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Microgeographic genetic structure in the yellow-pine chipmunk (*Tamias amoenus*)

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Abstract

While there is evidence for broad-scale genetic structure in small mammals, few studies have used variable DNA-based genetic markers to examine genetic differentiation at microgeographic (tens of kilometres) scales. Yellow-pine chipmunks (*Tamias amoenus*) live in the heterogeneous landscape of the Rockies in southwest Alberta and are generally restricted to areas of low elevation. We used seven microsatellite loci to determine whether chipmunks show evidence of population genetic structure among three closely situated sites (< 15 km) in the Kananaskis Valley, Alberta. We found evidence for genetic structure in the form of significant differences in allele frequencies among populations and significantly nonzero values of F_{ST} for both overall and pairwise population comparisons. However, F_{IS} values for each population were not significantly different from zero, suggesting little evidence for inbreeding within populations. Genetic differentiation probably occurs as a result of the strong effect of drift in very small ($N_e \approx 25$) populations of these animals even in the face of substantial immigration rates.

Keywords: genetic structure, immigration, microsatellite DNA, *Tamias amoenus*, yellow-pine chipmunk

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Introduction

There is evidence that populations of small mammal species show genetic structure (e.g. Kim *et al*. 1998; Stewart *et al*. 1999; Surridge *et al*. 1999). Much work has focused on the effects of metapopulation dynamics (e.g. Peacock & Smith 1997; Stewart *et al*. 1999) or social structure (e.g. Dobson *et al*. 1997; Surridge *et al*. 1999) on genetic differentiation, but there is very little information known regarding fine-scale genetic structure in these animals. Allozyme markers have been used to measure genetic differentiation in many studies investigating genetic structure in small mammals such as the Sciuridae (Dobson 1994; Sullivan 1996; Dobson *et al*. 1997; Perault *et al*. 1997), but few studies have used DNA-based markers such as microsatellites to quantify genetic differentiation among populations (Jarne & Lagoda 1996). An understanding of the pattern of genetic structure in a heterogeneous environment is of fundamental importance to evolutionary biologists because it forms the basis of hypotheses and predictions regarding gene flow and genetic diversity, as well as behaviours such as dispersal and philopatry.

The yellow-pine chipmunk (*Tamias amoenus*) is a small (45–75 g) sciurid which ranges in the mountainous areas from northern California to central British Columbia (Sutton 1992). It is generally restricted to areas of low elevation, either due to interspecific competition with the least chipmunk (*Tamias minimus*) (Sheppard 1971) or habitat selection (Meredith 1976). Chipmunks in mountainous regions may have restricted gene flow among populations due to a heterogeneous landscape which prohibits dispersal (e.g. Sullivan 1996; Perault *et al*. 1997). Evidence from allozyme markers suggests that populations of chipmunks living in mountainous terrain show genetic structure at fine spatial scales (< 10 km) (Perault *et al*. 1997).

Here, we determine whether yellow-pine chipmunks found on the eastern slopes of the Rocky Mountains show structure over short geographical distances (≤ 18 km) and assess levels of migration between subpopulations using assignment tests (Rannala & Mountain 1997; Cornuet *et al*. 1999).

