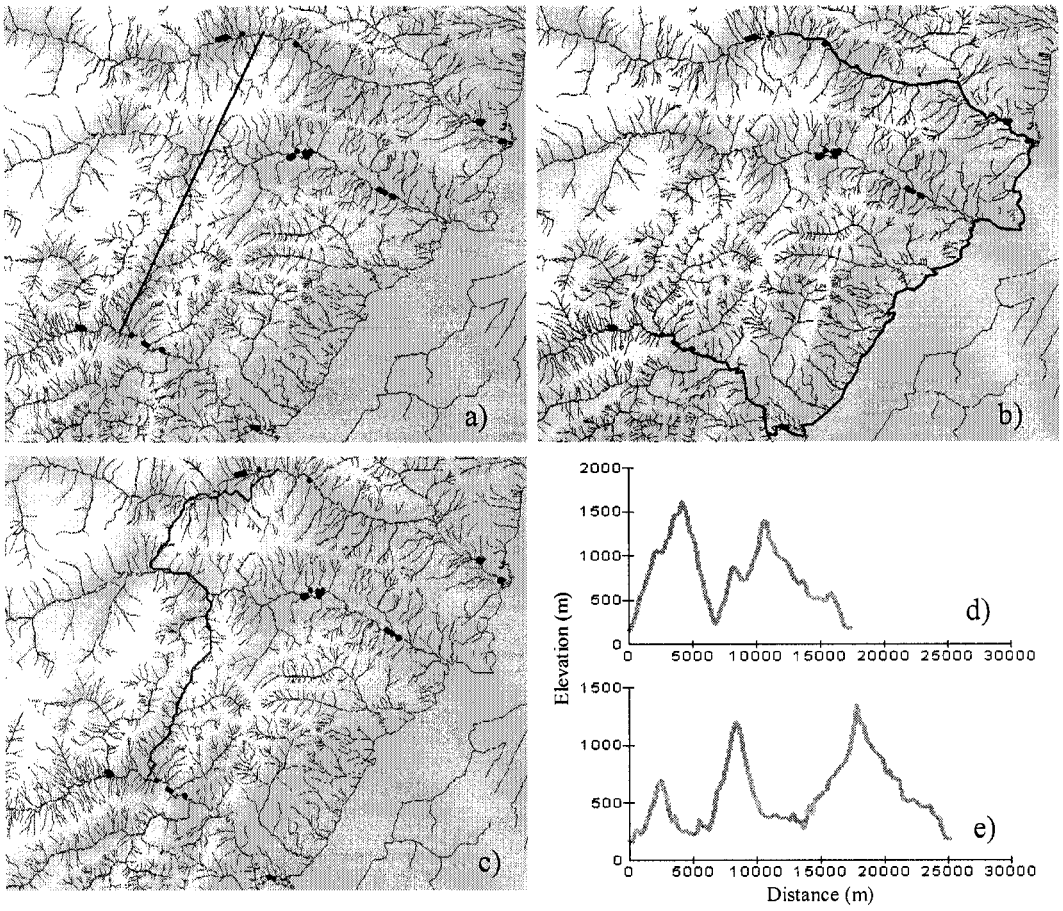

Fig. 3.2. Geographic distance measures, and elevation profile graphs, as estimated between the subpopulations DWI and HHI. (a) Euclidean distance, the shortest line between the subpopulations. (b) River distance, distance when travel is restricted to rivers and shoreline only. (c) Habitat-path distance, 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.

