Reproductive success and effective population size in woodrats (*Neotoma macrotis*)

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**Abstract**

Discrepancies between the census size and the genetically effective size of populations ($N_e$) can be caused by a number of behavioural and demographic factors operating within populations. Specifically, strong skew in male reproductive success, as would be expected in a polygynous mating system, could cause a substantial decrease in $N_e$ relative to census size. Because the mating system of *Neotoma macrotis* had previously been described as one nearing harem polygyny, I examined the distribution of reproductive success and genetic variation within a population of this species. Combining genetic data and three years of field observations, I show that variance in reproductive success does not deviate from poisson expectations within either sex and variance in success is similar between the sexes. Furthermore, both males and females had multiple partners across litters in addition to some evidence of multiple paternity within litters. Despite a lack of strong skew in reproductive success, an estimate of $N_e$ based on a number of demographic parameters suggests that the ratio of $N_e/N$ in this population is 0.48. Although the ratio of $N_e/N$ suggests that the population is experiencing higher rates of genetic drift than would be expected based on census size alone, the population maintains high levels of genetic diversity. Estimates of neighbourhood size and patterns of recruitment to the study site suggest that immigration plays an important role in this population and may contribute to the maintenance of high levels of genetic diversity.

**Keywords**: effective population size, mating system, *Neotoma*, reproductive success, woodrat

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**Introduction**

The effective size of a population ($N_e$) is that of an ideal population whose genetic composition changes in response to random processes in the same way as an actual population of size $N$ (Wright 1931). Because the effective size determines the degree to which genetic drift is acting, $N_e$ is a critical parameter in understanding the evolution of populations. Furthermore, because genetic diversity is lost at a rate of $1/2N_e$, effective size is a central concern to conservation managers (reviewed in Schwartz et al. 1998; Crandall et al. 1999).

Wright (1938) considered a number of factors that contribute to a difference between census and effective sizes of populations including: (i) temporal fluctuations in population size, (ii) variation in family size and (iii) deviation from a 1:1 sex ratio. Frankham (1995) showed that the single most important factor in reducing the ratio of $N_e/N$ is temporal fluctuation in population size with the long-term effective size being close to the smallest sized generation. Variation in family size (or reproductive success) reduces the ratio of $N_e/N$ by ~54%, whereas unequal sex ratios account for a 36% reduction (Frankham 1995; Frankham et al. 2002). Early estimates of effective size generally considered only one factor at a time and did not incorporate complexities such as age- and spatially structured populations and the influence that various mating systems can have on $N_e$. However, efforts have been made to consider a number of complexities including overlapping generations (Felsenstein 1971; Hill 1972; Nunney 1993) and breeding tactics (Chesser 1991; Nunney 1993; Sugg & Chesser 1994). Factors such as generation time, sex ratio, dispersal capabilities, mating habits and social structure have varying influences on effective size depending on species-specific characteristics of these parameters (Chesser 1991;
Nunney (1993; Sugg & Chesser 1994). For example, Nunney (1993) showed that when generation times are short, extreme polygynous mating systems can reduce the ratio \( N_e/N \) below 0.2 but when generation times are longer, the difference between effective and census size is much less pronounced. Thus, in order to estimate the ratio \( N_e/N \) for any population, a number of basic life history, mating and dispersal characteristics must be evaluated.

Because high variance in reproductive success can have such a strong influence on the ratio of \( N_e/N \), this study focuses on a population of woodrats (Neotoma macrotis) that was previously described as having a mating system nearing one of harem polygyny (Kelly 1989). Observations of radio-collared individuals and live trapping led Kelly (1989) to conclude that due to strong philopatry, first-order female relatives are spatially clustered in the habitat. Spatial clustering, according to Kelly (1989), allows a single male to monopolize breeding within a group of highly related females. A number of testable hypotheses concerning patterns of reproductive success and the distribution of genetic diversity within the population emerge from Kelly’s work: (i) variance in reproductive success among males should be significantly different from poisson expectations, (ii) variance in reproductive success should be significantly different between the sexes with less variance among females than males, (iii) males should have a greater number of different mates within a season than females, (iv) females that are mated by the same male should be highly related to one another, and (v) high levels of female philopatry should lead to significant subdivision within the population as measured by the inbreeding coefficient \( F_{IS} \). To test these hypotheses concerning the distribution of reproductive success and genetic diversity, I combine three lines of evidence: (i) variance in reproductive success among males, (ii) variance in reproductive success, and (iii) mean relatedness among potential mates within a season.