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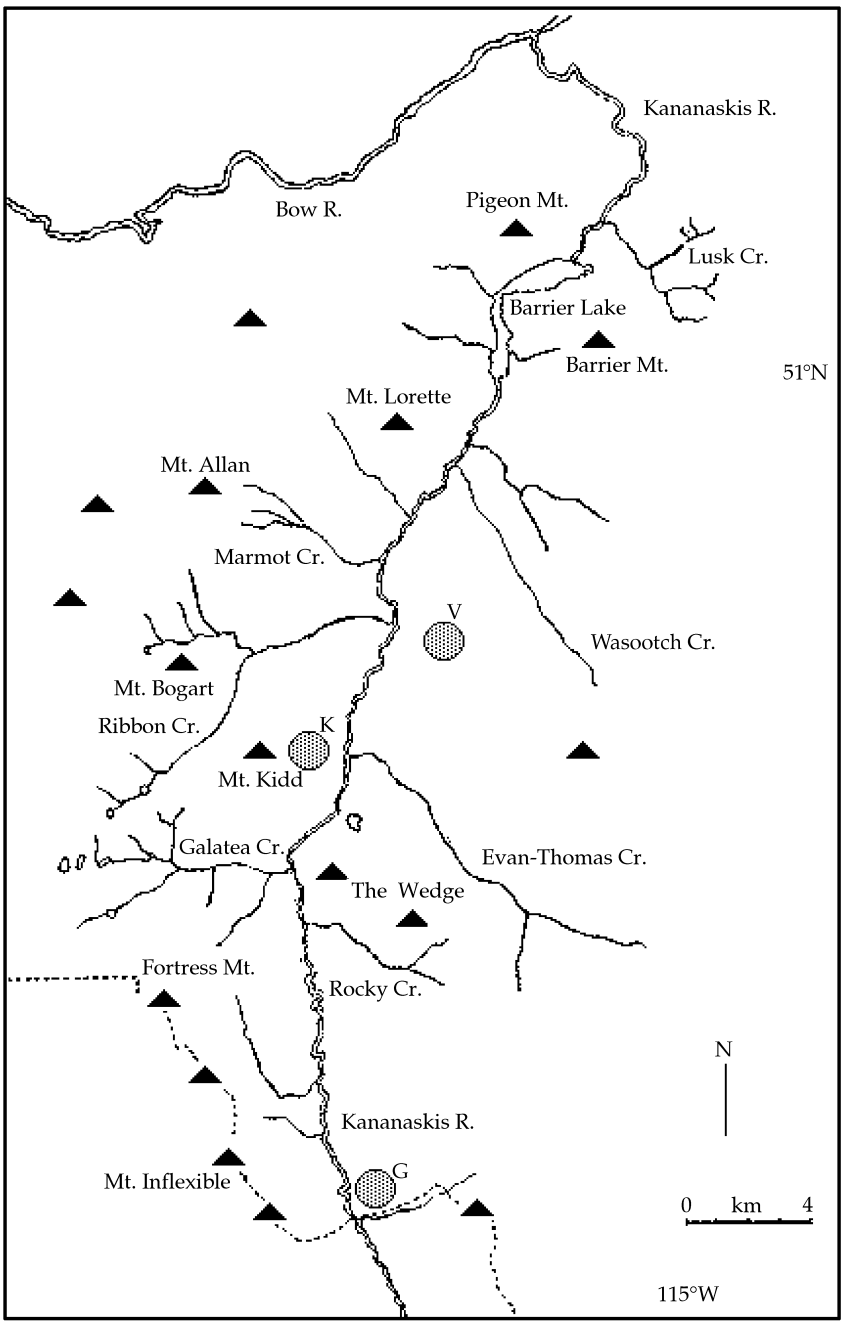

Fig. 1 Location of three subpopulations of the yellow-pine chipmunk sampled from the Kananaskis Valley, Alberta. Each subpopulation is represented by a circle with a superscript letter: V, Village; K, Kidd; G, Grizzly.

Methods

Adult yellow-pine chipmunks were sampled on three trapping grids (subpopulations) in the Kananaskis Valley, Alberta, in the Front Ranges of the Rocky Mountains (51° N, 115° W) (Schulte-Hostedde & Millar 2000). These grids were located at the base of Mount Kidd (3.8 ha), at Grizzly Creek (4.8 ha) and at the Kananaskis Village junction (2.4 ha) (herein referred to as Kidd, Grizzly and Village, respectively) (see Fig. 1). The distances between each of the three sites are; Kidd–Village 6 km, Kidd–Grizzly 14 km and Village–Grizzly 18 km. We hypothesized that these grids represented subpopulations because of the heterogeneous landscape and barriers between sites, including the Kananaskis River (Fig. 1). All grids were located on rocky creek beds and consisted of single Longworth traps placed approximately 20 m apart and baited with sunflower seeds, oats and cotton bedding. Each grid was trapped two mornings each week from early May to late August 1998. Upon capture, adult chipmunks were individually marked with ear-tags (Monel #1005) and a portion of the ear was removed for genetic analysis.

Tissue samples were immediately placed in individual Eppendorf tubes, placed in a cooler with ice packs, and then transported to a freezer and stored at –70 °C.

