

The Effects of Habitat Fragmentation on the Genetic Structure of Small Mammal Populations

M. S. Gaines, J. E. Diffendorfer, R. H. Tamarin, and T. S. Whittam

We present five case studies highlighting the effects of habitat fragmentation on the genetic structure of small mammal populations. The studies reflect different spatial scales and components of genetic variation. In marginal and central populations of *Sigmodon hispidus* we found less allozymic variation within the marginal population, whereas patterns of morphological variability were the converse. In the rice rat (*Oryzomys* spp.), nucleotide diversity in mtDNA was similar in an island population in the Florida Keys to mainland populations in the Everglades. This observation contrasts with insular vole populations (*Microtus* spp.), where isolation on islands results in genetic structuring. Temporal changes in abundance in mainland populations had no effects on genetic differentiation (F_{ST} values) because subpopulations did not experience bottlenecks. In an experimentally fragmented landscape, fragmentation influenced demographic processes but not genetic structure. We conclude that (1) with extreme fragmentation, small mammal populations become depauperate of genetic variation and differentiate genetically; (2) different components of genetic variation lead to different genetic structuring; (3) spatial and temporal scales should both be considered when examining genetic structure of populations; (4) demographic and ecological processes are more likely influenced by fragmentation than genetic structure; and (5) there is an interaction between demographic processes and genetic structure.

Human activities are destroying the natural habitats of terrestrial ecological communities at an alarming rate. As a result of this destruction, native habitats have become more fragmented: those that were once continuous are now subdivided into "islands" of suitable habitat surrounded by an unsuitable "sea" that has been modified by humans. As fragmentation increases, it leads to a decrease in average habitat patch size and an increase in average distance between patches. Both the loss of habitat and the isolation of habitat patches can reduce population sizes to such low levels that indigenous species go locally extinct.

Gilpin and Soulé (1986) distinguished between the causes underlying two kinds of population extinctions, deterministic and stochastic. Deterministic extinctions result from forces that inexorably lead to the disappearance of a population. For example, in the Florida Keys tropical hardwood hammocks and pinelands are being eliminated by real estate development, which if left unchecked will exterminate the communities of small mammals, birds, and other organisms that occupy these

habitats. Stochastic extinctions are those due to random events. Shaffer (1981, 1987) described four sources of variation that could result in the random extinction of a population: (1) demographic stochasticity due to random events in individual survival and reproduction; (2) environmental stochasticity due to unpredictable changes in abiotic or biotic factors; (3) natural catastrophes such as fires and floods, which occur at random intervals; and (4) genetic stochasticity in fitness due to genetic drift and inbreeding depression. The first three sources of variation are ecologically induced, whereas only the last is genetically induced.

There has been lively discussion among population biologists about the relative roles of ecological and genetic stochasticity in causing extinctions. Some ecologists have argued that the Alleé effect, in which densities become too low for populations to persist, plays a major role in extinctions. Population geneticists have focused on the role of genetic drift and inbreeding depression in small populations as a major cause of extinction. Lynch and Gabriel (1990) showed, for example, that the syn-

From the Department of Biology, University of Miami, Coral Gables, FL 33124 (Gaines and Diffendorfer), the Department of Biology, University of Massachusetts, Lowell, Massachusetts (Tamarin), and the Department of Biology, Pennsylvania State University, University Park, Pennsylvania (Whittam). We thank Jim Hamrick and Jim Patton for their critical comments on this manuscript. We are grateful to Dr. Xiaoyuan Kong for her technical assistance in the mtDNA sequencing of *Oryzomys*. Darung Wu generously provided some data on mtDNA RFLP variation in *Microtus ochrogaster* from her Master's thesis at the University of Kansas. Some of this work was supported by National Science Foundation grants BSR-8718088 and DEB-93-0865 as well as the University of Kansas General Research Fund to M.S.G. and Public Health Service grant HD 06621 to R.H.T. This paper was delivered at a symposium entitled "Genetics of Fragmented Populations" sponsored by the American Genetic Association at the University of Georgia on May 18, 1996.

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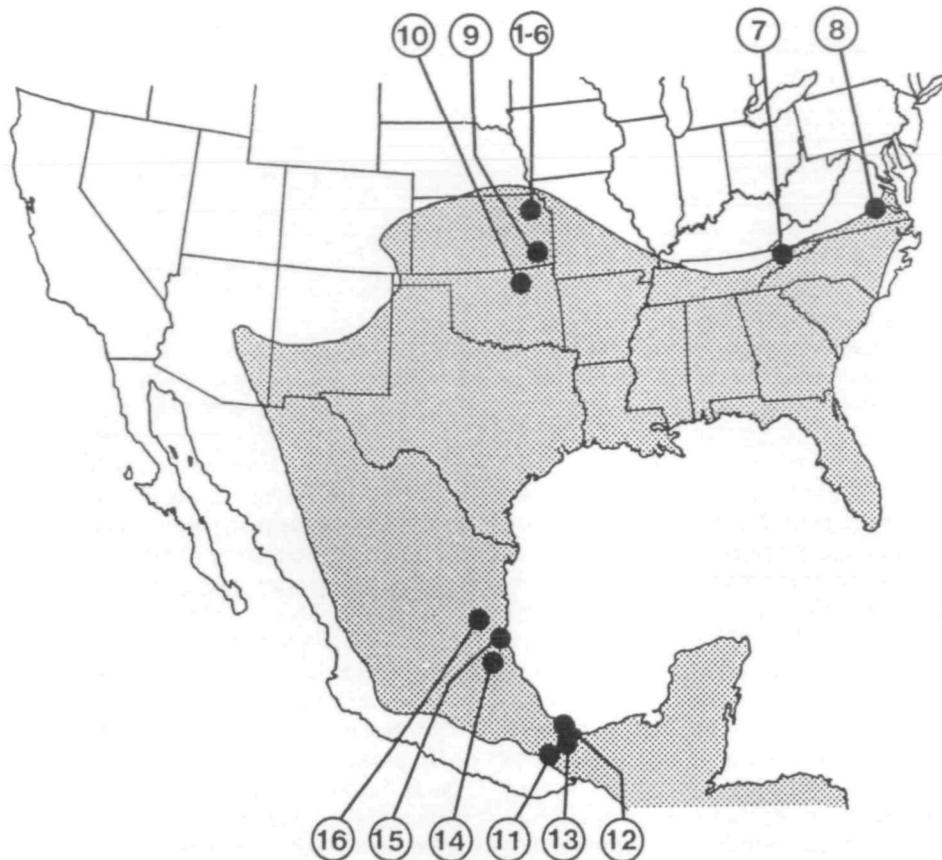


Figure 1. Locations sampled for cotton rats (*Sigmodon hispidus*) in Mexico and the United States. The stippled area represents the known distribution of cotton rats. Locations 1–10 were considered marginal and 12–16 central.

ergistic interaction between the accumulation of deleterious mutations in small populations can cause concomitant reductions in population size, an effect they refer to as “mutational meltdown.” Clearly, both ecological and genetic factors can contribute to population extinction. Nevertheless, Lande (1988) concluded from theoretical and empirical examples “that demography is usually of more immediate importance than population genetics in determining the minimum viable sizes of wild populations.”

