Natural History Note

The Genetic Effects of Ecological Disturbance: Flooding in Jumping Mice

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ABSTRACT: Pacific jumping mice (Zapus trinotatus) live in riparian habitats that are discontinuously distributed and subject to regular flooding. Both of these characteristics have a spatial component. Habitat-restricted dispersal frequently leads to spatial genetic structure among individuals, and flooding often imposes spatially specific mortality. Here I report that following a severe flood, an interaction between these factors resulted in an immediate reduction of genetic diversity and genetic divergence of the postflood population. Survival was spatially biased toward more closely related individuals, and this was propagated throughout the postflood population by changes in reproduction. Not only did the number of closely related breeding pairs increase, but so did the production of offspring by individuals. These changes precipitated strong genetic effects, including a reduction in observed heterozygosity, an increase in relatedness, a doubling of inbreeding levels, and significant genetic divergence from previous years.

Keywords: bottleneck, founder effects, genetic diversity, inbreeding, spatial genetic structure, Zapus trinotatus.

Introduction

Habitat patchiness is common in nature, and its occurrence is becoming increasingly widespread as a result of anthropogenic habitat fragmentation. Species affiliated with patchy habitats are often ecologically and behaviorally adapted to existence within these discontinuous environments. One of the most common of these adaptations is restricted dispersal (Dieckmann et al. 1999; Wiens 2001). In a subdivided habitat, individual movement between suitable habitat patches can entail substantial risk of mortality. Such risk can exert pressure on dispersing individuals, such that there is an advantage to limiting dispersal distance (Wiens 2001).

In such dispersal-limited species, we also expect the formation of spatial genetic structure among individuals

(Wright 1943; Epperson 1995). Such structure can result not only from short dispersal distances but also from other traits you might expect within patchily distributed species: persistent home range or territory use, philopatry, and nonrandom mating (Shields 1987; Smouse and Peakall 1999; Hansson et al. 2002). The presence of spatial genetic structure can also affect ecological systems and evolutionary dynamics. In particular, patterns of spatial relatedness among individuals can amplify the impacts of mortality events on genetic diversity (Barton and Wilson 1995; Leblois et al. 2006). For example, if survivors of an event share a high proportion of genes, the genes that survive will be biased toward those carried by the related survivors. This can result in rapid genetic divergence in the surviving population as well as possible increases in inbreeding, decreases in heterozygosity, and even reduced genetic diversity (Leblois et al. 2006). This may be especially true in cases where survival is spatially biased, such as disturbances that are spatial in nature (flooding, fire, logging, urban encroachment, etc.).

Interactions between habitat heterogeneity and disturbance are known to have profound influences on ecological processes across scales (Brown 2007), and habitats characterized by a patchy distribution are often prone to disturbance. Thus, the potential for an interaction between spatial genetic structure among individuals, as often found in patchy habitats, and genetic drift, as induced by disturbance, is especially interesting. These interactions are important from a population ecology perspective, particularly where natural disturbance is an integral part of a species' existence. They are also pertinent to conservation because changes in genetic variation, diversity, and inbreeding can affect species persistence, adaptability, and evolutionary trajectory (Frankel 1974; Frankham 2005; O'Grady et al. 2006). Moreover, the increase in habitat loss and fragmentation occurring in areas influenced by humans makes these interactions particularly relevant.

The Pacific jumping mouse (*Zapus trinotatus*) is a small North American rodent in the family Dipodidae that is distributed from southern British Columbia to northern California. They are affiliated with mesic and heteroge-

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neously distributed habitat types, especially riparian alder/ salmonberry (*Alnus-Rubus spectabilis*) and skunk cabbage (*Veratrum*) marsh ecosystems within Douglas-fir (*Pseudotsuga menziesii*) forest (Maser et al. 1981), but also alpine meadows and marshy thickets (Svihla and Svihla 1933). Dispersal is limited in this species (Vignieri 2005, 2007), and they exhibit migration largely along riparian pathways (Vignieri 2005). Work within the flood-impacted population demonstrated that animals show site fidelity and that these home ranges are persistent both within and across years (Vignieri 2007). Most relevant, and as predicted based on the characterized ecology of the species, spatial patterns of relatedness among individuals exist (Vignieri 2005, 2007).