Extraction of DNA was performed using QIAGEN® QIAmp tissue kits and samples were genotyped at seven microsatellite loci (EuAmMS35, –37, –41, –86, –94, –108 and –114) using primers described in Schulte-Hostedde *et al*. (2000).

To determine the extent of microgeographic structure, we evaluated variation in the seven microsatellites for samples collected from the three grids [Kidd $n = 47$ (27 males, 20 females); Grizzly $n = 20$ (11 males, nine females); Village $n = 16$ (eight males, eight females)] and tested for patterns of differentiation using a variety of indices. We used GENEPOP (Raymond & Rousset 1995) to determine allele frequency differences among and between the three subpopulations. We also used FSTAT (Goudet 1995), which uses an infinite allele mutation model, to calculate Weir & Cockerham's (1984) estimators of F statistics, θ (F_{ST}), and f (F_{IS}), and R_{ST} CALC (Goodman 1997) to calculate R_{ST}, a differentiation index which measures genetic differentiation based on a stepwise model of mutation (Slatkin 1995). Values of the differentiation statistics (θ and R_{ST}) were tested for significance from zero using permutation procedures described in Goudet (1995) and Goodman (1997). All α values from multiple tests were adjusted using the sequential Bonferroni correction as described in Rice (1989). To preserve biological relevance, we used the number of tests (microsatellites) within a population as k (Rice 1989) when testing for differences between observed and expected heterozygosity (Table 1), and differences in allele frequencies (Table 2). We also assessed the level of immigration using an assignment test implemented by the program IMMANC (Rannala & Mountain 1997). IMMANC uses multilocus genotypes to identify putative immigrants within each subpopulation and the most likely source of these immigrants. For example, we used it to test whether individuals captured on Kidd were more likely to be residents or immigrants from Village or Grizzly, based on genotype. This approach assigns the source of an individual by calculating the likelihood that the individual's genotype originated in the population from which it was sampled. The power of the test is dependent on three factors: the number of loci, the number of individuals sampled and the extent of differentiation among populations (Rannala & Mountain 1997). Because individuals which are identified

Table 1 Number of alleles, observed heterozygosity (H_O), expected heterozygosity (H_E) and P-value of exact tests calculated by Markov chain method as performed by GENEPOP (Raymond & Rousset 1995) for seven microsatellites of the yellow-pine chipmunk

Population/locus	No. of alleles	H_O	H_E	P
Village				
EuamMS35	4	0.940	0.720	0.576
EuamMS37	3	0.923	0.662	0.007*
EuamMS41	5	0.875	0.792	0.710
EuamMS86	5	0.563	0.593	0.712
EuamMS94	3	0.188	0.284	0.132
EuamMS108	3	0.500	0.492	0.782
EuamMS114	5	0.625	0.605	0.911
Overall				0.247
Kidd				
EuamMS35	5	0.652	0.633	0.832
EuamMS37	3	0.555	0.478	0.215
EuamMS41	5	0.565	0.665	0.377
EuamMS86	5	0.447	0.569	0.054
EuamMS94	3	0.255	0.249	0.617
EuamMS108	4	0.587	0.635	0.214
EuamMS114	8	0.787	0.726	0.920
Overall				0.337
Grizzly				
EuamMS35	4	0.700	0.609	0.494
EuamMS37	3	0.333	0.452	0.029
EuamMS41	4	0.950	0.691	0.034
EuamMS86	3	0.316	0.280	1
EuamMS94	4	0.474	0.519	0.641
EuamMS108	4	0.700	0.617	0.936
EuamMS114	6	0.700	0.745	0.676
Overall				0.257

*indicates a significant difference between observed and expected heterozygosity.