In this article we follow Lande’s advice and integrate population genetics and ecology to understand the effects of fragmentation on small mammal populations. Small mammals are ideal organisms for studying the effects of habitat fragmentation. First, a major focus in small mammal ecology has been how variation in patch size and quality affects population processes (for reviews see Hansson 1995; Lidicker 1995). Second, there is much information on dispersal of small mammals in patchy environments (Diffendorfer et al. 1995a; Gaines and McClenaghan 1980; Johnson and Gaines 1990). Third, small

mammals can be experimentally manipulated (Johnson and Gaines 1987).

Our purpose here is not to give a complete review of the work that has been done on fragmented populations of small mammals. Instead, we focus on several case studies that illustrate some of the major patterns and complexities drawn from our own research experiences. First, we examine patterns of genetic structure on several geographic scales, from subpopulations within an individual’s dispersal range to larger landscapes. In addition to various spatial scales of fragmented landscapes, we will investigate the effects of fragmentation on different types of genetic variation; including morphological variation, protein polymorphisms, restriction fragment length polymorphisms (RFLPs), and DNA base substitutions. Second, we will explore how demographic processes in an experimentally fragmented landscape in northeastern Kansas can be related to genetic structure. Finally, we reach some general conclusions about the effects of habitat fragmentation on the genetic structure of small mammal populations.

Allozymic and Morphological Variation in Central and Marginal Populations of the Hispid Cotton Rat (*Sigmodon hispidus*)

Evolutionary and population processes that occur in fragmented populations may also occur in marginal populations of a species distribution. Our contention is that some of the same mechanisms operating in populations in fragmented habitats to reduce genetic variability could also operate in marginal populations. One cautionary note is that although marginal and fragmented populations share many features, they do not share them all. For example, a recently colonized marginal population might be expected to have substantially less genetic variation than a similarly sized remnant of a genetically diverse population in a fragmented environment.

Soulé (1973) identified six factors accounting for the loss of variation in marginal populations. First, as individuals become more isolated from a pool of potential mates, the probability of mating with close relatives increases. Second, increased isolation may result in reduced gene flow. Third, founder events and bottlenecks result in genetic drift. Fourth, inbreeding and a lack of gene flow result in a smaller effective population size (N_e) in marginal localities. Fifth, the niche-width variation hypothesis predicts that less ecological variation leads to less genetic variability in marginal habitats. Finally, directional selection in marginal environments reduces variation. All six factors should also reduce variation in isolated patches in fragmented landscapes. This reduction will depend on the size of the isolated populations.

In 1980 we compared genetic variation in marginal and central populations of the hispid cotton rat (McClenaghan and Gaines 1980). This murid rodent was well suited for such a study for several reasons. The species is widely distributed (Figure 1). We wanted to sample populations from vastly different environmental regions to detect differences in genetic structure. Also, several lines of evidence suggest that populations of cotton rats near the northern edge of the species range are ecologically marginal (McClenaghan and Gaines 1980).

We sampled 647 cotton rats from 16 localities in the United States and Mexico (Figure 1). Ten populations in the United States were close to the northern edge of the species distribution and six popula-

Table 1. Estimates of genic and morphological variability in marginal and central populations of *Sigmodon hispidus*

Locality	Sample sizes		Genetic variation				
	All ages	Adults	<i>P</i> (%)	<i>H_i</i>	<i>CV_n</i>	<i>F_{ST}</i>	<i>s²CV_n</i>
Marginal	460	143	17.4	0.19	8.32	0.005	1.55
Central	187	79	26.1	0.23	4.91	0.024	1.12

P represents the mean proportion of polymorphic loci; *H_i* is the mean heterozygosity per individual; *CV_n* is the mean multivariable coefficient of variation computed from 16 morphometric variables measured from adults; *s²CV_n* is the variance in *CV_n*; *F_{ST}* is the mean measure of among-population variance over all polymorphic allozyme loci.

tions in Mexico were centrally located. To assess the amount of genetic variation within populations, we examined protein polymorphisms at 23 allozyme loci and estimated the within-population heterozygosity (*H_i*) and the proportion of polymorphic loci (*p*). To gauge the degree of genetic differentiation among populations, we calculated standard genetic distances (Nei 1972) and *F_{ST}* values (Wright 1965) based on electrophoretic variation at six polymorphic protein-encoding loci (*Lap*, *Trf*, *6-Pgd*, *Mdh-1*, *Mdh-2*, and *Got-1*). Phenotypic variation was assessed by measuring adult cotton rats for 16 conventional external and cranial characteristics. We quantified variability in each population as a multivariate coefficient of variation, *CV_n* (McClenaghan and Gaines 1980). *CV_n* is independent of the number of variables measured and is numerically comparable to the univariate coefficient of variation.

There was significantly less genetic variation within marginal cotton rat populations as compared to the central populations (Table 1). The mean *p* for marginal populations was lower than that for central populations ($U = 57, P < .01$) and the heterozygosity (*H_i*) was also significantly reduced ($U = 19, P < .05$). *F_{ST}* values for marginal populations were approximately five times lower than comparable values for the central populations, which was marginally significant ($U = 11.5, P < .09$). There was a statistically significant positive correlation between genetic distance and geographic distance in pairwise comparisons of localities ($r = 0.51, P < .01$). Thus, as geographic distance between populations increased, genetic distance increased.

We expected the genetic variance among marginal populations to be higher than central populations as a result of past genetic drift and reduced gene flow.

This was not the case. There are several hypotheses that can account for the genetic uniformity among marginal populations of the cotton rat. The one we favor is that the marginal populations were recently established as a consequence of a single northward colonization from the center of the species range, with a subsequent extension along an east-west axis. In addition, the amount of genetic variation among marginal populations may have decreased as a result of subsequent genetic drift and loss of rare alleles and fixation of common alleles.

The pattern of morphological variability is the converse of that for genetic variability; the average morphological variance of characters in marginal populations exceeds that of central populations (Table 1). The difference between the mean *CV_n* of the marginal and central populations was statistically significant ($F_{1,12} = 22.0, P < .01$). Because the total variance in morphological traits contains both an environmental and a genetic component, the higher values for *CV_n* in marginal populations may be due to greater environmental variance at the margin of the species distribution. There were no significant differences in the variance of *CV_n* among marginal populations compared to the variance of *CV_n* among central populations.

Habitat Fragmentation in Rice Rat (*Oryzomys*) Populations

Marsh rice rats (*O. palustris*) occur from southeastern Pennsylvania and southern New Jersey southward to the tip of Florida (excluding the Florida Keys) and westward to Texas (Wolfe 1982). Rice rats reach high abundances in mesic habitats such as low-lying forests, other natural areas with seasonal standing water, and irrigated agricultural areas. There have been several morphological studies of rice rats in North America (Goodyear 1991; Humphrey and Setzer 1989) and one genetic study using allozymes (Schmidt and Engstrom 1994). These studies focused on the systematics of *O. palustris*.