In this study, I characterize the impact of a natural flood on the population dynamics and genetics of this jumping mouse population, with a particular focus on the hypothesis that spatial genetic structure can facilitate rapid genetic divergence and increases in inbreeding. To do so, I used mark-recapture data to characterize demographic and spatial patterns of survival and parentage analysis to identify patterns of postflood reproduction. Additionally, using eight microsatellite markers, patterns of fine-scale spatial genetic structure, genetic diversity, inbreeding, and relatedness were determined before and after the flood to characterize structure and test for bottleneck effects and genetic divergence. While much work has been done on the impacts and importance of specieswide bottlenecks (Bouzat et al. 1998; Glenn et al. 1999; Hoelzel 1999; Whitehouse and Harley 2001; Leonard et al. 2005), this study provides insight into the mechanics of natural bottlenecks and founder events in action, about which we know considerably less (Keller et al. 1994, 2001; Queney et al. 2000; Eldridge et al. 2004; Fauvelot et al. 2006; Busch et al. 2007). This study uniquely demonstrates that interactions between disturbance, intrapopulation structure, and recovery can rapidly alter the genetic composition of small, structured, and semi-isolated populations.

Methods

Study Site

Population Study. I constructed a 25,600-m² trapping grid consisting of 250 traps spaced at 10-m intervals in June 2000 on a section of riparian habitat surrounded by a meander in the Dosewallips River on the Olympic Peninsula in Washington State (fig. 1). This habitat contains a small population of Pacific jumping mice semi-isolated on three sides by the river meander and on the fourth by a steep slope beneath a road. Trapping and nonlethal sampling was conducted during the active season (details in

Vignieri 2007) over 2,205 trap nights in 2000, 6,125 in 2001, and 7,105 in 2002.

The 2002 Flood. On January 6–7, 2002, a storm increased the flow of the river to 260 m³/s from the typical rate of 34 m³/s. Such a flow is estimated to have a recurrence rate of 25 years (Cenderelli et al. 2003). The overbank discharge in this flood resulted in a large degree of overwash (cross-sectional average flow width of 71.54 m and cross-sectional flow area of 121.02 m²), which scoured vegetation and washed away approximately 50 m² of river bank on the northeastern edge of the habitat patch.

Genetic Sampling and Analyses

I genotyped each individual at eight microsatellite loci, isolated from *Zapus trinotatus*, on a MegaBACE 1000 (Molecular Dynamics) automated sequencer. DNA extraction, isolation of microsatellite loci, names of loci, oligo sequences, determination of linkage disequilibria for loci, polymerase chain reaction conditions, and genotyping of individuals are as in Vignieri (2003). Per-locus observed and expected heterozygosities as averaged across all years were as reported by Vignieri (2007).

Demographic Flood Impacts

Pacific jumping mice hibernate from approximately September to March (Bailey 1936); thus mortality induced by the flood occurred while animals were hibernating in their nests. To quantify the spatial nature of this mortality I plotted the last capture location from the previous year for each animal to survive and be recaptured between both of the overwinter seasons, 2000–2001 and 2001–2002. I then constructed a 99% minimum convex polygon (MCP) around these points to create a "survivor region" for each of the overwinter seasons, within the program Biotas (Ecological Software Solutions). Additionally, I conducted a Poisson test for complete spatial randomness (Greig-Smith 1964), also in Biotas, to determine whether survival patterns varied from random in each of the overwinter seasons.

To determine whether flooding affected reproduction in the surviving population, I measured output of males and females before and after the flood. Parentage assignments were conducted using the program CERVUS (Marshall et al. 1998), followed methods in Vignieri (2007), and made with 95% confidence and manual confirmation of parentoffspring matches. Each juvenile assigned to a mother or father was recorded as that individual's offspring, and each individual assigned an offspring was counted as a parent. I then compared counts of offspring assigned to mothers and fathers across years. I used ANOVA and planned com-



Figure 1: Diagram of the sample grid consisting of traps placed 10 m apart along a 220° compass heading (trap locations indicated by dots) and the preflood (*unshaded*) and postflood (*shaded*) survivor regions in a population of jumping mice before and after a severe flood. *Inset*, aerial photograph of habitat patch corresponds to diagram. After Vignieri (2007).

parisons to assess the difference in offspring production before and after the flood and linear regression to test for a correlation between offspring output and adult census size. Further, I calculated pairwise relatedness, *pR*, within the program RELATEDNESS (Queller and Goodnight 1989), between the male and female in each identified breeding pair (those individuals identified as the parents of a sampled juvenile) to investigate whether there were population-level changes in the proportion of closely related breeding pairs. I tested for significance of changes using *G*-tests with the expected proportion of pairs based on those observed in the preflood years.