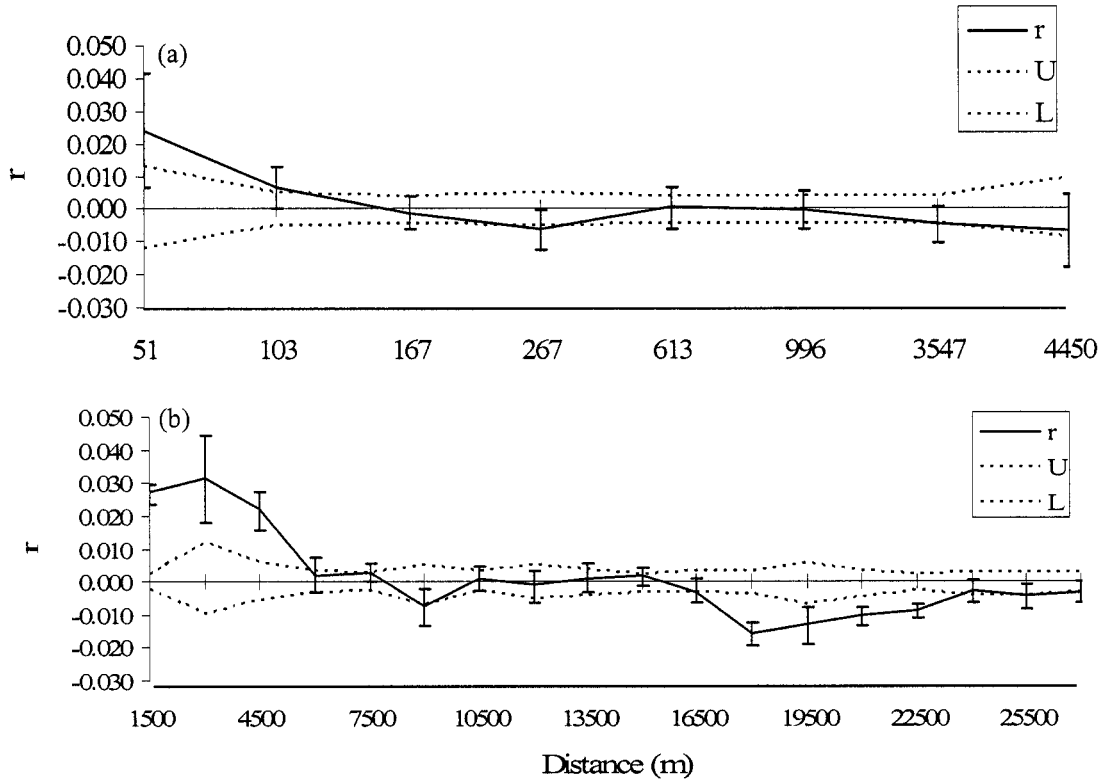

Fig. 3.3 Spatial autocorrelation correlograms indicating multilocus genetic correlation with distance in meters at two levels, (a) only amongst individuals from within the same subpopulations, *rc*, and (b) amongst individuals across all subpopulations, *r*. Dashed lines indicate 95% confidence intervals 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

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Appendix A: Isolation and Characterization of Microsatellite Markers for the Pacific Jumping Mouse

The Pacific jumping mouse (*Zapus trinotatus*) is associated with riparian, marshy, and meadow habitat (Maser *et al.* 1981). These habitats are patchily distributed throughout the geographic range of the species within the Pacific Northwest. The association of this species with such habitat patches results in a non-continuous distribution of individuals throughout the landscape. Interbreeding individuals within patches should form a semi-isolated sub-population that could exchange intermittent migrants with surrounding patches, as predicted by metapopulation theory (Levins 1969).

I am investigating relatedness and connectivity at multiple levels (within a sub-population, between sub-populations and between groupings of sub-populations) within this patchily distributed species. This requires examination of *Z. trinotatus* at multiple levels -- from breeding structure and reproductive success within a patch, to gene-flow and population structure across patches. This examination requires markers flexible and powerful enough for use at both the individual and population levels. Accordingly, I developed a suite of microsatellite markers for *Zapus trinotatus*.

Genomic DNA was extracted from liver tissue acquired from a salvaged trap mortality, using a Dneasy extraction kit (Qiagen). I used an

enrichment protocol followed by PCR screening adapted from Hamilton *et al.* (1999). This protocol involves the ligation of a blunt ended oligonucleotide primer (SNX) to restricted DNA fragments in order to facilitate post-PCR enrichment. Based on a technique developed at the Marine Molecular Biotechnology Laboratory (University of Washington), I modified this protocol by combining the restriction and ligation into one overnight step. In this step 250.0ng (5µl) of genomic DNA was digested and ligated to SNX in the presence of 13.0µl sterile distilled H_2O, 6.0µl buffer #2 (New England Biolabs, NEB), 6.0µl rATP[10mM], 23.4µl double stranded SNX[5mM], 0.6µl BSA[10mg/ml], 2.0µlHincII (NEB), 2.0µlXmn1 (NEB) and 2.0µl T4 DNA ligase (400U/ml NEB). This digestion/ligation mix was incubated overnight in a MJ Research PTC 100® thermalcycler using the following cycling conditions, 37°C (10 minutes) 16°C (30 minutes) for 22 cycles, followed by a final single cycle of 65°C for 20 minutes.