To elucidate the genetic population structure of marsh rice rats (*O. palustris*) in a highly fragmented environment, we sampled individuals from tropical hardwood tree islands in Everglades National Park. We collected from a constellation of 17 hammock islands at Rock Reef Pass in the central Everglades and 6 islands at Chekika in the east Everglades. The two localities are approximately 30 km apart. Distances between islands within the two

Table 2. Average nucleotide diversity within and between three populations of *Oryzomys*

	Number	Central Everglades	East Everglades	Keys
Central Everglades	20	0.0151	—	—
East Everglades	6	0.0258	0.031	—
Keys	15	0.0211	0.0221	0

Diversity is measured as the average number of substitutions per nucleotide site.

localities ranged from 20–360 m. Island area ranged from 0.0005–0.45 ha. In addition, we trapped a disjunct population of silver rice rats (*O. argentatus*) on Raccoon Key (Monroe County in the Lower Florida Keys). This species occurs only in the Lower Keys (Spitzer and Lazell 1978) and is classified as endangered by the U.S. Fish and Wildlife Service. From a systematics standpoint, there has been disagreement on whether the silver rice rat should have species or subspecies status (Goodyear 1991; Humphrey and Setzer 1989).

To assess the impact of habitat fragmentation on genetic structure and isolation of populations, we examined nucleotide variation in the D-loop of mtDNA within and between two *Oryzomys* populations in the east and central Everglades and one population in the Florida Keys. Because of its insular geography and restricted habitat, we hypothesized that within the Florida Keys, effective population sizes should be small and should reduce variation relative to populations in the Everglades. Also, we expected genetic differences between the Keys and Everglades populations to exceed the differences between the two Everglades populations.

We isolated DNA from tail tips and used oligonucleotide primers to amplify a 291 bp segment within the HV1 region of the mtDNA D-loop. Nucleotide sequences were determined by a silver DNA sequencing system (Promega Co.).

We calculated the diversity of the mtDNA sequence data using the method of Lynch and Crease (1990). The average number of substitutions per nucleotide site given by their Equation 1 is summarized in Table 2. A total of 34 sites out of 291 were polymorphic ($P = .12$). The average nucleotide diversity within populations was $\nu(w) = 0.0151$. It is noteworthy that the Keys population had no detectable mtDNA variation, which is consistent with the idea that this population has experienced a small effective size, either a pronounced bottleneck or a recent founding event.

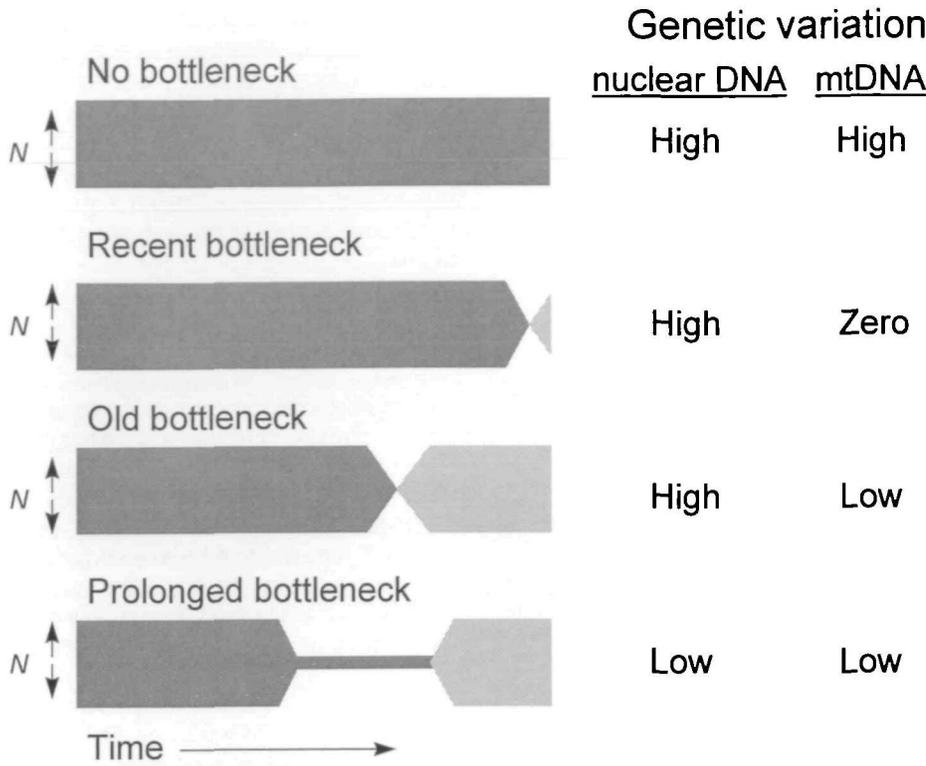


Figure 2. Conceptual model of changes in the variation of nuclear and mitochondrial DNA under different temporal patterns of genetic bottlenecks. (This figure was modified from Wilson et al. 1985, p. 391.)

The impact of a bottleneck on the amount of genetic variation is different for nuclear than for mitochondrial genes and depends on the duration of the bottleneck (Wilson et al. 1985). The qualitative outcome is shown in Figure 2. The width of the bar denotes the standing population size (N) and the effects of the timing of bottlenecks on the level of genetic varia-

tion (right side columns in the figure). A very recent bottleneck, as depicted in the second row of the figure, can substantially reduce mtDNA variation without a significant reduction in genetic variation in nuclear genes. Given sufficient time, the mtDNA diversity can recover, as shown in the third row where the bottleneck occurred in the more distant past. However,

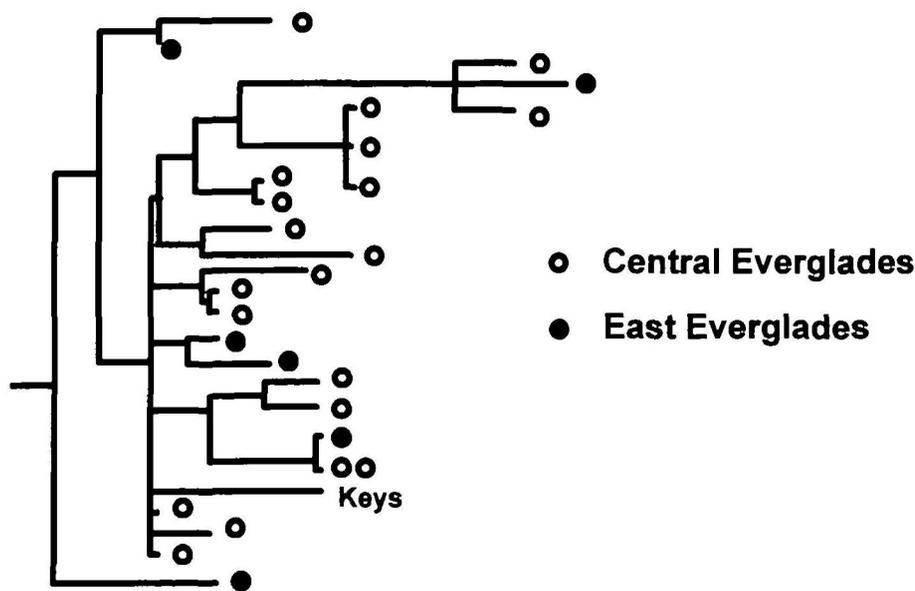


Figure 3. Neighbor-joining tree for rice rats (*Oryzomys palustris* and *Oryzomys argentatus*) in the central Everglades, east Everglades, and the Lower Florida Keys.

if the bottleneck is prolonged, both nuclear and mitochondrial variation can be reduced to low levels (Figure 2, bottom row).