Interactions between Survival and Spatial Genetic Structure

To characterize a possible interaction between spatial patterns of survival and spatial genetic structure among survivors I constructed detailed "genetic landscape shape" (GLS) interpolation surfaces (Miller 2005) for all adults in the years preceding and following the flood. I similarly constructed GLS surfaces based on all members of the preand postflood populations (i.e., both adults and juveniles) to determine how flood-induced demographic changes in offspring production affected overall patterns of genetic distance. Following the procedure outlined in Miller (2005), a Delauney triangulation connectivity matrix was constructed between home range centroids identified for each individual (as described in Vignieri 2007). Genetic distances between individuals were calculated following Miller (2005, eq. 3). Calculated raw genetic distances were then assigned to landscape coordinates at the midpoints of the connectivity network edges. Patterns of genetic structure across the network were inferred through an inverse distance-weighted interpolation (with a distance weight of a = 0.5; Watson and Philip 1985; Watson 1992) across a uniform grid laid over the entire trapping area (see eq. 1 in Miller et al. 2006). A grid of 11 × 30 cells was used to best match the 10-m trap spacing and dimensions of the trapping grid (other dimensions were

Table 1: Pre- and postflood measures of genetic diversity

Year	$N_{\rm A}$	$N_{\rm J}$	$A_{\rm R}$	$F_{\rm is}$	$H_{\rm e}$	$H_{\rm o}$	$D_{\rm HW}$	$B_{\rm W}$
Preflood:								
2000	60	36	94	.019	.834	.823	.070	.004**
2001	71	24	98	.017	.834	.826	.070	.009**
Postflood:								
2002	35	52	94	.043**	.822	.787**	<.001***	.014*

Note. N_A = number of adults captured in each year; N_J = number of juveniles captured in each year; A_R = allelic richness across all eight loci; F_{is} = Wright's inbreeding coefficient; H_e = expected heterozygosity; H_o = observed heterozygosity; D_{HW} = deviation from Hardy-Weinberg equilibrium; and B_W = Wilcoxon tests for evidence of a bottleneck. Significance is indicated by asterisks for (1) F_{is} as a deficit of heterozygotes, indicative of inbreeding, within a year, (2) H_o as a deviation from that expected under Hardy-Weinberg proportions within a year across all loci, (3) D_{HW} as an overall deviation from Hardy-Weinberg equilibrium within years and across loci, and (4) B_W as a bottleneck-induced excess of heterozygosity within a year.

* $P \le .05$.

** $P \le .01$.

*** $P \leq .001$.

tested to ensure that grid size did not affect surface morphology). This procedure produced an interpolation across a rectangular grid 30 cells wide and 11 cells deep (with a cell roughly equal to 10 m²); however, the actual trapping grid is irregular, as it was set to fill the natural landform created by a river meander. Thus, the interpolation surface was pruned to match the exact dimensions of this grid through the removal of values interpolated for cells in areas outside of the habitat patch.

Spatial patterns of survival were plotted on GLS to determine whether survival patterns interacted with spatial patterns of genetic distance. I used *G*-tests to determine whether patterns of genetic distance among individuals were different inside and outside of the flood survival range (in the preflood year) and before and after the flood.

