



How isolated are Pleistocene refugia? Results from a study on a relict woodrat population from the Mojave Desert, California

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Abstract

Pleistocene vicariance is often invoked to explain the disjunct populations of animals in habitat refugia throughout the southwestern United States. The combined effects of small population size and isolation from the rest of the contiguous range are thought to result in genetic differentiation of relict organisms.

Here, we describe a relict population of dusky-footed woodrats (*Neotoma fuscipes* Baird) found in a pinyon-juniper-oak community in a small mountain range within the Mojave Desert. We compare morphological and genetic data for these individuals with two populations within the contiguous range, and with another species of woodrat (*Neotoma lepida*). We also examine the distributional overlap between contemporary oak species and dusky-footed woodrats, and estimate the potential oak woodland habitat available during the late Quaternary.

As expected, both the morphological and genetic analysis confirm that the relict population is *N. fuscipes*. Within the limitations of our data, we detect no evidence of differentiation. Instead, the relict population forms a paraphyletic group with the nearest population within the contiguous range. This may be explained by the combined influences of a shorter period of isolation and a greater effective population size than was originally expected.

The linkage between contemporary oak and dusky-footed woodrat distributions is very tight, reinforcing the idea of an obligate relationship between the two.

We estimate that at ~8000 ybp, pinyon-juniper-oak woodlands may have covered ~53% of the central Mojave, forming large contiguous areas of habitat. Although considerably more fragmented, at present ~12% of the area consists of relict woodlands.

Our results suggest that there may be numerous other woodrat refugia, with a relatively high degree of connectiveness between the larger ones. Animals within them may effectively function as a single metapopulation, buffering against occasional stochastic extinction events.

Keywords

Oak/juniper woodlands, biogeography, Pleistocene vicariance, climate change, d-loop evolution, *Neotoma fuscipes*.

INTRODUCTION

The late Quaternary was a period of considerable climate and vegetational change. As glacial ice sheets receded and climatic and precipitation regimes altered, numerous fluctuations

occurred in the distributions of both plants and animals (Graham, 1986; Brown & Lomolino, 1998). In many locations within the southwestern United States, montane and coniferous woodlands were fragmented. These vicariance processes resulted in discrete relict 'islands' of montane/woodland habitat, surrounded by lower elevation semidesert grassland and/or desert scrub (e.g. Brown, 1971, 1978; Patterson, 1982; Sullivan, 1994; Brown, 1995). The analysis

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Table 1 Selected records of fossil pinyon-juniper-oak woodlands within the southern Mojave Desert. Modern lower extent is between 1200 and 1500 m (Wells & Berger, 1967; Munz, 1974; Rowlands *et al.*, 1982)

Reference	Location	Plant species present	Elevation (m)	Radiocarbon date (ybp)	Comment
Van Devender 1977	Lucerne Valley, CA	<i>Juniperus</i> spp.	510	9600	
Van Devender 1977	Redtail Peaks, CA	<i>Juniperus</i> spp.	520	9160, 8900	
Van Devender 1977	Whipple Mtns, CA	<i>J. osteosperma</i> , <i>Pinus</i> spp.	520	9920	
Leskinen, 1975	Sacatone Wash, NV	<i>Q. dunnii</i>	730	9490	
Spaulding, 1990	Brown Buttes, Marble Mtns, CA	<i>Juniperus</i> spp.	840	8900	Not present by 7900; essentially modern vegetation by 4400
Wells & Berger, 1967	Turtle Mtns, CA	<i>Juniperus</i> spp.	850	19,500, 13,900, 12,600	
Leskinen, 1975	Newberry Mountains, NV	<i>Q. dunnii</i> , <i>Q. chrysolepis</i>	850	9500	
Spaulding, 1990	Skeleton Hills, NV	<i>J. osteosperma</i>	910	36,600 to 15,500	Absent by 9200
King, 1976	Lucerne Valley, CA	<i>J. osteosperma</i>	1006	12,100, 11,100, 8300, 7800	Absent after 7800, not present today
Wells & Berger, 1967	Lucerne Valley, CA	<i>J. osteosperma</i> , <i>Pinus</i> spp.	1070	9140, 7800	Not replaced by desert scrub until 7800
Spaulding, 1977 and 1990	Sheep Range, NV	<i>J. osteosperma</i> , <i>Pinus</i> spp.		3500 to 2000	Neopluvial?
Spaulding, 1990	Mercury Ridge, Spotted Range, NV	<i>J. osteosperma</i>	1100	7800	
Wells & Jorgensen, 1964	Frenchman Flat, NV	<i>Juniperus osteosperma</i>	1100	27,400, 17,450, 10,100	
Wells & Jorgensen, 1964	Frenchman Flat, NV	<i>J. osteosperma</i>	1280	7800	
Van Devender & Spaulding 1979	Robbers Roost, CA	<i>J. osteosperma</i> , <i>Pinus monophylla</i> , <i>Q. turbinella</i>		13,800 to 12,800	