Our finding of no mtDNA variation in the Keys population suggests that *O. argentatus* experienced a recent bottleneck that virtually eliminated mtDNA variation within the population. We predict that this bottleneck was very recent (see below) so that the level of genetic variation in nuclear genes remains high (the situation shown in the second row of Figure 2). At this point we have not obtained the data on nuclear genes to test this prediction.

Interestingly the Keys population had a unique sequence in the mtDNA D-loop that was not found in either of the Everglades populations. The average nucleotide diversity between populations was $v(b) = 0.023$. Contrary to our expectation, nucleotide diversity between the Keys population and the Everglades populations was not significantly greater than the diversity between the central and east Everglades populations. The statistic that corresponds to the G_{ST} (Nei 1973) at the nucleotide level is $N_{ST} = v(b)/[v(b) + v(w)]$. For the *Oryzomys* data, $N_{ST} = 0.60$. This value is comparable to N_{ST} values obtained by Lynch and Crease (1990; Table 2) for nucleotide diversity between populations at the species level.

We inferred a phylogenetic tree of the mitochondrial sequences (Figure 3) to gain insight into the evolutionary genetics of fragmented rice rat populations. The tree was constructed with the neighbor-joining method (Saitou and Nei 1987) and rooted by a homologous sequence from *Mus spratus*. The tree shows that the mitochondria from rice rats in the central and east Everglades are not genetically distinct. We found a few identical base sequences in rice rats from both populations. Furthermore, the Lower Keys population is not very different from the two Everglades populations based on the branch length. The short branch lengths and starlike phylogeny supports the idea that the differentiation of the Everglade and Keys populations as measured by mtDNA divergence occurred at about the same time and relatively recently.

In the last 6000 years the Lower Keys have undergone several cycles of submergence and emergence with changes in sea level (Fairbridge 1974). When sea levels peaked at 4 m and 3 m above present levels (6000–4700 and 4300–3400 years BP, respectively) the freshwater marsh habitats of the rice rats in the Keys and most of

the Everglades were completely submerged. More recently (2000–1600 years BP) sea level dropped to 2 m below its present level, resulting in exposure of much of the bottom of Florida Bay and the shallower basins and channels that separate the Lower Keys. Such a drop in sea level would favor the development of marsh habitats and favor the dispersal of rice rats into the archipelago. Thus, according to Babour and Humphrey (1982), the establishment of *Oryzomys* populations in the Lower Keys and their genetic differentiation from mainland populations in the Everglades has taken place recently and no more than the 3000 years ago. Our findings are consistent with Humphrey and Setzer's (1989) suggestion that the silver rice rat should not be given species status. Thus the population in the Lower Keys has not had enough evolutionary time to diverge genetically.

Habitat Fragmentation in Vole Populations

Microtine rodents add another dimension to the effect of habitat fragmentation on small mammal populations because they undergo periodic fluctuations in numbers. These multiannual cycles in abundances must be superimposed on the distribution of individuals in space to gain a complete understanding of the genetic structure of vole populations. First, we examine allozymic variation in mainland and island populations of the meadow vole (*Microtus pennsylvanicus*) and the beach vole (*M. breweri*) in Massachusetts. Second, we will use variation in allozymes and in RFLPs of mtDNA to examine the genetic structure of prairie voles (*M. ochrogaster*) in eastern Kansas.

Island Versus Mainland Voles

In an earlier study, Kohn and Tamarin (1978) reported electrophoretic data for mainland populations of the meadow vole in southeastern Massachusetts and the island beach vole on Muskeget Island, Massachusetts, a 1 mi² island located off Nantucket Island (Tamarin 1978). The beach vole is restricted to Muskeget Island, which separated from nearby islands and the mainland in the Cape Cod region of Massachusetts as little as 3000 years ago. In that time, the beach vole has differentiated enough to achieve species status (Moyer et al. 1985; Tamarin and Kunz 1974). The beach vole differs from the mainland meadow vole in tooth, skeletal size, pelage, and life-history characteris-

Table 3. F_{ST} values for the *Trf* and *Lap* locus in the beach vole (*M. breweri*) on Muskeget Island and the meadow vole (*M. pennsylvanicus*) on the mainland in southeastern Massachusetts

Populations	Within population H_s			Between population F_{ST}	
	<i>N</i>	<i>Trf</i>	<i>Lap</i>	<i>Trf</i>	<i>Lap</i>
Muskeget Island	953	0.103	—	0.004	—
Mainland	322	0.482	0.470	0.027	0.027

tics; the beach vole is larger, with coarser and lighter pelage. It has a smaller litter size (Tamarin 1977b).

In each species, four localities were sampled on a regular basis (Kohn and Tamarin 1978). All of the Muskeget Island trapping areas were within 1 km of each other. Three of the four mainland sampling areas were within 6 km of each other in Barnstable County; the fourth area was about 50 km to the northwest, across the Cape Cod canal in Plymouth County (Tamarin 1977b). The only electrophoretic locus polymorphic in both populations was the *Trf* locus; the *Lap* locus was also polymorphic in the mainland populations. F_{ST} values were calculated in both species according to the methods of Gaines and Whittam (1980).

According to our F_{ST} values (Table 3), populations of the beach vole are virtually unstructured and the meadow vole is somewhat heterogeneous. Unlike the lower F_{ST} values between Muskeget Island populations (0.004) and between the mainland populations (0.027), comparisons for all populations combined indicates a high degree of heterogeneity (0.221). These values are expected based on our understanding of the ecology of the populations. The four subpopulations on Muskeget Island were in continuous habitat and had Trf^E frequencies that were very similar (0.93–0.97). The mainland populations, however, were geographically dispersed, three in Barnstable County on Cape Cod and one in Plymouth County, Massachusetts. Allelic frequencies varied between 0.38 and 0.60 for Trf^E and between 0.44 and 0.70 for Lap^S . Combining the two species increased the range of the Trf^E frequencies from 0.38 to 0.97, and thus greatly increased the variance. On the mainland, overall F_{ST} values were identical for the two loci. When high and low abundances were compared on the mainland (the island species was always at peak abundances), F_{ST} values for transferin were virtually identical (high abundance = 0.041; low abundance = 0.044).

However, the F_{ST} values for *Lap* differed at high and low densities; higher at high densities (0.044) and lower at low densities (0.014). The H_s values for *Trf* (Table 3), for the mainland population are four times higher than the island population ($t = 27.0$, $df = 3$, $P < .001$). Thus heterozygosity is much higher in the mainland populations.

Our F_{ST} and H_s values indicate that the beach vole is a homogeneous population that has diverged from the meadow vole to a large extent, whereas the meadow vole populations have not diverged much from each other. This seems to be the case ecologically as well. There are differences between the species in ecological and other life-history parameters varying from dispersal patterns to litter sizes (Tamarin 1978).