Individuals were captured using Tomahawk live traps baited with peanut butter and oats. Two traps housed in a wooden shelter were placed near each woodrat house. Traps were set for three consecutive nights at ~8-week intervals between August 1997 and March 2000. Traps were opened at sunset, checked within 4 h of sunset, then checked again and closed at sunrise. During the 1998 and 1999 breeding seasons (February to September), live-trapping was increased to 4–5 nights per week. To avoid disrupting the mating activity of the study subjects, traps were checked within 5 h of sunset and then closed for the night.

At first capture, all animals were ear-tagged (Monel 100S, National Band and Tag Co.), sexed, weighed and a small piece of ear pinnae was removed with sterile surgical scissors and stored in 95% ethanol for genetic analyses. Weight and reproductive status were monitored throughout the breeding season and mother–offspring relationships were established by transfer of fluorescent pigment powders between individuals (Ribble 1991). To minimize inhalation of pigmented powder by the animals (Stapp et al. 1994), only a small amount of powder was applied to the area immediately surrounding the teats of lactating females.

**Genetic analyses**

DNA was isolated using a standard phenol–chloroform extraction followed by ethanol precipitation (Sambrook et al. 1989). Individuals were genotyped for six microsatellite loci under the conditions described in Matocq (2001). Four loci, Nfu1, Nfu4, Nfu5 and Nfu6, were developed specifically for the study population (Matocq 2001). The remaining two loci, Nma10 and Nma11, were originally designed for N. magister (Castleberry et al. 2000). Fluorescently labelled polymerase chain reaction (PCR) products were electrophoresed on 6% denaturing acrylamide gels on an ABI 377 (Applied Biosystems). Fragment sizes were analysed and genotypes were assigned using the GENESCAN and GENOTyper software (Applied Biosystems).

Linkage disequilibrium and deviations from Hardy–Weinberg equilibrium were tested using ARLEQUIN (Schneider et al. 2000). The frequency of null alleles was estimated using CERVUS (Marshall et al. 1998). Paternity was assessed using the likelihood-based approach implemented in CERVUS (Marshall et al. 1998). Mother–offspring relationships were identified using the field methods described above and assumed to be known for the genetic assignment of paternity. Any male caught on the study site at any point during the reproductive season (1998, \( N = 28 \); 1999, \( N = 22 \)) was considered as a candidate father for every pup reared during that season. A total of 78 juveniles representing 48 litters were included in the study (1998, \( N = 22; 1999, N = 26 \)). Simulations were run with 10,000 cycles; 28 and 22 candidate males for each year, respectively;

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**Materials and methods**

**Field studies**

The study was conducted on a 580 m stretch of riparian/oak woodland along Big Creek at the Hastings Natural History Reservation in Carmel Valley, California. The current study site was included in the studies of both Linsdale & Tevis (1951) and Kelly (1989). The focal population of this study has been considered Neotoma fuscipes in the prior literature (Linsdale & Tevis 1951; Kelly 1989) but is now recognized as Neotoma macrotis, a species distinct from N. fuscipes (Matocq 2002a).
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0.99 as the proportion of individuals genotyped; 0.01 as the genotyping error rate; and 70% of true fathers assumed to be included in the sample (Kraaijeveld-Smit et al. 2003).

Two tests were implemented to assess if the Big Creek population had recently experienced a genetic bottleneck. One test examined the shape of the frequency distribution of alleles. Theory predicts that under any mutation model, the majority of alleles at microsatellite loci will be at low frequencies, whereas fewer alleles will be maintained at intermediate frequencies (Nei et al. 1976; Luikart et al. 1998). As such, nonbottlenecked populations should exhibit characteristic L-shaped allelic frequency distributions. Significant deviations from an L-shaped distribution in the Big Creek population were tested using a coalescent simulation approach as implemented in Bottleneck (Piry et al. 1999). A second test for recent bottlenecks relied on the prediction that bottlenecked populations lose alleles more rapidly than heterozygosity. As such, expected heterozygosity ($H_E$) based on numbers of alleles in the population will exceed heterozygosity expectations ($H_{BE}$) based on drift–mutation equilibrium (Luikart & Cornuet 1998). In nonbottlenecked populations, on average, 50% of loci will exhibit a deficit in heterozygosity ($H_E < H_{BE}$) and 50% will show an excess of heterozygosity ($H_E > H_{BE}$). A sign test and Wilcoxon’s signed-ranks test (as implemented in Bottleneck, Piry et al. 1999) were used to assess whether the Big Creek population exhibited an excess of heterozygosity. A two-phase mutation model (both single-step and multistep mutations possible) was assumed with the probability of single-step mutations set at 0.80 and 0.95 in and multistep mutations possible) was assumed with the zygosity. A two-phase mutation model (both single-step