of allozymes, morphometric data and mtDNA sequences of several mammalian species has suggested that late Quaternary vicariance processes influenced genetic differentiation and gene flow (Patterson, 1982; Riddle & Honeycutt, 1990; Hayes & Harrison, 1992; Sullivan, 1994). This is not surprising since animals in refugia are likely to demonstrate the effects of both isolation and small effective population size, given their restricted opportunities for dispersal (Wright, 1978; Sullivan, 1994). Intervening stretches of arid habitats such as semidesert grasslands and desert scrub appear to function as effective barriers to dispersal and hence gene flow, especially for small montane mammals (e.g. Hooper, 1938; Spevak, 1983; Lomolino *et al.*, 1989; Sullivan, 1994).

Pinyon-juniper-oak woodlands were widespread throughout much of the Mojave Desert as recently as 7,800–9000 ybp (Wells & Jorgensen, 1964; Wells & Berger, 1967; Leskinen, 1975; King, 1976; Harris, 1985; Betancourt *et al.*, 1990; Spaulding, 1990; Table 1). Although the Mojave Desert had been dominated during the Miocene and Pliocene by a live oak woodland savanna (Chaney *et al.*, 1944; Axelrod, 1977), by the late Quaternary much of this area was predominantly pinyon-juniper woodland, with oaks restricted to more mesic locations (Wells & Jorgensen, 1964; Wells & Berger, 1967; Leskinen, 1975; Spaulding, 1990). Increasing aridity and warmer climates during the Holocene resulted in local extirpation and/or elevational displacement of woodland vegetation. Estimates suggest, for example, a displacement of ~600–800 m for *Quercus chrysolepis* (Canyon live oak) since 9500 ybp (Leskinen, 1975), and displacement of ~600 m for pinyon-juniper woodland (Wells & Berger, 1967; Spaulding, 1990; Table 1). Currently, small discontinuous relicts of pinyon-juniper-oak habitat are found at elevations greater than ~1200–1400 m on a number of mountain ranges within the Mojave (Wells & Berger, 1967; Munz, 1974; Vasek & Thorne, 1977; Rowlands *et al.*, 1982). These have not been well characterized, however, and little information is available about associated montane species that may be present and/or their evolutionary divergence (Vasek & Thorne, 1977).

In 1990, we live-trapped a relict population of woodrats in upper Cottonwood Wash at the Jack and Marilyn Sweeney Granite Mountains Desert Research Center in the Mojave Desert (F. A. Smith and P. A. Kelly, pers. observ.). On the basis of their large size and distinctly marked hind feet, the animals were tentatively identified as dusky-footed woodrats (*Neotoma fuscipes*). The woodrats were approximately 100 km from the nearest known contiguous 'mainland' population of *N. fuscipes* (Fig. 1), and inhabited a refugium of pinyon-juniper-oak woodland. Later investigation of museum holdings at the Los Angeles County Natural History Museum yielded several additional specimens collected in 1976 from approximately the same area. In 1997–98, several dozen additional specimens were live-trapped in Cottonwood Wash (M. Matocq, pers. observ.).