Although F_{ST} values are reasonable qualitative estimates of population differentiation, these values are not predictors of the kinds of changes that have taken place or their ecological consequences. To learn of these changes, in-depth ecological studies are needed, the kind that can document the actual changes taking place between populations and within species. For example, there were large differences in the nature of the dispersal process in the two populations (Tamarin 1977a). In the beach vole, dispersal is a simple process: dispersers are a random sample of the resident population for age structure and sex ratio. In the meadow vole, dispersers are not a random sample of the resident population; in addition, meadow voles move longer distances.

Prairie Voles in Eastern Kansas

Allozymes. In our earlier work on the genetics of prairie voles, we focused on temporal patterns of allozymic variation in fluctuating populations (Gaines et al. 1978). We monitored genetic changes at five electrophoretic loci—*Trf*, *Lap*, *6-Pgd*, *Est-1*, and *Est-4*—over 3 years in four populations. Changes in allele frequency at the *Trf* and *Lap* loci were correlated with density. An analysis of different components of fitness among *Lap* and *Trf* genotypes, including survival rates, breeding activity, and growth rates, indicated that changes in allelic frequency at these loci were due to selection. In a follow-up study (Gaines and Whittam 1980), we applied the Lewontin–Krauer test for selective neutrality to temporal variation in gene frequency at the five loci in the same four populations. Contrary to our early results, we found that changes in gene frequencies

Table 4. Measures of genetic diversity in Kansas voles

Source	Within population variation	Between population variation	
	H_s	Genetic distance	G_{ST}
Allozymes	0.316	0.0025	0.033
mtDNA	0.668	0.0035	0.199

were primarily due to nonselective forces. We attributed this apparent inconsistency to differences in the temporal scale used in the two analyses. Our earlier components of fitness analysis were done separately on different phases of a density cycle (increase, peak, decline). The Lewontin–Krauer test was done over the entire cycle. Since vole populations experience repeated bottlenecks of varying sizes during the low phase, genetic drift may counteract the effects of selection during population increases and peak phases of the density cycle.

Here we reanalyze the same data in a spatial context to determine if there is genetic structuring in prairie vole populations. The four live-trapped grids (A, B, C, and D) were located on University of Kansas land, 11 km northeast of Lawrence, Kansas. Grids A, B, and D were all within 1.2 km of each other; grid C was 3.5 km from the main study area. The grassland habitat of voles in eastern Kansas is fragmented by wooded areas, roads, and farms. We calculated F_{ST} values for the five loci among the four populations during high and low densities. The density phases for the four prairie vole populations were synchronous, which is typical for microtine rodents (Chitty 1996). We predicted that F_{ST} values would be higher at low densities compared to high densities due to increased genetic variance among populations resulting from genetic drift. There was no significant difference in the mean F_{ST} value for the five loci at high densities ($F_{ST} = 0.030$) and at low densities ($F_{ST} = 0.033$). This similarity between low- and high-density populations may be a due to the short duration of the bottleneck (Gaines et al. 1978).

We calculated genetic distances between the four grids by pooling allelic frequencies over the density cycle. Genetic distances were low, ranging from 0.0010 to 0.0053, with an average of 0.0025 (Table 4). There was no significant correlation between genetic distance and geographic distance.

mtDNA. We used RFLPs to examine fine-

scale mtDNA heterogeneity among prairie voles at six localities on the Nelson Environmental Study Area of the University of Kansas. The maximum distance between any two localities was approximately 1650 m, whereas the minimum distance was approximately 360 m. We attempted to collect at least 10 voles per locality. Fifty-nine animals were trapped and brought back to the laboratory for mtDNA analysis. Live-trapping data from nearby localities indicated that populations were declining during the mtDNA study.

We found a total of 12 mtDNA haplotypes using two restriction enzymes, *HaeIII* and *Sau96I*. Eight other restriction enzymes did not result in polymorphisms. Both *HaeIII* and *Sau96I* revealed extensive mtDNA sequence heterogeneity among populations and also a very large amount of sequence polymorphism within populations. Of the 12 mtDNA haplotypes, AA, CB, and DB were found in four populations, AA, BB, BA, FC, and GC were found in two populations; CA, CD, EB, and FA were unique to one population.

To compare intrapopulation mtDNA composite haplotype diversity, we used an index of nucleon diversity (h) from Nei and Tajima (1981). Values close to zero indicate no mtDNA composite haplotype diversity within populations, whereas values close to one indicate maximum diversity. The nucleon diversity for localities A, B, C, D, E, and F were 0.759, 0.800, 0.765, 0.744, 0.200, and 0.733, respectively. We have no explanation as to why locality E had about 75% lower diversity than the other localities. The mean nucleon diversity over all localities was 0.668 (Table 4). This is exactly the same value obtained by Plante et al. (1989) in declining populations of *M. pennsylvanicus* in Canada.

We used the overall nucleotide diversity (π) to calculate net nucleotide diversity between pairs of localities (δ) following the methods of Nei and Tajima (1981). δ is equivalent to genetic distance. This value approximates the genetic distance of 0.0025 from electrophoretic data in four populations (see above). As was the case for the electrophoretic data, there was no significant correlation between genetic and geographic distances in pairwise comparisons of localities.

According to Nei (1973), the nucleon diversity of a subdivided population can be partitioned into within- and between-subpopulation (locality) components. The G_{ST} statistic, which is equivalent to F_{ST} , represents the fraction of genetic variation within an entire population that is due to

interlocality genetic differences. The observed G_{ST} value among localities in our study is 0.199 ($\chi^2 = 11.75$, $df = 5$, $P < .05$), which indicates about 20% of the observed variation in mtDNA could be attributed to interlocality variation. The mean F_{ST} calculated at low population densities for the five electrophoretic loci was an order of magnitude lower ($F_{ST} = 0.0329$) than the G_{ST} from mtDNA.

Taken together, our two analyses of genetic structuring of fragmented prairie vole populations based on allozymes and mtDNA RFLPs suggest that variation within populations is high and variance among populations is small. Genetic distances between populations based on electrophoretic data and RFLPs of mtDNA were low. The G_{ST} based on mtDNA RFLP analysis was an order of magnitude higher than the mean F_{ST} values calculated from five electrophoretic loci. This result is not surprising because the N_e for mtDNA is expected to be about four times smaller than for nuclear genes. Another contributing factor is the lower dispersal rates of females compared to males.

An Experimental Study of Habitat Fragmentation

Two studies of small mammals are under way at the Nelson Environmental Study Area (Figure 4). Site 1 is an ongoing study of small mammal community organization and population dynamics conducted by Dr. Norm Slade. Site 2 is an experimental study of habitat fragmentation located approximately 0.5 km away. The fragmentation study was begun in 1984 when the farm field was disked and allowed to enter secondary succession. Mowing between the patches maintains a low turf, which is qualitatively and quantitatively different from the unmowed patches (Robinson et al. 1992). The experimental system consists of three patch sizes arrayed in 5000 m² rectangles called "blocks." Large blocks consist of one, continuous 50 m × 100 m patch; medium blocks of six, 12 m × 24 m patches; and small blocks of fifteen, 4 m × 8 m patches.