Genetic estimate of $N_e$

At equilibrium, expected heterozygosity should be equal to $4N_e\mu/(4N_e\mu + 1)$ (Hartl & Clark 1989 eqn 3.15). This equation can be rearranged to provide an estimate of effective population size based on genetic variation:

$$N_{eG} = H/4\mu(1 - H)$$

(2)

Average expected heterozygosity ($H$) was estimated across all microsatellite loci with eqn 8.6 of Nei (1987) and used in the above equation. A mutation rate ($\mu$) of $10^{-3}$ was used (Weber & Wong 1993; Bouteiller & Perrin 2000).

Neighbourhood size

The spatial extent of the deme or randomly mating group is, in part, determined by dispersal capabilities (Dobzhansky & Wright 1943). Given that the study area is not completely isolated from surrounding occupied habitat (MD Matocq, unpublished data), the spatial extent of the deme likely exceeds the sampled area. In order to estimate the number of individuals contributing to the genetic diversity of the study population, the following equation was used:

$$N_{de} = 4\pi\delta^2$$

(3)

where $\delta$ is the average density of breeding adults and $\sigma^2$ is the one-way dispersal variance. The one-way dispersal variance was calculated as one-half the mean squared distance between birth and breeding site (Wright 1978).

Results

Population characteristics

Numbers of breeding adults in the population were similar in the 1998 ($N = 56$) and 1999 ($N = 48$) seasons (Tables 1 and 2). The sex ratio in each season expressed as (no. males / no. males + no. females) was 0.50 in 1998 and 0.46 in 1999.

Turnover among adult males was significantly greater than among adult females with average (SD) tenure on the site (time between first and last capture) during the breeding
season (max. = 360 days assuming a 6-month breeding season) for males being 99 (±59.7) days and 173 (±96.1) days for females (Mann–Whitney U = 466; N = 44, 44; P < 0.001). Differences in turnover within the population could also be seen in the proportion of adults that remained on the site to breed the following season. Of the 26 adult females in the 1999 season, 10 (38%) were adults from the previous season, whereas only 6 (27%) of the 22 males in 1999 had been reproductively active adults on the study site the previous season. Of the 32 juveniles born in 1998 (N = 19 females, 13 males), only 13 remained on the site through at least part of the 1999 breeding season (N = 9 females, 4 males). Although many of the disappearances from the study site could be due to mortality, given the amount of dispersal onto the study site, it seems reasonable to assume that at least some of the individuals born on site dispersed successfully. As a result of both juvenile and adult dispersal or mortality, the 1999 breeding population was composed of 40% immigrants (55% males; 27% females). This estimate does not take into account individuals that may have dispersed to the site prior to 1998.

Genetic variation

One locus, Nfu6, deviated significantly from Hardy–Weinberg equilibrium due to the presence of a null allele, the existence of which was confirmed by comparing the genotypes of several known mother–offspring pairs. As a result, this locus was excluded from further analyses. Mean expected heterozygosity at the five loci used in the parentage analysis was 0.85 with observed values ranging from 0.81 to 0.94 (Table 3). All loci were in Hardy–Weinberg equilibrium with negligible frequencies of null alleles (Table 3). Mean polymorphic information content was 0.84 with total exclusionary power of 0.983 for the first parent and 0.998 for the second parent. No evidence of linkage disequilibrium was found.