Neotoma fuscipes Baird is considered by many to be an obligate oak (*Quercus* spp.) and/or woodland specialist, although this supposition has not been rigorously examined (Hooper, 1938; Linsdale & Tevis, 1951; Murray & Barnes, 1969; Chew & Woodman, 1974; Atsatt & Ingram, 1983;

Kelly, 1989, 1991). Currently, the species is restricted to a band of mostly oak and/or riparian woodland habitat along coastal and central California, stretching from southern Oregon to the northern end of Baja California (Hooper, 1938; Hall, 1981; Fig. 1). Fossil records indicate, however, that during the Pleistocene *N. fuscipes* was found considerably farther east into what is now the Mojave Desert (Harris, 1985; Jefferson, 1991). Most likely, *N. fuscipes* also receded westward and to higher elevations as vegetation shifted.

Here, we compare the relict population found at the Granite Mountains to two other groups: *N. lepida*, the desert woodrat, which is found throughout the Mojave Desert and which lives in sympatry with *N. fuscipes* along the coast, and several 'mainland' populations of *N. fuscipes*. Our comparisons incorporate both genetic and morphologic data. Our aim was to confirm the initial identification of the relict population, and then examine the phylogenetic relationship between the relict population and other groups of woodrats. We anticipated that some divergence would have occurred, given the likely small effective population size, as well as the long period of isolation. In view of the apparent tight linkage between oak and/or juniper woodlands and dusky-footed woodrats, we also compare their present and past distributional overlap, and estimate the extent of woodland habitat potentially available during the late Quaternary.

METHODS

Sampling localities and morphological comparisons

Relict population

The woodrats tentatively identified as *Neotoma fuscipes* were located in the Granite Mountain Range approximately 100 km east of Barstow, San Bernardino County, California (24° 47' N, 115° 43' W; Fig. 1). They were trapped in an area known as Cottonwood Wash, at about 1460 m elevation. The flora consisted of a *Yucca-Opuntia-Coleogyne* scrub under-community (Vasek & Barbour, 1977), with the addition of cottonwoods (*Populus fremontii*), juniper (*Juniperus californica*) and Canyon live oak (*Quercus chrysolepis*; Fig. 2). In August 1990, sixteen large Sherman live-traps were set at the base of large free-standing dens within oak trees. From these five woodrats were caught (three adults and two juveniles; Appendix 1, Fig. 2). Further trapping was conducted in August 1997 and in April and July of 1998, and several dozen additional individuals were caught. Bait consisted of apple slices, grain and/or peanut butter and oats; several cotton balls were added for insulation. Upon initial capture, woodrats were uniquely identified by attaching a numbered fingerling tag to each ear. The animals were sexed, weighed, and reproductive condition assessed. Measurements of mass and estimates of the lengths of the body, head, tail, ear and hind-foot were made for most animals in the field. We did not anaesthetize the animals, consequently body length is probably underestimated. The other morphological characters were much easier to measure accurately on live animals. Photographs of the face, hindfoot, and tail were taken in



Figure 1 Physiographic map indicating the localities of different *Neotoma* populations used in the study. Note that fully 30% of the Mojave Desert is hilly or mountainous (Rowlands *et al.*, 1982). Legend as follows: GM, Granite Mountain relict population; SB, San Bernardino *N. fuscipes simplex*; HR, Hastings *N. fuscipes luciana*. Two Rancholabrean fossil site of *N. fuscipes* are indicated: KC, Kokoweef Cave and AC, Antelope Cave in the Ivanpah Mountains (Harris, 1985; Jefferson, 1991). The P indicates the location of the Providence Mountains. A 2° longitude by 3° latitude rectangle is outlined; topographical contours within this area were analysed (see text). Figure redrawn after Bender (1982) and Barbour & Major 1977.