Small mammals have been censused on the continuous site since 1977 and were trapped on the fragmented site from 1984 through 1992 using standard mark-recapture techniques [see Foster and Gaines (1991) and Swihart and Slade (1990) for details on trap locations and methodology]. The two most common small mammals on the two sites are cotton rats and prairie voles.

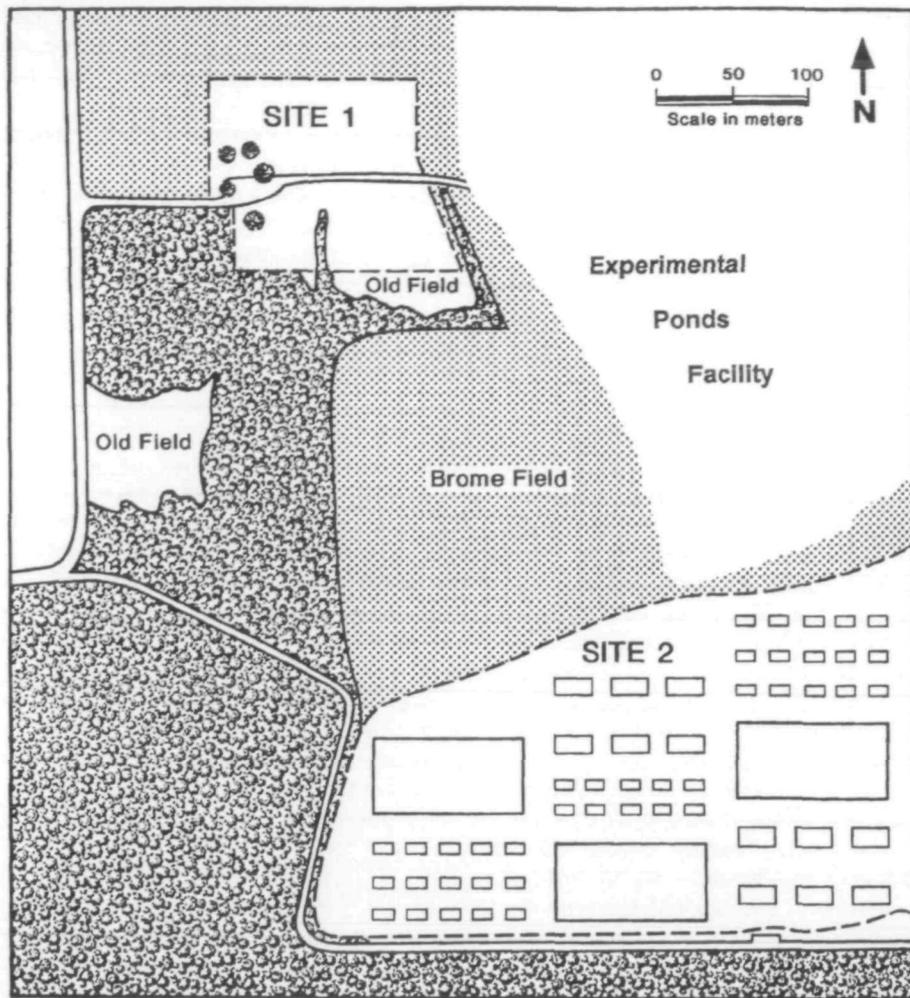


Figure 4. Two study areas located at the Nelson Environmental Study Area, 12 km northeast of Lawrence, Kansas. Site 1 contains approximately 1.9 ha of old-field habitat. Site 2, an experimentally fragmented area, contains 1.9 ha of old-field habitat in 6.9 ha of mowed grass. The 40 small patches are each 4 m × 8 m; the 12 medium patches are 12 m × 24 m; the three large patches are 50 m × 100 m. One large patch is a large block; a group of six medium patches is a medium block; a group of 10 or 15 small patches is a small block. Blocks are separated by 16–20 m and the centers of the two sites are approximately 500 m apart.

We make use of these data in two ways. First, we present data on movements of individuals at two scales. At a larger scale, we discuss long-distance dispersal events between the two sites. At smaller spatial scales we present movement between blocks within the fragmented site. Second, we present data regarding local demography on just the fragmented site. Our goal is to use empirical estimates of movement and abundances to predict the genetic structure of populations in the fragmented system and to estimate the spatial scale at which movement influences local demography and perhaps genetic structure.

Large-scale (≈ 0.5 km) dispersal events between the two sites are rare, with less than 1% of the marked animals in any given population moving to the other (Diffendorfer et al. 1996). Similarly, Foster and Gaines (1991) trapped the woods to the

south of the fragmented site and the brome field to the north for 1 year using 450 traps. They determined that only 4% of the marked animals on the fragmented site immigrated from the two areas, a distance of 200 m or less. These data suggest that demographically the two study sites are essentially autonomous, with local births and deaths, not immigration or emigration, influencing changes in population size. Given these data, the scale at which movements can influence local demography seems relatively small for our mammals and we therefore studied the impacts of movements on local demography at even smaller spatial scales—that of movement between the blocks on the fragmented site.

Animals switching between blocks can move distances of 20–140 m. Cotton rats and prairie voles had very different pat-

terns of movement on the two sites (Figure 5), with cotton rats moving mainly between the three large blocks, while prairie vole movement was much more cosmopolitan in nature. Despite what appears to be many movements between patches in Figure 5, movements between the blocks were infrequent. Cotton rats and prairie voles had similar and low rates of movement with 7–9% of the animals on the site moving between blocks. For both species, the correlation between the proportion of the animals on a block that were either immigrants or emigrants and the abundance on the block was high and negative (Diffendorfer et al. 1996). Thus, at low abundances, movements can have substantial impacts on local demography and a greater impact on genetic structuring.

Based on our results, we suggest that the spatial scale at which movements affect local population dynamics is no more than 150 m for the two species of small mammals we studied. Given this conclusion, we examined how movements and local demography interact to produce genetic structuring in an experimentally fragmented system.

We calculated a predicted G_{ST} over the entire fragmented site by combining the data on movement with estimates of effective population size over the entire 7.7 years of the study. The analyses were done for time periods when abundances were either low or high. We calculated G_{ST} as $G_{ST} = 1/(4N_e m \alpha + 1)$, where N_e is the effective population size, m is the migration rate (the number of migrants per generation where migrants are assumed to successfully breed in the new population); and $\alpha = (n/(n-1))^2$, where n is the number of subpopulations ($n = 8$). Effective population size was estimated as $N_e = 4N_m N_f / (N_m + N_f)$, where N_m and N_f are the numbers of breeding males and females. Our assumption is that all reproductive animals contribute equally in terms of reproducing offspring. Males were considered reproductive if their testes were descended and females if their nipples or vagina were swollen or if they were obviously pregnant. The value of m was estimated as the total number of reproductively active animals to have switched, divided by the total number of reproductively active animals captured at least two times (animals must be captured twice to switch) during time periods determined by low and high abundances. Because m is measured as a per generation rate of migration, we then divided the proportion of animals that switched by the number of gen-