Table 2 P-values of Fisher exact test between and among three subpopulations of the yellow-pine chipmunk performed by GENEPOP (Raymond & Rousset 1995) from allele frequencies of seven microsatellites

	Village–Grizzly	Village–Kidd	Grizzly–Kidd	Pooled
EuamMS35	0.022	0.038	0.476	0.044
EuamMS37	0.019	0.007*	1	0.027
EuamMS41	0.024	0.003*	0.361	0.005*
EuamMS86	<0.001*	0.224	0.005*	0.002*
EuamMS94	0.192	0.900	0.015	0.053
EuamMS108	0.070	0.019	0.975	0.088
EuamMS114	0.067	0.663	0.632	0.463
Overall	—	—	—	<0.001*

*indicates a significant difference.

as putative immigrants may originate from unsampled subpopulations, we used the exclusion procedure (Bayesian method) of GENECLASS (Cornuet *et al*. 1999) to establish whether any individuals could be identified as immigrants from subpopulations other than the three we sampled. GENECLASS uses a similar approach to IMMANC but calculates a likelihood value which relates each individual to the three subpopulations. If the value is below a threshold probability (in our case 0.01) then the individual is excluded from that subpopulation, i.e. it did not emigrate from that location. If all three subpopulations are excluded for a given individual, then it is reasonable to surmise that the individual may have emigrated from an unsampled subpopulation. To determine any sex differences in immigration and dispersal, we used two approaches. First, we used contingency table analysis to determine whether those individuals identified as putative immigrants by IMMANC differed from a 1 : 1 sex ratio. Second, we used the program KINSHIP (Goodnight & Queller 1999) to determine differences in pairwise relatedness (r) between individuals of the same sex within each of the three subpopulations. We calculated a mean r-value for all female pairings and a mean r-value for all male pairings. The simulation procedures of KINSHIP were also used to identify pairs of individuals with r-values that were significantly greater than that expected for unrelated individuals following Gibbs *et al*. (2000). We did this by using the overall microsatellite allele frequencies to determine the 95% confidence interval for expected r-values for unrelated individuals. We then classified pairs of individuals with r-values exceeding this cut-off as 'related'. The procedure was repeated for each population. The numbers of statistically significant relationships among all female pairs were compared to those found among all male pairs using contingency table analysis.

Results

The number of alleles per microsatellite locus ranged from three to eight (Table 1). Only one locus showed significant deviation ($P < 0.007$) from Hardy–Weinberg equilibrium (EuamMS37 — Village and Grizzly). This deviation was due to heterozygote excess (Table 1). Among the three subpopulations, f was not significantly different from 0 ($P = 0.563$) overall and for all individual microsatellite loci ($P > 0.05$).

Exact tests of allele frequencies revealed significant differences in allele frequencies among the three subpopulations (Table 2). Specifically, Village–Grizzly had significant allele frequency differences at one of the seven loci (14.3%), Grizzly–Kidd had significant allele frequency differences at one of the seven loci (14.3%), and Village–Kidd had significant allele frequency differences at two of the seven loci (28.6%) (Table 2). Among all three subpopulations, two of the seven loci (28.6%) showed significant differences in allele frequencies (Table 2). In addition, for all pairs of subpopulations, θ was significantly different from 0 ($P \leq 0.015$), as was the overall θ ($P = 0.001$) (Table 3). There were no significant differences in ρ ($P > 0.05$), however, there was a trend toward significant differentiation between Village and Grizzly ($P = 0.055$) (Table 3).

Table 3 Overall and pairwise comparisons of yellow-pine chipmunk population differentiation estimated by θ (Goudet 1995) and ρ (Goodman 1997)

	θ	*P*	ρ	*P*
All	0.036	0.001*	0.007	0.153
Village–Kidd	0.038	0.001*	0.001	0.368
Village–Grizzly	0.083	0.001*	0.033	0.055
Grizzly–Kidd	0.019	0.015*	0.006	0.220

*indicates a significant difference.

Table 4 Results of immigration test for yellow-pine chipmunks using IMMANC (Rannala & Mountain 1997)

	Putative source		
Sample	Village	Kidd	Grizzly
Village	16	0	0
Kidd	3	40	4
Grizzly	1	0	19

Rows indicate sample grid, columns indicate potential source grid.