Enrichment of the resulting fragments was conducted (following Hamilton *et al.* 1999) using streptadavin-labeled magnetic beads (Dynal MPC®-E) and biotin-labeled repeat oligonucleotides (Operon Technologies). First, the biotin-labeled repeat was attached to the beads through biotin-streptadavin binding, resulting in magnetic beads carrying a $(GACA_4)$ repeat motif. The digested/ligated DNA was then added to these beads and, at optimum binding temperature (48°C), allowed to hybridize to the repeat

motif. Non-hybridized fragments were then discarded through a series of washes at 48°C with increasing stringency. Following the wash, the resulting fragments were released from the biotin-labeled repeat oligonucleotides, through exposure to high temperature (95°C), and increased through asymmetric PCR. The products of this PCR were transformed into competent cells (TOPO TA Cloning Kit for Sequencing Version E, Invitrogen). Resulting colonies were screened using M13 forward and reverse primers and those containing inserts between 300-1500bp were sequenced using DYEnamic™ET Terminator and visualized on a Megabace 1000 (both Amersham) automated sequencer. One-hundred ten of the positive clones were sequenced and 25 primer pairs were designed using the program C-Primers (Greg Bristol and Robert Anderson, UCLA).

Resulting primer pairs were initially screened on the donor individual using a gradient thermalcycler (MJ Research Tetrad®) at twelve increasing annealing temperatures between 48°C and 65°C. Nine of the primer pairs produced clear products and were optimized for annealing temperature and cycling conditions. PCR reactions were carried out in a volume of 10µl containing 1X Reaction buffer (500mM KCL, 100mM Tris-HCL, and 1%Triton® X-100, Promega Corporation), 0.16mM of each dNTP (0.2mM of each for Ztri18), 2.0mM $MgCl_2$ (2.2mM $MgCl_2$ for Ztri4 and Ztri11 and 2.5mM $MgCl_2$ for Ztri6), 0.3µM of each primer, 0.1U Promega *taq* and

~150ng template DNA. Amplifications occurred through one denaturing cycle at 95°C for 2 minutes, 25 cycles of denaturing for 30 seconds at 94°C, annealing at *Tm* for 30 seconds and extension at 72°C for 22 seconds, followed by one final cycle of extension at 72°C for 5 minutes.

DNA from sampled tail tips was extracted using a Dneasy-96 (Qiagen) tissue extraction kit. Ten individuals were randomly selected to test for variability in the nine resulting loci. PCR products were electrophoresed on 6% polyacrilamide gels and visualized on a FluorImager (Amersham) gel reading system. All nine loci were found to be polymorphic. After initial screening of loci, samples from all populations were genotyped and visualized on a Megabace 1000 (Amersham) automated sequencer and alleles were scored using Genetic Profiler version 1.5 (Amersham). As data were compiled, it became clear that one of the primer pairs was amplifying two clear, polymorphic, non-overlapping, unlinked loci (Ztri19 and Ztri19+); this tenth locus was included in all further analyses.

All ten of the successfully amplified microsatellite loci were screened in 228 individuals from nine sub-populations, or three population groupings. Levels of variability were relatively high. Mean number of alleles per locus varied from 6.4 to 11.3 across sub-populations. Heterozygosities were high in all loci but one (Ztri6), from 0.688-0.912. In the case of Ztri6, the observed heterozygosities were significantly lower than expected, 0.190 versus 0.841,

and it was significantly out of Hardy-Weinberg proportions across all populations. This locus was dropped from all further analyses. Additionally, one pair of loci was found to be linked across all populations, one of these was subsequently dropped and is not included in this report. None of the remaining eight loci were consistently out of Hardy-Weinberg proportions or significantly out of linkage disequilibrium across all populations (analyses conducted in GENEPOP,Raymond and Rousset 1995).

The high degree of variability found in the final 8 markers indicates that they will be useful for analyses of parentage and reproductive success, as well as investigations of population structure and gene flow. They are likely to be applicable in other *Zapus* species and may be especially valuable in the endangered *Zapus hudsonicus preblei.* They may also be useful in other Dipodid rodents, a group within which few microsatellites have been identified.

Table A.1 Characteristics of optimized *Zapus trinotatus* microsatellites. *Tm* is annealing temperature. H_o is observed heterozygosity. H_E is Nei's (1978) unbiased expected heterozygosity. N_a is the number of alleles observed across all populations (228 individuals) *indicates the addition of a fluorescent label at the 5'end.