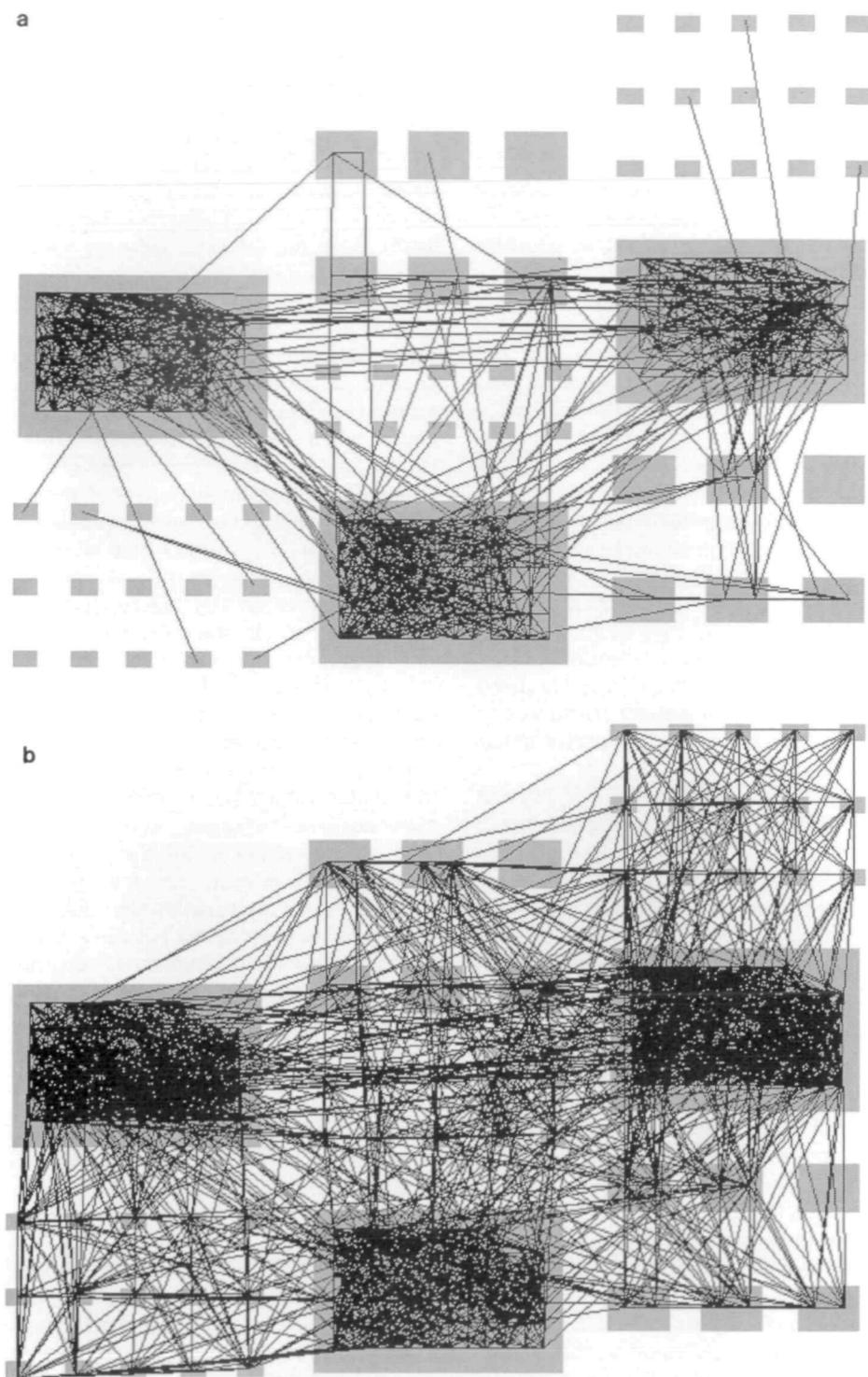


Figure 5. Individual movement patterns over 7 years on the experimentally fragmented study area for (a) cotton rats (*Sigmodon hispidus*) and (b) prairie voles (*Microtus ochrogaster*).

Table 5. Predicted G_{ST} values for prairie voles and cotton rats on the experimentally fragmented study area

Species	Low density			High density		
	N_e	m	G_{ST}	N_e	m	G_{ST}
<i>Microtus ochrogaster</i>	62	0.016	0.15	1,239	0.003	0.04
<i>Sigmodon hispidus</i>	78	0.015	0.13	203	0.016	0.05

erations at which population abundances were either high or low. The generation time for cotton rats and voles is approximately 2 months.

Our G_{ST} estimates based on demographic data predict that at high abundances there will be little genetic structuring within the fragmented site for both species (Table 5). Surprisingly the results were similar for both species despite very different patterns of movement and average abundances across the blocks. In our system, cotton rats are found almost exclusively on the large blocks, whereas voles are distributed on all three block sizes (Diffendorfer et al. 1995b; Foster and Gaines 1991; Gaines et al. 1992). Despite these differences, the predicted genetic structure was almost identical. This result highlights the unique intricacies in the interactions between demographic processes and genetic structure. In our case, two different demographic responses to fragmentation lead to the same genetic structure.

Our G_{ST} estimates were similar to those found by Plante et al. (1989) in meadow vole populations inhabiting a system of four grids (0.25 ha each) spaced 50–70 m apart. They estimated G_{ST} at 0.060 and 0.093 from mtDNA at high and low abundances, respectively. Given the greater distances between patches in the Plante et al. (1989) study and their use of mtDNA, the slightly larger G_{ST} estimates they found at high abundances should be expected. At low abundances, their G_{ST} was lower than our estimates. However, due to a possible Wahlund effect, their estimate of G_{ST} during the low abundances may be conservative. Thus, our values of G_{ST} predicted from demographic data alone seem to match real data from a similar system of small mammals. We intend to sample our experimental study area to estimate genetic structure and relate these values back to those predicted from demographic data.

The G_{ST} values we calculated from trapping data should be viewed with caution. There are two potential biases. An animal may move from block to block within the study area but may not be trapped. Thus the values of m we calculated may be an underestimate of the true migration rate. If so, then G_{ST} estimates should be smaller. Conversely, our estimate of N_e assumes that reproductive males and females contribute equally in terms of reproduction. Any variation in male or female reproductive success will lower N_e , thus increasing G_{ST} .

Conclusions

Our analysis of genetic structuring of small mammal populations over different spatial scales and with different levels of genetic variation lead to five general conclusions about the effects of habitat fragmentation on evolutionary and ecological processes.

Only in extreme cases of fragmentation, when there is little or no gene flow, will populations become depauperate of genetic variation and differentiate genetically. We have two examples to support this point: rice rats in South Florida and voles in eastern Massachusetts.

In rice rats, an analysis of the base sequence of the D-loop in mtDNA indicated that populations in the Everglades had a relatively high nucleotide diversity. The Florida Keys population, which is believed to have been isolated from the Everglades population for 3000 years (Humphrey and Setzer 1989), had no variation, a finding consistent with the impact of a recent genetic bottleneck. A comparison of nucleotide diversity between the Everglades and Keys populations revealed the populations were not genetically distinct, although the Keys population had some unique nucleotide substitutions. The mtDNA haplotypes fit a starlike phylogeny, suggesting that the differentiation of the Everglades and Keys populations as measured by mtDNA divergence occurred recently. The reduced mtDNA variation in the Keys and the absence of genetic differences between the Everglades populations makes it plausible that the population in the Keys is in the process of undergoing speciation. Our conclusions should be viewed as preliminary given our small sample sizes. We are in the process of sampling more localities in the Keys.