Immigrant analysis using IMMANC (Rannala & Mountain 1997) had variable power to detect immigrants. Power to detect immigrants ranged from 0.445 (sample from Kidd, putative source Grizzly) to 0.921 (sample from Grizzly, putative source Village). Putative immigrants were identified in two subpopulations ($P < 0.05$). Only one of 20 (5%) individuals from Grizzly was identified as an immigrant (source — Village). The intermediate subpopulation, Kidd, had the highest number of putative immigrants; seven of 47 (14.9%) individuals were identified as potential immigrants, three from Village and four from Grizzly. None of the individuals from Village were identified as immigrants (Table 4). Analysis using GENECLASS (Cornuet *et al*. 1999) only classified one individual (from Village) as not originating from any of the three subpopulations we sampled ($P < 0.01$ for all three subpopulations). Of the eight putative immigrants identified from IMMANC, six were males. Contingency table analysis indicated that this was not significantly different from an expected 1 : 1 sex ratio ($\chi^2 = 2$, d.f. = 1, $P = 0.157$). If males are more likely to disperse than females (e.g. Dobson 1982), then levels of relatedness should be higher among adult females than among adult males within each subpopulation. We used the program KINSHIP (Goodnight & Queller 1999) to determine mean values of r for pairwise comparisons among males and

Table 5 Mean relatedness as calculated by KINSHIP (Goodnight & Queller 1999) among male and female yellow-pine chipmunks at three subpopulations in the Kananaskis Valley

	Among males	Among females
Village	0.0050	−0.0671
Kidd	−0.0213	0.0226
Grizzly	−0.0581	0.1944

among females. Females at Grizzly appeared to be more closely related to each other than males were to each other, whereas in the other two subpopulations, relatedness among males and females appeared to be about equal (Table 5). The *r*-values required to distinguish pairs of significantly related individuals were very high (Village, 0.526; Kidd, 0.589; Grizzly, 0.572) suggesting that KINSHIP had little power to distinguish among various levels of relatedness. Nonetheless, we compared the number of statistically significant relationships among both males and females for each of the subpopulations. None of the *r*-values calculated for same sex pairings at Village were significant, however, at Grizzly and Kidd more female pairs than male pairs had *r*-values that were classified as significant [Grizzly: male, 0/55 *r*-values were significant, female, 6/36 *r*-values were significant ($\chi^2 = 9.81$, $P = 0.0017$); Kid: male, 11/351 *r*-values were significant, female, 16/190 *r*-values were significant, ($\chi^2 = 6.48$, $P = 0.010$)].

Discussion

Significant differences in allele frequencies and significant values of θ provide convincing evidence that there is genetic differentiation among these three subpopulations of chipmunks. R_{ST} values indicated a trend toward differentiation between Grizzly and Village. Curiously, despite the assertion that θ (Weir & Cockerham 1984) underestimates the degree of genetic differentiation among populations (Slatkin 1995; Goodman 1997), R_{ST} was more conservative than θ. Estimates of R_{ST} can have high variance, especially under situations such as ours of small sample sizes and few loci (Gaggiotti *et al*. 1999). This may explain why R_{ST} did not detect the same degree of differentiation as θ.

The observed pattern of differentiation is consistent with an isolation-by-distance model (Hartl & Clark 1987) in which the more geographically distant subpopulations are, the more genetically differentiated they become (Slatkin 1987). There is clear evidence of this among our three subpopulations, which are arranged in a linear fashion along the Kananaskis Valley (Fig. 1). The highest value of θ (0.108) occurs between Village and Grizzly, the most distant subpopulations. The only measure of ρ which shows a trend toward differentiation is between Village and Grizzly. Finally, the proportion of individuals identified as putative immigrants is highest at Kidd, the middle site. Low levels of dispersal may be the mechanism by which isolation-by-distance occurs. The proportion of individuals assigned as putative immigrants is lowest at the two subpopulations which are furthest apart (Grizzly and Village), suggesting that immigration rarely occurs between the two areas. Least (*Tamias minimus*) and Uinta (*Tamias umbrinus*) chipmunks show low levels of gene flow between features such as slopes along the mountain crestline and drainages within the slopes of the Uinta mountains (Perault *et al*. 1997). Chipmunks may be unable to cross the barren mountains and extreme environmental conditions associated with high altitude habitats (Perault *et al*. 1997). However, Meredith (1974) described movements by nonbreeding yearling yellow-pine chipmunks up to 1000 m. Radiotelemetry data from our study suggest that some breeding female chipmunks make daily movements up to 400 m from their nest (Schulte-Hostedde, unpublished data). Although anecdotal, this suggests that chipmunks are capable of dispersing widely. Dobson (1994) found high rates of gene flow (measured using allozymes) among populations of Columbian ground squirrels (*Spermophilus columbianus*), which live in discrete patches (meadows) of varied size in the Rocky mountains of southwestern Alberta. Pika (*Ochotona princeps*), which also live in discrete patches on the Bodie Hills of northern California, also show high rates of gene flow among talus fields; no evidence of genetic structure was detected using multilocus DNA fingerprints (Peacock & Smith 1997). Further studies on the effects of landscape features of mountainous environments on dispersal in chipmunks are required to understand gene flow and its consequences for genetic structure.