1990. The pelage condition, colouration, and other markings were noted during examinations. Ear tissue and hair clippings were taken from selected animals. Tissues from three individuals (MDM182, MDM186, MDM189; Appendix 1) were used in our molecular analysis.

Comparative populations

Museum specimens were obtained from the Los Angeles County Natural History Museum (LACNHM), University of New Mexico Museum of Southwestern Biology (MSB), the Museum of Vertebrate Zoology at the University of California Berkeley (MVZ), and from personal trapping records (Appendix 1). Information taken from each included the subspecies, location trapped, museum catalogue number, sex, date of capture, total length, tail length, ear length, hindfoot length, mass (if reported), reproductive condition, collector and collector catalogue number. Body length was determined by subtracting the tail measurement from the overall length. Data were analysed with one-way analysis of variance (ANOVA), using the SPSS (Version 6.1.1) statistical package for the

Macintosh. Woodrats are sexually dimorphic, with males larger than females. Means were not corrected, however, since the ratio of males to females was approximately equal in each population. Previous morphometric analyses on woodrats have demonstrated that ear, hindfoot and skull length can be used to distinguish between species and subspecies of *Neotoma* (e.g. Carraway & Verts, 1991; Hayes & Richmond, 1993).

Samples used for the molecular analysis were obtained from live-trapping woodrats at the following locations: MDM216, MDM217, and MDM218, April 1998, San Bernardino Mountains, Cushenberry Canyon, 8.0 miles east of Big Bear City on State Route 18, San Bernardino Co.; MDM1, JLP16817, and MDM12, April 1997, Hastings Natural History Reservation, Carmel Valley, 26 miles south-east of Carmel on G16, Monterey Co. The *N. lepida* (MDM22) included in the analysis were collected April 1997 along Arroyo Seco Road, 2 miles north-east of the junction of Arroyo Seco and Carmel Valley Roads, Monterey Co. From each animal, liver and/or ear tissue was removed, immediately preserved in 95% ethanol, and subsequently



Figure 2 Photographs taken by P. A. Kelly in 1990 at the Jack and Marilyn Sweeney Granite Mountains Desert Research Center, California: (a) A male woodrat caught 26 August 1990 from Upper Cottonwood Canyon, at approximately 1480 m elevation. Inset: the dusky hindfoot is a diagnostic characteristic and is the basis for the specific name (*fusc* = Latin meaning ‘dusky’ and *pedalis* meaning ‘of or belonging to the foot’; Carraway & Verts, 1991); (b) Vegetation at upper end of Cottonwood Wash. The terrain is rocky with pockets of oak (*Quercus chrysolepis*), juniper (*Juniperus californica*), and cottonwoods (*Populus fremontii*), interspersed with an understory of *Yucca* (*Yucca* spp.), cactus (*Opuntia* spp.), and blackbrush (*Coleogyne ramosissima*). Vegetative communities are described in Stein & Warrick (1979), and Smith (1996).

stored at room temperature. Several samples were taken from animals that are part of an ongoing behavioural study of *N. fuscipes*; for these individuals, only a small snippet of ear tissue was sampled.

Molecular techniques

Genomic DNA was isolated from the ethanol preserved liver or ear tissue using a standard salt extraction and ethanol precipitation (e.g. Medrano *et al.*, 1990). A 430 base pair fragment of the mitochondrial DNA control region (D-loop) was amplified via PCR and sequenced using degenerate primers designed by E. Lacey at the MVZ; these were based on primers I and III described in Fumagalli *et al.* (1997). Primer sequences were as follows: 5'-ACCAYYARCACCCA-AAGCTRA-3' and 5'-CCTGAAGTARSAACCAGWWG-3'. Amplification reactions were conducted in a volume of 25 µl with final concentrations of 1x PCR buffer (Boehringer Mannheim), 1.5 mM MgCl₂, 0.2 mM of each deoxynucleotide, 200 ng of each primer, 0.6 units of Taq DNA polymerase (Boehringer Mannheim), and 1 µg of total genomic DNA. Amplifications were performed in a PTC-100 thermocycler (MJ Research, Inc.) with 30 cycles of the following program: 94 °C, 1 min; 55 °C, 1 min; and 72 °C, 1 min. Double-strand DNA was purified using the QIAquick PCR Purification kit (Qiagen). Double-strand product was cycle-sequenced using TaqFS and run on a 377 Automated Sequencer according to manufacturer specifications (Applied Biosystems, Inc.). The only deviation from manufacturer instructions was to cut in half the total volume of the cycle sequencing reaction (e.g. 10 µl instead of 20 µl) but final reagent concentrations remained the same. Sequence data was submitted to GenBank; accession numbers are AF091253 through AF091260.