In the Muskeget Island population of voles, we found that heterozygosity at the *Trf* locus was approximately four times less than in the mainland population (0.103 versus 0.482), indicating a lack of genetic variation on the island. The F_{ST} measuring variation between Muskeget Island and the mainland was 0.221, indicating a moderate level of genetic differentiation between the two populations. These populations have been isolated for approximately 3000 years (Kohn and Tamarin 1978). Note that the F_{ST} value between populations on the mainland, a somewhat fragmented area that may have low levels of gene flow between populations, is an order of magnitude lower than the F_{ST} value between the mainland and the island.

Hence low levels of gene flow are sufficient to ameliorate genetic differentiation. The low F_{ST} between populations on the island (0.004) may be due to a combination of a lack of variation and continuous habitat.

Different components of genetic variation lead to different results in the analyses of genetic structure of populations. We have two examples: A comparison of morphological and allozymic variation in marginal and central populations of cotton rats and a comparison of allozymic variation and mtDNA RFLPs in Kansas vole populations.

In cotton rats, we found that allozymic variation is lower in marginal populations than in central populations, but morphological variation was higher in marginal than in central populations. Morphological traits are polygenic and can be influenced greatly by the environment. The higher variance in morphological traits in marginal populations may be attributed to greater environmental fluctuations at the edge of the range of cotton rats compared with more environmentally stable conditions in the center of this species distribution in Mexico.

Voies in Kansas showed very different patterns of genetic structuring depending on the level of variation studied. Genetic differentiation between populations based on G_{ST} was six times higher with mtDNA RFLPs than with allozymic variation. The higher level of genetic structuring with mtDNA is due to two factors. First, the effective population size for mtDNA is one-quarter that of allozymic variation. Second, male voles have higher dispersal rates than females (Johnson and Gaines 1987). Thus gene flow for allozymic variation is higher than that for mtDNA. Other authors have found that levels of genetic structuring are greater for mtDNA than for nuclear genes (Avise et al. 1979; Crease et al. 1990; DeSalle et al. 1987; Hale and Singh 1987; Karl and Avise 1992).

Spatial and temporal scales need to be considered when examining the genetic structure of populations. Obviously one expects differentiation between populations to increase as geographic distance increases. All else being equal, large-scale comparisons between populations should result in higher levels of genetic differentiation than smaller-scale comparisons. However, patterns of genetic structure will depend on the interaction between the geographic distance between populations and the vagility of the species in question. This interaction between dispersal and the spatial structure of the landscape is vital to understanding the impacts of frag-

mentation on genetic structure. Our experimental study of fragmentation on prairie voles and cotton rats indicates that although fragmentation alters movement patterns and demography, it has little impact on genetic structure (i.e., low G_{ST} estimates). If fragmentation occurred at a larger scale for these species, we would expect genetic structuring.

Genetic structuring must be viewed in a temporal context (Lidicker and Patton 1987). Over short time scales, temporal changes in abundances can alter genetic structure. Voies undergo periodic bottlenecks when populations crash, which should lead to a reduction of genetic variation within populations and an increase in the differentiation between populations. In our analysis of F_{ST} values from allozyme data for meadow and prairie voies, we did not find greater genetic differentiation at low abundances. In some cases F_{ST} values were higher at peak abundances than at low abundances, while in other cases there was no density effect. However, as predicted, G_{ST} values estimated from demographic data on the experimentally fragmented study were higher at low abundances.

We are uncertain about the causes of these discrepancies. In the four populations of prairie voies in eastern Kansas, low abundances were still between 10 and 20 animals—enough animals to capture most of the genetic variation in the populations. Thus, at low abundances, populations really did not experience severe bottlenecks and F_{ST} values did not change. On the fragmented site, effective population sizes between high and low abundances were extremely different and had large influences on our G_{ST} estimates.

These results indicate the potential for genetic structure to change through time and underscore the need to study the genetic structure of populations longitudinally. Furthermore, these results indicate that studies of genetic structure done as snapshots in time may lead to erroneous results. If population geneticists were to characterize the genetic structure of vole populations with samples taken at low abundances, the results could be different than at high abundances.

At larger temporal scales evolutionary history becomes tantamount in understanding genetic structuring. After 3000 years in the Florida Keys, rice rats may be in the early stages of genetic differentiation. Although the Keys population has been given endangered species status, differences in morphology from the Ever-

glades population are subtle (Humphrey and Setzer 1989). A comparison of vole populations in eastern Massachusetts after 3000 years of isolation indicates genetic and morphological differences between the Muskeget Island population and those on the mainland. These results indicate isolated populations can diverge at different rates depending on their history.

Demographic and ecological processes are more likely to be influenced by fragmentation than genetic events. In both of our studies with extreme isolation (Muskeget Island and the Florida Keys) we saw obvious effects on genetic structure. However, in both cases the populations have survived for over 3000 years. This result indicates that genetic factors alone at the scales we measured are not sufficient to cause extinction. Although the rice rat in the Florida Keys is listed as an endangered species, the likely factor causing low numbers is a demographic response to the loss of habitat, which in turn could influence the genetic structuring we have measured. The point here is that short-term demographic responses most likely have caused the rice rat decline, not genetic feedback on population numbers (i.e., inbreeding depression or genetic drift).

Many demographic and ecological processes in our experimentally fragmented system in Kansas were impacted by habitat fragmentation, yet there was little impact on genetic structure (i.e., low predicted G_{ST} values). These results, taken together with the results from the Florida Keys, suggest that habitat fragmentation affects demographic and ecological processes which may or may not feed back on genetic structure. The interesting question is determining at what temporal and spatial scales ecological and demographic processes feed back on genetic structure and how this interplay is modulated by habitat fragmentation. Clearly, under conditions where fragmentation results in isolated, small populations, the effects of genetic drift through these bottlenecks can be strong, affecting both variation within local populations and differentiation among populations.

There is an interaction between demographic processes and genetic structure. Population abundances can be reduced by both abiotic and biotic factors, which in turn leads to genetic drift and inbreeding. These genetic processes may in turn feed back on demography to further reduce population numbers. The genetic effects may be most pronounced when a population bottleneck is maintained over many

generations, thus reducing genetic variation for both mitochondrial and nuclear genes (Figure 2). In the experimental study of habitat fragmentation, the nature of the interaction between demographic and population genetic processes on small mammals is unpredictable. Prairie voles and cotton rats had different demographic responses to habitat fragmentation, yet showed similar patterns of genetic structuring based on estimated G_{ST} values. We feel that in most cases, patterns of genetic structure will be the consequences of changes in ecological processes. Therefore we support Lande's (1988) contention that understanding the effects of habitat fragmentation on the dynamics of the interaction between ecological and genetic processes may give the best insights into the causes of population extinction. Population geneticists and ecologists must do critical experiments to illuminate the nature of these interactions.

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