Parentage and reproductive success

Using an 80% confidence level, 71 of 78 offspring (91%) could be assigned to a sampled male. At a 95% confidence level, 51 of 78 pups (65%) could be assigned to sampled males. Success in assigning offspring to a sampled male was lower in 1998 (95% confidence level = 59%; 80% confidence level = 88%) than in 1999 (95% confidence level = 70%; 80% confidence level = 93%). In both years, the observed assignments exceeded those expected by simulations at the 95% (1998: 59 vs. 46%; 1999: 70 vs. 50%) and 80% (1998: 88 vs. 78%; 1999: 93 vs. 80%) confidence levels. Four of the seven (57%) cases of nonassignment at the 80% confidence level were due to lack of power to exclude at

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**Table 1** Male reproductive success during two breeding seasons in a population of *Neotoma macrotis*. Successful males were those that sired at least one pup to the point of emergence from the nest. \(I_{bm}\) is the standardized variance in male reproductive success.

<table>
<thead>
<tr>
<th>Season</th>
<th>No. pups assigned</th>
<th>No. candidate males</th>
<th>No. sires</th>
<th>Mean (var) no. pups per successful male</th>
<th>Mean (var) no. pups all males</th>
<th>Poisson expected mean</th>
<th>(I_{bm})</th>
</tr>
</thead>
<tbody>
<tr>
<td>1998</td>
<td>28 (88%)</td>
<td>28</td>
<td>13 (46%)</td>
<td>2.15 (1.14)</td>
<td>1.0 (1.70)</td>
<td>1.80</td>
<td>1.70</td>
</tr>
<tr>
<td>1999</td>
<td>43 (93%)</td>
<td>22</td>
<td>14 (64%)</td>
<td>3.07 (3.61)</td>
<td>1.95 (4.52)</td>
<td>2.97</td>
<td>1.19</td>
</tr>
</tbody>
</table>

**Table 2** Female reproductive success during two breeding seasons in a population of *Neotoma macrotis*. Successful females were those that raised at least one pup to the point of emergence from the nest. \(I_{bf}\) is the standardized variance in female reproductive success.

<table>
<thead>
<tr>
<th>Season</th>
<th>No. pups</th>
<th>No. breeding females</th>
<th>No. successful mothers</th>
<th>Mean (var) no. pups/successful female</th>
<th>Mean (var) no. pups all females</th>
<th>Poisson expected mean</th>
<th>(I_{bf})</th>
</tr>
</thead>
<tbody>
<tr>
<td>1998</td>
<td>32</td>
<td>28</td>
<td>17 (61%)</td>
<td>1.65 (0.74)</td>
<td>1.0 (1.11)</td>
<td>1.10</td>
<td>1.11</td>
</tr>
<tr>
<td>1999</td>
<td>46</td>
<td>26</td>
<td>16 (62%)</td>
<td>2.69 (1.83)</td>
<td>1.65 (2.87)</td>
<td>2.49</td>
<td>1.05</td>
</tr>
</tbody>
</table>

**Table 3** Summary statistics for five microsatellite loci sampled in a population of *Neotoma macrotis* over two breeding seasons. \(H_O\) = observed heterozygosity, \(H_E\) = expected heterozygosity, \(PIC\) = polymorphic information content.

<table>
<thead>
<tr>
<th>Locus</th>
<th>N</th>
<th>No. alleles</th>
<th>(H_O)</th>
<th>(H_E)</th>
<th>PIC</th>
<th>HW</th>
<th>Null Freq.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nfu1</td>
<td>193</td>
<td>16</td>
<td>0.87</td>
<td>0.84</td>
<td>0.82</td>
<td>0.70</td>
<td>NS −0.02</td>
</tr>
<tr>
<td>Nfu4</td>
<td>181</td>
<td>16</td>
<td>0.94</td>
<td>0.90</td>
<td>0.88</td>
<td>0.79</td>
<td>NS −0.03</td>
</tr>
<tr>
<td>Nfu5</td>
<td>195</td>
<td>13</td>
<td>0.92</td>
<td>0.88</td>
<td>0.87</td>
<td>0.75</td>
<td>NS −0.02</td>
</tr>
<tr>
<td>Nma10</td>
<td>190</td>
<td>19</td>
<td>0.81</td>
<td>0.82</td>
<td>0.81</td>
<td>0.68</td>
<td>NS +0.01</td>
</tr>
<tr>
<td>Nma11</td>
<td>184</td>
<td>11</td>
<td>0.86</td>
<td>0.82</td>
<td>0.80</td>
<td>0.65</td>
<td>NS −0.03</td>
</tr>
<tr>
<td>Mean</td>
<td>15</td>
<td>15</td>
<td>0.85</td>
<td>0.85</td>
<td>0.84</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total exclusionary power</td>
<td>0.998</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
least two candidate fathers. These results suggest that the majority of true fathers were included in the sample. With the exception of one male at one locus, no fathers had mismatches with their assigned offspring.