Sequences were edited in the program Sequence Navigator (Applied Biosystems, Inc.) and aligned by eye. Pairwise distances were estimated using the Kimura (1980) two-parameter model. Maximum-parsimony and 50% majority-rule consensus trees for the DNA sequence matrix were constructed using a heuristic search in PAUP (version 3.1.1; Swofford, 1993). The robustness of nodes were evaluated by bootstrap using 100 replicates.

Distributional comparisons

The common observation that *N. fuscipes* is found in close association with oak woodlands (e.g. Linsdale & Tevis, 1951; Atsatt & Ingram, 1983; Kelly, 1989) led us to wonder how robust the relationship actually is. Accordingly, we examined the present day distribution of various oak species found within California and Oregon and compared them to that of *N. fuscipes*. Range maps at 1 : 100,000 scale were scanned into Adobe Photoshop, aligned and overlaid. Total area occupied and areas of sympatry and allopatry were measured using NIH image (Version 1.6.2). Three replicates were conducted for each area measure; the mean is presented here. Measurement error for small areas (< 50 km²) was approximately 1 km²; that for the larger areas was under 10 km². The distribution of *Neotoma fuscipes* was taken

from Hall (1981); those for *Quercus agrifolia* (California live oak), *Q. chrysolepis* (Canyon live oak), *Q. lobata* (Valley oak), and *Q. garryana* (Oregon oak) were taken from Little (1971). Several oaks whose range was almost entirely encompassed within the area occupied by these species were not analysed (e.g. *Q. douglasii*, blue oak and *Q. kelloggii*, California black oak).

The extent of pinyon-juniper-oak woodlands within the Mojave Desert was estimated for three periods during the late Quaternary using data derived from woodrat palaeomiddens (Table 1). Plant macrofossils from the southern portion of the Mojave Desert suggest that the elevational extent of pinyon-juniper-oak woodlands was ~900 m at ~8000 ybp, ~1200 m at 3,500–2000 ybp, and ~1400 m today (Wells & Jorgensen, 1964; Wells & Berger, 1967; Leskinen, 1975; King, 1976; Vasek & Thorne, 1977; Harris, 1985; Spaulding, 1990). The late Holocene neopluvial between 3000 and 2000 ybp was proposed by Spaulding (1977, 1990). Based on plant macrofossils preserved in woodrat palaeomiddens, he concluded that pinyon-juniper-oak woodlands were displaced downwards by ~100–200 m during 3,000–1500 ybp.

Topographical maps at 1 : 500,000 scale were scanned into Adobe Photoshop, and area measurements were made with NIH Image as described above. The total area above 900, 1200 and 1400 m (the approximate extent of woodlands at 8,000, 3,000–2,000, and 0 ybp) was estimated. Because of the enormous area within the Mojave Desert at ~900 m, we arbitrarily limited our analysis to a 2° by 3° rectangle, which included the Granite Mountains and the San Bernardino 'mainland' population (115°–117° longitude by 34°–37° latitude; Fig. 1). Hence, we have considerably underestimated the total extent of contiguous area within the Mojave Desert at ~8000 ybp (much of the desert lies at or around 900 m). We estimated the potential population size of dusky-footed woodrats by multiplying the area by typical densities derived in other studies. Woodrat density varies considerably, even within 'suitable habitat'; literature values range from 1 to 61 per hectare (i.e. 100–6100 woodrats/km²; Linsdale & Tevis, 1951; Cranford, 1977; Kelly, 1989; Carraway & Verts, 1991). Here, we use a very conservative estimate of 2 animals/ha (or 200 woodrats/km²) to arrive at a lower limit.