Population Comparisons Before and After the Flood

A Wilcoxon signed rank test under the two-phase mutation model (with 70% TPM) was used, within the program Bottleneck (Cornuet and Luikart 1996), to test for a bottleneck-induced deficit of heterozygosity (H_{FX}) in preand postflood populations. In addition, measures of genetic diversity were estimated before and after the flood. To determine whether the overall relatedness of individuals within the population increased, I estimated the relatedness coefficient, R, among all individuals, adults, and juveniles, and between adults and juveniles in each year using the program RELATEDNESS (Queller and Goodnight 1989). I tested for significant differences between these values through t-test comparisons of jackknife pseudovalues (which corrects for possible pseudoreplication) as implemented within the RELATEDNESS program. To determine whether there was an increase in inbreeding, I estimated F_{is} (Wright 1978) with the program FSTAT (Goudet 2001) and used a randomization procedure to determine significance. In addition, I tested each year for deviation from Hardy-Weinberg equilibrium (D_{HW}) using the exact test of Guo and Thompson (1992) within GENEPOP (ver. 3.4; Raymond and Rousset 1995). To test for a reduction in genetic diversity I measured allelic richness (A_R) and the levels of observed and expected heterozygosity (H_o and H_e) across all loci in each year within the program TFPGA (ver. 1.3; Miller 1997). I used a Wilcoxon paired sign-rank test (Zar 1999) to test for differences between pre- and postflood levels of heterozygosity across loci.

To investigate whether the flood precipitated genetic divergence, I compared allele frequency distributions between years using Fisher's exact test (Raymond and Rousset 1995) and used Fisher's combined probability test (Sokal and Rohlf 1995) to determine significance across loci in TFPGA (ver. 1.3). I determined the level of postflood divergence through estimation of pairwise F_{st} between years (Weir and Cockerham 1984), and significant differences of these values from 0 were determined using a nonparametric permutation approach (Excoffier et al. 1992) within the program Arlequin (ver. 2; Schneider et al. 2000).

Results

Demographic Flood Impacts

In the preflood 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. Unlike total size, the flood substantially altered age structure in the population. In 2000 and 2001, adults represented 63% and 75% of the population, respectively. Following the flood only 40% of individuals captured were adults—half the number captured in preflood years (table 1). Overwinter survival decreased by 44% following the flood, with 34 individuals captured in 2000 recaptured in 2001 versus 19 captured in 2001 and recaptured in 2002.

Roughly half the sampled juveniles were assigned parents in each year (14, 12, and 24, respectively). The total number of individuals identified as parents did not increase following the flood (parents₀₀ = 21, parents₀₁ = 14, parents₀₂ = 14) despite the twofold increase in the number of juveniles. However, the mean number of offspring identified per parent did increase ($M_{00} = 1.4$, $N = 36; F_{01} = 1.5, SE = 0.34, N = 36; F_{02} = 2.7,$ SE = 0.67, N = 20; ANOVA, P = .001), and there was a strong negative correlation between the census number of adults and the mean number of offspring produced per breeding adult ($R_{males}^2 = 0.664$, $R_{females}^2 = 0.955$, $R_{all}^2 =$ 0.665; P = .03). Following the flood there were upward shifts in both the distribution of related breeding pairs (G = 23.87, df = 7, P = .001; fig. 2A) and the average number of offspring produced by pairs of a given pR(G = 42.87, df = 7, P < .001; fig. 2B).

Spatial Flood Impacts

The postflood survivor region was 9,000 m² as compared to 15,850 m² for that over the nonflood winter season (fig. 1). Survivor capture points were distributed in a significantly nonrandom way postflood (P = .01, $\chi^2 = 6.28$) but not preflood (P = .16, $\chi^2 = 2.01$).

In the adult GLS, G-tests revealed that the proportion of cells falling below the average genetic distance as computed across the surface in the preflood year (0.739) was higher inside the survival range than it was outside (fig. 3A; G = 6.68, df = 1, P < .01). Further, following the flood, the proportion of all cells with below-average (0.737) genetic distance increased (fig. 3B; G = 5.86, df = 1, P < .05). In the population-wide GLS, 94% and 100% of the cells fell below the average adult GLS genetic distance pre- and postflood, respectively, demonstrating that the vast majority of recruits to the population were locally generated in both cases (fig. 3C, 3D). However, the inclusion of new recruits in the year following the flood decreased population-wide GLS genetic distance (Adult_{post} = 0.737, Population_{post} = 0.715) nearly three times more than it did in the preflood year (Adult_{pre} = 0.739, Population_{pre} = 0.731).



Figure 2: Population level increase in relatedness among mates, and production of offspring by related mates, following severe flood in 2002. *A*, Number of breeding pairs identified with given pR; *B*, average number of offspring produced by pairs with given pR. The number of pairs contributing to the average in *B* can be found in *A*.