All adult females showed signs of reproductive activity but only 17 (61%) and 16 (62%) individuals were successful in rearing at least one juvenile to emergence from the nest in each year, respectively. A similar proportion of the male population reproduced successfully with 13 (46%) and 14 (64%) successful breeders in each year. Across years, there was no significant difference in the proportion of males and females successfully breeding in the population (Fisher’s exact test, \( P > 0.05 \)). Considering only those adults who successfully reared at least one juvenile to emergence from the nest/house, the sex ratios were 0.43 and 0.47 for each season, respectively.

In 1998 and 1999 successful males sired an average of 2.15 (1.14, var.) and 3.07 (3.61) pups, whereas successful females reared an average 1.65 (0.74) and 2.69 (1.83) young (Tables 1 and 2). Including unsuccessful individuals reduces within year population averages to 1.70 (1.50) and 1.95 (4.52) for males and to 1.0 (1.11) and 1.65 (2.87) for females. The poisson expectation of reproductive success in 1998 and 1999 was 1.8 and 2.97 pups for males and 1.1 and 2.49 for females. The standardized variance of success for males \( \left( t_{pm} \right) \) was 1.70 and 1.19, whereas for females \( \left( t_{pf} \right) \) it was 1.11 and 1.05. Observed variance in reproductive success was not significantly different from poisson expectations for either sex in each year (\( I\text{-test}, P > 0.05 \)). Variance in reproductive success was not significantly different between the sexes in either year (\( I\text{-test}, P > 0.05 \)).

Of 25 litters that had two or more pups, five (20%) showed evidence of multiple paternity. Of the 13 females that had \( \geq 2 \) litters in a single season, 6 (46%) had litters that were fathered by different male partners. Of the seven (54%) females whose successive litters were produced with the same partner, five were in isolated portions of the study site in areas that were seldom occupied by more than one adult pair. Twelve (60%) of 20 males that sired multiple litters within a season had different female partners. In 6 (50%) of these 12 cases, males appeared to breed nearly simultaneously with 2–3 females (based on estimated date of juvenile birth).

Of 28 different females that bred successfully, 11 (39%) had multiple male partners either within or across litters (and years) and of 24 different males that bred successfully, 14 (58%) had multiple female partners. There was no significant difference in the proportion of males and females that had more than one mate (\( P > 0.05 \), Fisher’s exact test). On average, males had 1.87 (0.92) different mates, which was not significantly different from the 1.54 (0.74) different mates of females (\( P > 0.05 \), Mann–Whitney U-test).

When males mated with multiple females within a single season, either simultaneously or sequentially, the females had an average relatedness of 0.004 and –0.065 in each year; this is not significantly different from the average pairwise relatedness of females on the site (–0.006 and –0.021 in each year, \( P > 0.05 \)). Of 26 possible pairs of females, 4 (15%) pairs were related at the 0.25 level and 2 (8%) were related at the 0.5 level.

Recent genetic bottlenecks and population subdivision

Assuming a two-phase mutation model, the population does not appear to have experienced a recent genetic bottleneck. Tests performed separately on the 1998 and 1999 samples with a range of single-step mutation probabilities showed similar results. Both the sign test and Wilcoxon’s signed-ranks test showed that the population was in mutation–drift equilibrium (\( P > 0.05 \)). Furthermore, allelic frequency distributions did not deviate from the expected L-shape.

Taken as the average across all loci, \( F_{IS} \) in the 1998 population was –0.047 and –0.020 in the 1999 population. Neither result was significantly different from zero (Bonferroni corrected \( P = 0.01 \)).