Locus/ Accesion #	Microsatellite sequence in clone		Primer Sequence (5'□3')	Allele size range	*Tm* (°C)	H_O	H_E	N_a
Ztri2	$(TGTC)_3(GTCT)_2(GTCC)_2$-	F	*CCCAGCTTCTGTGGAAAGGC	131-277	58.1	0.847	0.944	36
AY341377	$(GTCT)_6(GTCCGTCT)_7(GTCT)_6$	R	TGGCATATGAGAGCAGCAGAGTC					
Ztri24	$(GA)_2(CAGA)_{11}$	F	*CAGAGTCTCATTCCCCTTAATAGC	156-197	58.1	0.793	0.894	11
AY341384		R	TTGTGTGGCCAAACTTCCTAC					
Ztri3s	$(GTCT)_2(GT)_3(GTCT)_7$	F	*GACCCTATCCCAAAGAATATGGACAAGAG	224-255	58.1	0.833	0.834	15
AY341378		R	TTTGTCCCAGAATCATTGCCAGG					
Ztri17	$(GA)_6(GACA)_{16}$	F	*AGTGGGGCTTGCTAAAAGACAG	178-233	58.1	0.912	0.894	16
AY341381		R	GTTTGGTGTGGTGTATGCACG					
Ztri18	$(CT)_{16}$	F	*AACTGTTGTATTGGTGATGATTTCTC	97-152	62.1	0.912	0.934	26
AY341382		R	TCCATAATAGTAAATGAGCTGTCCC					
Ztri4	$(CAGA)_{14}$	F	*CATTCCAACTCCATACCCAGTCTAAAGG	363-400	62.1	0.837	0.832	10
AY341379		R	CGCCCCCATTTTTTCTTCCAG					
Ztri6	$(GACA)_{10}(GA)_3$	F	*GCAAGAGATGAAAAATGTCCATGTG	192-229	62.1	0.190	0.841	10
AY341380		R	GTTCGTTTACAGCGGCAGGAG					
Ztri19	$(GA)_6(GACA)_{10}(GA)_5$	F	*GCAAAGGCATGAAATGACGTGC	204-232	62.1	0.728	0.751	11
AY341383		R	CCCGCATAAGCCAGACCCAC					
Ztri19+	UNKNOWN	F	*GCAAAGGCATGAAATGACGTGC	240-259	62.1	0.688	0.751	13
		R	CCCGCATAAGCCAGACCCAC					

NOTES TO APPENDIX A

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VITA

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EDUCATION
University of Washington, (2005) Zoology, PhD
University of California, Berkeley (1993) Integrative Biology, BA

POST-DOCTORAL RESEARCH
University of Sussex, (2005-2006) Centre for Evolutionary Studies, Leverlhulme Fellowship

RESEARCH EXPERIENCE
University of Washington (1998-2005), Graduate research assistant. Effects of habitat heterogeneity on population structure of the Pacific jumping mouse.
University of Washington (1996-1998) School of Fisheries, Research assistant Population structure of northern fur seal. NOAA, National Marine Mammal Laboratory (1996), Field research assistant, Population and foraging ecology of Pribilof Island northern fur seals.
University of Washington, (1995) Wildlife Biology, Field research assistant, Den site selection of northern flying squirrels
University of California, Berkeley (1993-1994), Integrative Biology, Field research assistant, Ecological interactions of two species of Pteropodid bats in the Samoan Islands
University of California, Berkeley (1992-1993), Field Station for Behavioral Research. Behavioral endocrinology of spotted hyenas.
University of California, Berkeley (1992) Integrative Biology, Research assistant. Mate guarding and dominance behavior in midas cichlids.

TEACHIING ASSISTANTSHIPS AND LECTURES
Guest lectures in Biogeography, Conservation Biology, and Mammalogy (2001-2004), Teaching assistantships in Biogeography (1999-2001) and Vertebrate Zoology (1998).

DEPARTMENTAL AND SCIENTIFIC SOCIETY SERVICE

Faculty appointments committee (2003), graduate program committee (2002-2003), graduate representative to the faculty (2001), Burke Museum mammalian diversity outreach program (2001-2003), American Society of Mammalogists International relations committee (2000-present), American Society of Mammalogists Conservation of land mammals committee (2000-present), organizer of Zoology graduate student symposium (1999).

INVITED SEMINARS

(1) Influence of riparian connectivity on gene flow in the Pacific jumping mouse (*Zapus trinotatus*). (2005) Cooperative fish and wildlife research unit seminar series, Department of Natural Resources.