Genetic Effects

Interestingly, Wilcoxon tests revealed the signature of a bottleneck in all three years (table 1). Average relatedness among all comparisons did not change between the first two years, and thus these populations were combined such that all subsequent relatedness comparisons consisted of preflood (2000 and 2001) and postflood (2002). Relatedness among all individuals and among adults increased nearly threefold following the flood (fig. 4A, 4D). Increases in relatedness among juveniles and between adults and juveniles were smaller but also significant (fig. 4B, 4C). F_{is} values in the two preflood years were similarly low and were not significantly different from 0, but F_{is} in the year following the flood doubled (table 1) and showed a significant deficit of heterozygotes (table 1). Expected heterozygosities were similar in all three years (table 1), as were allelic richness values (table 1). Observed heterozygosities in the first two years did not differ from expectation. However, observed heterozygosity in the postflood population was different from that expected under Hardy-Weinberg proportions and significantly lower than that of the previous years (table 1; $P_{00-02} = .01$ and $P_{01-02} = .05$).



Figure 3: Overlap between flood survival region and patterns of genetic distance for adult jumping mice existing within a habitat patch created by a river meander; before (A) and after (B) winter flood; and change in patterns of genetic distance following recruitment (i.e., including both adults and juveniles) before (C) and after (D) flood. Genetic distance relationships are represented across a genetic landscape surface that corresponds to the dimensions of the habitat patch, and survival range is surrounded by an irregular pentagon. Interpolation cells with values that fall at and below average genetic distance across the surface for adults in each year are indicated by darker shading and those that fall above by lighter shading. Genetic distance values for each cell are coded according to the scale bar, and X- and Y-axes indicate distance along the sampling grid, with X parallel to and Y perpendicular to the river.

Only the postflood population was significantly out of Hardy-Weinberg equilibrium (table 1).

The postflood population diverged genetically from the preflood population as revealed through significant allele frequency differences ($P_{00-02} < .001$, $P_{01-02} = .024$). Allele distributions did not differ between the two preflood years ($P_{00-01} = .209$). Similarly, low but significant F_{st} values were found between the pre- and postflood populations ($F_{st-00-02} = 0.003$, $F_{st-01-02} = 0.003$; both $P \le .05$), whereas F_{st} between the preflood years was three times lower and not significantly different from 0 ($F_{st-00-01} = 0.001$; $P \ge .05$).

Discussion

Pacific jumping mice live in extremely dynamic habitats prone to regular flooding. In this study we have observed how such floods, and the recovery process that follows them, directly shape the population. In particular, the survival of, and increased reproduction by, mice in a distinct region of the habitat resulted in significant changes in the genetic diversity and composition of the population.

Survivors and Recovery

Survival decreased by nearly half, precipitating a moderate bottleneck in abundance; nonetheless, the population re-



Figure 4: Relatedness coefficient, R, in a population of jumping mice as determined before (2000 and 2001 combined) and after (2002) the flood, among all individuals, adults, and juveniles. Bars around estimates are standard errors produced by jackknife resampling of loci. All comparisons reveal significant differences determined through *t*-tests conducted on jackknife pseudovalues; among adults and all individuals, P < .001; among juveniles and between adults and juveniles, P < .05.

covered to nearly preflood size by the end of the following season, with twice the number of juveniles. This rapid recovery to near preflood size is interesting given that jumping mice hibernate for the majority of the year, produce only a single litter per year, and have a relatively small litter size (4-6; Bailey 1936). However, the increase in the mean number of offspring produced following the flood and a trend for increased "production" of juveniles when the number of census adults was low suggest a numerical response. There are three main, nonexclusive, processes that could have contributed to this response: (1) increased juvenile production, (2) increased juvenile survival, and (3) increased juvenile retention. In all cases increases could have been facilitated by decreased intraspecific competition expected to follow a population decline. It is likely that a combination of these processes were acting. Importantly, however, our main concern here is not how the number of related offspring increased following the flood but whether these offspring were produced locally.