Estimates of effective population size

Demographic parameters were estimated directly from the Big Creek woodrat population (Linsdale & Tevis 1951; Kelly 1989; this study). Adult survivorship (surviving from year 1 to year 2) was estimated to be 0.39 from cohort analyses (Kelly 1989) and 0.38 based on adult females that remained in the population through 1998 and 1999. For the 1998–99 data, it was assumed that a more reasonable estimate of survivorship would be made using only the more sedentary of the two sexes, females. Neither approach can differentiate between mortality and dispersal, but these estimates are the most accurate currently available. Averaging the two available survivorship values, mean adult life span was estimated to be 1.6 years. Mean maturation time for both sexes was estimated to be 0.9 of a year. Under exceptional conditions, some individuals can successfully breed within 6 months (Kelly 1989), but are generally between 9 and 12 months of age (Linsdale & Tevis 1951; Kelly 1989; this study). Using \( M = 0.9 \) and \( A = 1.6 \), leads to \( T = 1.5 \). (Nunney & Elam 1994). Sex ratio was taken as the average within-season ratio of successful breeders, 0.44 (Tables 1 and 2), which was similar to the value when all adults on site were included (0.48). Female fecundity \( (b_f) \) was averaged across years as 2.17 pups. Standardized variance in reproductive success for each sex \( (t_{pm} \text{ and } t_{pf}; \text{Nunney 1993, Nunney & Elam 1994}), \) averaged across years, was 1.45 and 1.08, respectively (Tables 1 and 2). Using eqn 1, the ratio of \( N_e/N \) was estimated to be 0.48. Thus, the census values of 56 and 48 individuals within each season represent demographically determined effective sizes \( (N_e) \) of 26.9 and 23.0, respectively.
Average heterozygosity across all five loci was estimated to be 0.85. Using this estimate of genetic diversity in eqn 2, the genetically determined effective size ($N_{ge}$) of the Big Creek population was estimated to be 1416 individuals.

The average density of breeding adults ($\bar{\sigma}$) in the study area was ~40/ha. Average birth-to-breeding site dispersal distance was 79.8 ($\pm$ 103.3) m ($N = 9$ females, 4 males). Assuming 0.004 individuals/m² and a one-way dispersal distance was 79.8 ($\pm$ 103.3) m ($N = 9$ females, 4 males). Assuming 0.004 individuals/m² and a one-way dispersal variance ($\sigma^2$) of 8113 m², eqn 3 leads to an estimate of a neighbourhood ($N_{na}$) that includes 408 individuals.

Discussion

The notion of the effective population size is not only central to the study of evolution, but also explicitly links behavioural and demographic processes with the maintenance and apportionment of genetic variation within and among populations.

Reproductive success

Contrary to predictions made by Kelly (1989), my study population could not be characterized by harem polygyny with harem females composed of related females. Similar proportions of males and females were reproductively successful and variance in reproductive success was not significantly different between the sexes. Furthermore, neither sex deviated from poisson expectations of reproductive success. Not all males mated with multiple females, but those that did, either simultaneously or sequentially, did so with females that were unrelated to each other. Lack of relatedness among female mates reflects high rates of female dispersal, which results in neighbouring females being unrelated to one another (Matocq & Lacey in press). Some individuals of both sexes were monogamous across litters within seasons but in the majority of cases, this occurred in relatively isolated, low-density areas of the study site. Approximately half of males and females had multiple partners across litters in addition to the cases of multiple paternity within litters. Given the relatively coarse resolution of trapping data, it is difficult to determine precisely the potential for multiple matings among individuals. Certainly, the high degree of turnover in the study population had a strong influence on the opportunity for remating the same partner. During the time of this study, the mating system of this population is most well characterized as some form of promiscuity. Nonetheless, annual differences in factors such as survivorship and population density could alter both male and female breeding tactics. Genetic data have shown that mating patterns in *Neotoma cinerea* are also best characterized by promiscuity (Topping & Millar 1998), although evidence of multiple paternity is lacking in this species.

Simulations suggest that incorporating more than one male partner per female increases effective size relative to those expected from polygyny and even monogamy (Sugg & Chesser 1994). Given that the current study provides evidence of multiple paternity in this species, depending on the frequency of this phenomenon, it may have important implications for the relationship of $N_{e}$ to $N$. Rates of multiple paternity found here are lower than those documented for other murid rodents (50–80%; Baker et al. 1999) and voles (33% Boonstra et al. 1993) but larger sample sizes are needed to determine the frequency of this phenomenon in woodrats.