Our approach is overly simplistic in several ways. First, we have ignored the considerable geographical variation in the elevational distribution of vegetative communities over the 2° by 3° rectangle. Realized habitats and the timing of biotic changes were/are influenced by factors such as latitude, slope aspect and underlying substrate (e.g. Vasek & Barbour, 1977; Spaulding, 1990). By using an elevation of 900 m, we are actually underestimating the true extent of woodlands at ~8000 ybp. Fossil evidence suggests, for example, that woodlands were found as low as 510 m at 9600 ybp within the southern and eastern portion of the Mojave Desert (e.g. Van Devender, 1977; Table 1). Further, they may have persisted at elevations as low as 800–900 m as late as 7800 ybp in some sites (e.g. Wells & Berger, 1967; Leskinen, 1975; King, 1976; Spaulding, 1990; Table 1). Second, although we are estimating the extent of pinyon-juniper-oak woodlands,

we suspect that oaks are the critical factor in influencing dusky-footed woodrat presence and abundance. Typically, the highest population densities are found in densely covered oak habitat (as high as 61 animals/ha; Linsdale & Tevis, 1951; Kelly, 1989, 1991), and the lowest in arid chaparral (e.g. Spevak, 1983; Carraway & Verts, 1991). Given the paucity of data, we have made no effort to estimate the density of oak within the pinyon-juniper woodland habitat, although it appears to be reasonably abundant (e.g. Vasek & Thorne, 1977, pers. obs.). We have also assumed that dusky-footed woodrats can occupy the more mesic woodland communities that exist or formerly existed at higher elevations on some of the taller mountain ranges. Given the wide altitudinal range seen among contemporary *N. fuscipes* (e.g. Hooper, 1938; Linsdale & Tevis, 1951; Hall, 1981), this is likely to be a valid assumption. Third, as we mentioned earlier, woodrat abundance varies considerably even in preferred habitat. Here, we have used the lowest densities reported in the literature to arrive at a first approximation of potential dusky-footed woodrat population size. Thus, we may be underestimating the actual population by an order of magnitude. Fourth, time gaps in the woodrat palaeomidden sequences make it difficult to pin down precisely the times of woodland extirpation and/or isolation. Further, some times series provide conflicting evidence. We have relied mostly on the work of Spaulding (1977, 1981, 1990), Wells & Jorgensen (1964), Wells & Berger (1967), Leskinen (1975), King (1976), Van Devender (1977), and a synthesis by Harris (1985) for our approximations. Finally, we would point out that this is a heuristic exercise; our aim is to arrive at a reasonable lower approximation of the total population size possible at various times for comparative purposes.

RESULTS

Morphological comparisons

Analysis of the morphological data yielded clear differences between the various *Neotoma* populations (Table 2). *Neotoma lepida* were significantly smaller in all morphological attributes than the mainland *N. fuscipes* (one-way ANOVA, $P < 0.0001$ in all instances; Table 2). They were also significantly smaller than the relict animals in body mass,

ear, hindfoot, and tail length. Although overall body length of *N. lepida* was smaller than that of the relict *Neotoma* at the Granites, it was not significantly so (Table 2). Given that body mass was significantly different between the two groups, we suspect that differences in methodology led to an underestimate of body length for the relict population. Unlike the other groups, morphological measurements of the relict *Neotoma* population were made on live and unanaesthetized animals. This probably impacted the estimate of body length the most, since other morphological characters (e.g. ear, hindfoot and tail length) were easier to accurately measure on live animals. All values for the relict and mainland *N. fuscipes* fell within the range of those reported in the literature for the species as a whole (e.g. Carraway & Verts, 1991).