Although the study population is somewhat isolated and migration among habitat patches is limited in jumping mice (Vignieri 2005), migration into the population could have also contributed to the recovery, as observed in other systems (Keller et al. 2001; Berthier et al. 2006; Fauvelot et al. 2006). In fact, in the postflood adult GLS there are three upslope areas where genetic distance among adults is elevated (visible as light areas in fig. 3*B*), a pattern that could be due to adult migration into the population or a

breakdown in structure due to movement of residents. More broadly, however, the results of the study support the hypothesis that population recovery was primarily locally driven. In particular, relatedness increased not only among adults and among juveniles as separate demographic groups but also between adults and juveniles (i.e., juveniles were more closely related to adults in the population after the flood than they were before). This result is strongly supported by the population-wide GLS analyses, which show that in both years juveniles throughout the habitat patch were related to resident adults and thus locally produced. This pattern was amplified in the year following the flood, in which population-wide genetic distances decreased substantially from those found in the population before the flood. This further demonstrates that the increase in the number of juveniles found in the postflood population was due to increased production (or survival) of offspring by surviving adults. These results are contrary to those expected for increased migration (wherein we would expect to see increases in genetic distance, especially following inclusion of juveniles) and clearly show that migration contributed minimally to postflood genetic structure. This finding is also consistent with strong habitat affiliation, relatively long life span (5-7 years), stable home range use, and limited dispersal distances characteristic of jumping mice. A similar result was observed by Peakall and Lindenmayer (2006), who found that populations of bush rats (Rattus fuscipes) exposed to experimental perturbation were genetically more similar to their predisturbance population than to neighboring populations. In contrast, Fauvelot et al. (2006) found that recovery in postfire populations of butterflies (*Drupadia theda* Felder) was directly related to their proximity to source populations and thus dependent on migration. It is likely that postdisturbance recovery is highly dependent on an interaction between the natural history of a species (e.g., dispersal ability and propensity) and the connectedness of the impacted population to source populations.

Genetic Effects

The change in overwinter recapture rates indicated a moderate, but clear, bottleneck in abundance. Interestingly, however, excess heterozygosity was present in all three years. A bottleneck-induced excess of heterozygosity is transitory but is detectable for 0.2-4 Ne generations (Luikart et al. 1998). Estimates of N_e made in each of the three years (using the method of Hill [1981] within the program NeEstimator [Peel et al. 2004]) indicate a 95% confidence range of $N_{a} = 46-132$. Assuming a 1-year generation time, which is consistent with jumping mouse natural history, a bottleneck within this population would be detectable for 9.2-528 years. While severe floods are relatively infrequent, they do happen at the rate of roughly one every 25 years. Given this level of regularity and the time required for the transitory signal to dissipate, it appears that the test for heterozygosity excess cannot differentiate the current bottleneck from those in the past. Instead, these results suggest that disturbance-induced bottlenecks are a regular component of this population.

Examination of the interaction between survival, relatedness, and reproduction provides a more direct approach for understanding how decline and recovery influence genetic composition. Genetic distance among animals living in the survival region before the flood was lower than it was for animals living outside of this region; this pattern could be due to persistent philopatry of mice in the upslope, and more stable, region of the patch. The elevated relatedness present among the survivors was propagated throughout the postflood population through a change in reproductive patterns. Not only was there an upward shift in the distribution of pairwise relatedness between mates, but this shift coincided with an increase in the average number of offspring produced per pair and the average number of offspring produced by more closely related pairs. Importantly, not all mated individuals were closely related. These results suggest that relatively small increases in the relatedness of breeding pairs can increase inbreeding and amplify relatedness at the population level.

Conclusions and Implications

Disturbances are quite common in nature. Similarly, spatial genetic structure among individuals is a component of many natural populations (Epperson and Li 1997; Sumner et al. 2001). Interactions between mortality, genetic structure, demographics, and genetic variation are likely to be typical responses to environmental change within natural populations. Thus, detailed knowledge of these interactions can help us to better understand evolutionary processes in systems subject to disturbance. Additionally, anthropogenically induced climate change is predicted to precipitate large increases in both the frequency and severity of spatial disturbance events such as fire and flooding within the next 100 years (Fowler and Hennessy 1995; Hennessy et al. 1997; McCarthy et al. 2001; Brown et al. 2004). An improved knowledge of how populations respond to disturbance may help us to foster persistence in species influenced by such anthropogenically induced increases.

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Riparian jumping mouse habitat along the Dosewallips River (photograph by Sacha Vignieri); *inset*, Pacific jumping mouse with ear tag (photograph by Rolf Ream).