PRESENTATIONS

(1) Streams over mountains: influence of riparian connectivity on gene flow in the Pacific jumping mouse (*Zapus trinotatus*) (2005) Anna M. Jackson award presentation, American Society of Mammalogists. **(2)** Understanding connectivity in patchy environments, limited gene-flow and unexpected migration patterns in the Pacific jumping mouse, *Zapus trinotatus* (2004) Society for Conservation Biology. **(3)** Dispersal as a driver? Effects of local processes on regional patterns in the Pacific jumping mouse (*Zapus trinotatus*) (2004). Ecological Society of America. **(4)** Effects of habitat restricted gene-flow in a patchily distributed species, the Pacific jumping mouse (*Zapus trinotatus*) (2004) Society for the Study of Evolution.**(5)** Does habitat heterogeneity restrict gene-flow? Fine scale genetic structure in the Pacific jumping mouse (*Zapus trinotatus*) (2004) American Society of Mammalogists. **(6)** Can we predict range wide effects from local results: hierarchical population structure in the Pacific jumping mouse (2003) American Society of Mammalogists. **(7)** Can local results predict regional effects: hierarchical population structure in Pacific jumping mice. (2002) Society for Conservation Biology/British Ecological Society. **(8)** Connections between hierarchical population levels (2001) American Society of Mammalogists. **(9)** Predicting patch occurrence across the geographic ranges of four small mammals in Washington. (2000) Pacific Ecology Conference. **(10)** A predictive spatial model for occurrence patches within the ranges of four small mammal species. (2000) Graduate Student Symposium, Zoology Department, University of Washington. **(11)** Predicting patch occurrence across

the geographic ranges of four small mammals in Washington. (2000) American Society of Mammalogists.

AWARDS

EPA STAR fellowship (2003-2006) $100,000 ($27,000 declined), British Ecological Society scholarship for attendance at joint meeting of BES and Society for Conservation Biology (2002) $175, Department of Biology travel award (2002) $450, Richard C. Snyder Award (2002 and 1999) $950, American Society of Mammalogists grant in aid of research (2001 and 2002) $2000, Sigma Xi grant in aid of research (2000) $900, Anna M. Jackson award-American Society of Mammalogists (2005) $750.

PROFESSIONAL SOCIETY AFFILIATIONS

American Society of Mammalogists, Ecological Society of America, Society for the study of Evolution, Society for Conservation Biology

REVIEWER FOR

Biological Conservation, Conservation Biology

JOURNAL PUBLICATIONS

(1) Vignieri, SN (2005) Streams over mountains: influence of riparian connectivity on gene flow in the Pacific jumping mouse (*Zapus trinotatus*). *Molecular Ecology* **(2) Vignieri, SN** (2003) The isolation and characterization of eight highly variable microsatellite markers in the Pacific jumping mouse (*Zapus trinotatus*) *Molecular Ecology Notes* 3, 638-640. **(3)** Drea, CM, **SN Vignieri**, and SE Glickman, (2002) Responses to olfactory stimuli in spotted hyenas (*Crocuta crocuta*): I. Investigation of environmental odors. *Journal of Comparative Psychology* 116, 331-341. **(4)** Drea, CM, **SN Vignieri**, HS Kim, ML.Weldele, and SE Glickman, (2002):II. Discrimination of conspecific scent. *Journal of Comparative Psychology* 116, 342-349. **(5)** Hoekstra HE, JM Hoekstra, D Berrigan, **SN Vignieri**, A Hoang, CE Hill, P Beerli, and JG Kingsolver (2001) Strength and tempo of directional selection in the wild. *Proceedings of the National Academy of Sciences* 98, 9157-9160. **(6)** Kingsolver JG, HE Hoekstra, JM Hoekstra, D Berrigan, **SN Vignieri**, CE Hill, A Hoang, P Gibert, P Beerli (2001) The strength of phenotypic selection in natural populations. *The American Naturalist* 157, 245-261. **(7)** Kingsolver JG, HE Hoekstra, JM Hoekstra, D Berrigan, **SN Vignieri**, CE Hill, A Hoang, P Gibert, P Beerli (1999) The strength of phenotypic selection in natural

populations: A review *American Zoologist* 39, 9A-10A. **(8)** **Vignieri, SN** (in prep for *Ecology*) The connection between ecological mechanisms and genetic patterns: natal dispersal and mating system drive local genetic structure in the Pacific jumping mouse. **(9)** **Vignieri, SN** (in prep for *Nature*) Spatial structuring among individuals precipitates rapid post-flood founder effects in the riparian Pacific jumping mouse. **(10) Vignieri, SN** (in prep for *Evolution)* An interaction between fine-scale spatial genetic structure and a spatially oriented flood results in rapid population divergence in the riparian Pacific jumping mouse.

OTHER PUBLICATIONS

Species accounts for invasive *Rattus* and *Sus spp.* in Boersma, P. D., S. H. Reichard, and A. van Buren. (in press). *unWanted: 101 Invasive Species in the Pacific Northwest*. University of Washington Press.