Discrepancies in estimates of $N_{e}$

In this population of woodrats, the variance in reproductive success for both males and females, a slight skew in the sex ratio and short generation times led to effective population size being lower than the census size. That is, the rate of genetic drift or loss of variation is higher because of the basic life history and mating characteristics of the population. Nonetheless, high levels of genetic diversity are maintained at the local level, which results in a genetic estimate of effective size ($N_{ge}$) that exceeds the census size by two orders of magnitude. Large discrepancies between census size and $N_{ge}$ have also been found in shrews (Bouteiller & Perrin 2000). Discrepancy between the genetic estimate of $N_{e}$ and census size could be due to a number of factors including subdivision of the focal population into a number of breeding groups, recent reductions in population size and/or a neighbourhood size that exceeds the census area.

As originally proposed by Wright (1951), $F$-statistics did not consider the effects of breeding group structure within subpopulations (reviewed by Sugg et al. 1996). Just as differentiation among subpopulations can contribute to the maintenance of genetic variation in the total population, differentiation among breeding groups can influence maintenance of variation within a subpopulation. That is, under certain circumstances, increased coancestry among adults within breeding groups can increase effective population size and could result in higher levels of genetic diversity than would be expected based on an assumption of random mating in the subpopulation. Based on Kelly’s (1989) original description of spatially and (presumptively) genetically related females mating with the same male, the existence of breeding groups would be an important consideration in estimates of effective size and the apportionment of genetic variation. Despite the qualitative evidence for breeding groups provided by Kelly, genetic data presented here and in Matocq & Lacey (in press) provide no evidence for such groups, based either on actually determined matings or on estimates of $F_{IS}$.

Another factor that could lead to low census estimates but high genetic estimates is if current population size is
small relative to that characteristic of historic populations (Gerber & Templeton 1996). From the distribution of allelic frequencies and the lack of excess heterozygosity, the population does not appear to have experienced recent genetic bottlenecks. Censuses of the Big Creek population over the past 50–60 years show fairly stable population sizes (Linsdale & Tevis 1951; Kelly 1989; this study), but the possibility of slow declines of populations in the region over longer timeframes cannot be eliminated.

Finally, another factor that would result in higher genetic estimates of effective size than census size is the large neighbourhood size that may characterize this species. The sampling area (Big Creek) is not isolated from surrounding areas of suitable and occupied habitat (Linsdale & Tevis 1951; Kelly 1989; this study), thus, it is likely that many more individuals are contributing to the maintenance of the genetic diversity sampled here than the individuals captured during this study (Bouteiller & Perrin 2000; Storz et al. 2002). The large estimate of neighbourhood size suggests this may be the case even though the estimate is likely to be low given the lack of good dispersal data. Although a more complete understanding of neighbourhood size in woodrats requires better estimates of dispersal, the high level of immigration to the study site suggests that movement between (sub)populations plays an important role in the dynamics of this population and, in particular, the maintenance of genetic diversity. As such, a large part of the discrepancy between census size and $N_e$ can likely be explained by a deme size that exceeds the focal census area.

Conclusions

These data suggest that although characteristics of the mating system and life history of these woodrats may contribute to loss of genetic variation over time, the movement of individuals among (sub)populations likely contributes to the maintenance of diversity within (sub)populations. In addition to these demographic and behavioural mechanisms, the level of genetic diversity that characterizes this woodrat population is also strongly influenced by the high historic, regional diversity of this portion of the Central Coast of California (Matocq 2002b). Thus, genetic variation in the study population is the result of both high regional diversity and the dispersal characteristics discussed here that maintain diversity on a more local scale. Because this study suggests that, if left in isolation, individual woodrat populations will lose diversity due to particular characteristics of their mating and demographic systems, these findings have important implications for the long-term maintenance of genetic diversity in a small, geographically isolated, endangered population of woodrats in the Central Valley of California (Williams 1993).

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References


The author’s research program seeks to combine molecular genetic techniques with field studies to elucidate historic and ongoing processes that determine the geographical distribution of genetic diversity within and among wild populations. Ongoing research projects are focused primarily on understanding mechanisms that generate and maintain species boundaries in the genus *Neotoma*. © 2004 Blackwell Publishing Ltd, *Molecular Ecology*, 13, 1635–1642