Although evidence of genetic structure suggests that dispersal is low, there is some evidence that male chipmunks are more likely to disperse than females (e.g. Dobson 1982). Although putative immigrants were not significantly male-biased ($P = 0.157$), the power of our test was low due to a small sample size ($n = 8$). Sex-specific patterns of pairwise relatedness indicated that females are more likely to be closely related to each other than are males. This pattern would occur if females are philopatric and male chipmunks disperse from natal home ranges.

Two hypotheses may explain why significant genetic differentiation develops among chipmunk subpopulations that are spatially close to each other. Differentiation may be the result of founder events which are followed by population expansion, or subpopulations which regularly exchange individuals may be nonetheless subject to genetic drift. We favour the latter hypothesis for several reasons. First, inbreeding was not evident within any subpopulation, as the F_{IS} estimator *f* was not significantly different from 0 under any circumstance. Therefore, it is unlikely that these subpopulations are formed by founder events.

Second, the number of animals sampled at each site represents up to 90% of each subpopulation (Schulte-Hostedde, unpublished data). Although population estimates have not been made, unmarked individuals were rarely captured. This means that these subpopulations are very small and genetic drift may act very quickly to produce differences in allele frequencies between them (Hartl & Clark 1987). The effects of genetic drift are magnified if the effective population size is smaller than the census population (Hartl & Clark 1987), and this is the case when there is high variance in male reproductive success (Nunney 1993). Levels of variation in individual reproductive success are unknown in chipmunks, but males compete intensely amongst each other for mating opportunities, suggesting that males may differ in reproductive success (Callahan 1981). If genetic drift is the mechanism leading to the observed differentiation, it must be strong because the results of the assignment test (IMMANC) suggested substantial immigration into the intermediate population (Kidd).

The analysis of patterns of immigration has an important caveat. The program IMMANC assigned each individual as originating from one of the three subpopulations (Village, Kidd, or Grizzly). It is known that there are other subpopulations of chipmunks between these three subpopulations (Schulte-Hostedde, unpublished data), therefore individuals which emigrated from these intermediate subpopulations may not have been identified as immigrants. We have tried to control for this by using the exclusion procedure of GENECLASS (Cornuet *et al*. 1999). The fact that only one individual, from Village, was identified as not having originated from one of the three subpopulations suggests that immigration from other subpopulations may be low.

The interactions between these factors (low dispersal, high genetic drift, variance in male reproductive success) may result in a metapopulation model, in which small subpopulations are established by several individuals and become extinct and disappear relatively quickly (Hanski & Gilpin 1991). These populations may be small enough for genetic drift to take place, thus resulting in genetic differentiation among subpopulations. Metapopulations may have a high risk of losing genetic variation through genetic drift because effective population size can be one or two orders of magnitude lower than the total number of individuals in the overall population (Gilpin 1991).

The consequences of genetic structure on the behavioural ecology of yellow-pine chipmunk is not immediately clear. Social structure can have important implications in the determination of fixation indices (Sugg *et al*. 1996), however, chipmunks have a very simple social structure; solitary individuals defend territories around a single burrow entrance (Broadbrooks 1970). The most complex social unit consists of a female and her young. The absence of inbreeding, the results of the immigrant assignment test (IMMANC), and anecdotal information suggest that dispersal does occur, although the degree of dispersal is unclear. Assessing the levels of dispersal and factors influencing individual variation in reproductive success must be done in order to understand fully the factors producing genetic differentiation on a microgeographic scale in these animals.

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