The morphological analysis also suggested some degree of divergence among the three *N. fuscipes* populations. Several attributes differed between all three groups, including body and hindfoot length (Duncan and Scheffe multiple range tests, $P < 0.05$; Table 2). Yet, the Granite Mountains were not the most unique population. Tail length was indistinguishable between the Granite and San Bernardino *N. fuscipes*, but significantly larger for the Hastings population (Scheffe multiple range test, $P < 0.05$; Table 2). While ear length of all *N. fuscipes* was significantly larger than that of *N. lepida*, it did not vary among the various groups of *N. fuscipes* ($P > 0.05$). Several morphological characters (e.g. body length, body mass) were significantly related to gender (one way ANOVA, $P < 0.0001$), but because the sex ratios of the various groups were approximately equal (Appendix 1), the interaction did not influence our results.

Genetic analysis

A total of 417 base pairs of the mtDNA control region were analysed. Of these, 347 positions (83%) were invariant and forty-three of the variable positions (10% of the total or 43/70 = 61% of the variable) were uninformative. As expected on the basis of the morphological comparisons (e.g. Table 2) and observed life history characteristics, the genetic analysis confirmed that the relict population at the Granites was indeed *N. fuscipes*. A distance analysis using a Kimura two-parameter correction of the data (Kimura, 1980) suggested that the mean distance among *N. fuscipes* populations was

Table 2 Results of morphological analysis. Sample sizes are given below location and species. Means and the standard error of the mean are given; those which are significantly different in a one-way ANOVA are indicated by different superscripts (see text for details; $P < 0.001$ in all cases). The ratio of males/females was approximately equal for each locality. Exact trapping localities are shown in Fig. 1.

Variable	<i>N. lepida</i> (16)		San Bernardino <i>N. fuscipes</i> (18)		Hastings <i>N. fuscipes</i> (50)		Granite Mtns* <i>Neotoma</i> (17)	
Body Length	156.5 ^a	4.13	185.5 ^b	4.73	214.1 ^c	1.67	164.3 ^a	2.88
Tail Length	130.1 ^a	2.08	166.4 ^b	4.11	193.4 ^c	2.27	177.1 ^b	2.44
Hindfoot Length	29.5 ^a	0.40	35.8 ^b	0.42	40.9 ^c	0.28	32.5 ^d	0.23
Ear Length	28.7 ^a	0.40	32.7 ^b	0.88	31.9 ^b	0.20	30.9 ^b	0.47
Body Mass†	130.1 ^a	4.69	158.3	11.67	244.3 ^b	4.9	167.9 ^c	9.05

*Measures were made on live animals.

†Body mass was available for only three animals from San Bernardino.

Table 3 Kimura Two-parameter distance matrix (Kimura, 1980). Distances below the diagonal are for transversions only. GM, Granite Mountains *N. fuscipes*; SB, San Bernardino *N. fuscipes*; H, Hastings *N. fuscipes*; NI, *N. lepida*. Considering all substitutions, mean within *N. fuscipes* distance was 0.046; mean *N. lepida* v. *N. fuscipes* distance was 0.119.

	GM1	GM2	SB1	SB2	H1	H2	H3	NI
GM1	—	0.0449	0.0449	0.0146	0.0527	0.0500	0.0552	0.1186
GM2	0.0048	—	0.0146	0.0476	0.0661	0.0633	0.0659	0.1275
SB1	0.0048	0.0000	—	0.0476	0.0501	0.0474	0.0552	0.1100
SB2	0.0000	0.0048	0.0048	—	0.0634	0.0606	0.0632	0.1216
H1	0.0073	0.0073	0.0073	0.0073	—	0.0170	0.0295	0.1245
H2	0.0097	0.0097	0.0097	0.0097	0.0024	—	0.0220	0.1100
H3	0.0121	0.0121	0.0121	0.0121	0.0048	0.0024	—	0.1187
NI	0.0486	0.0486	0.0486	0.0486	0.0514	0.0487	0.0513	—

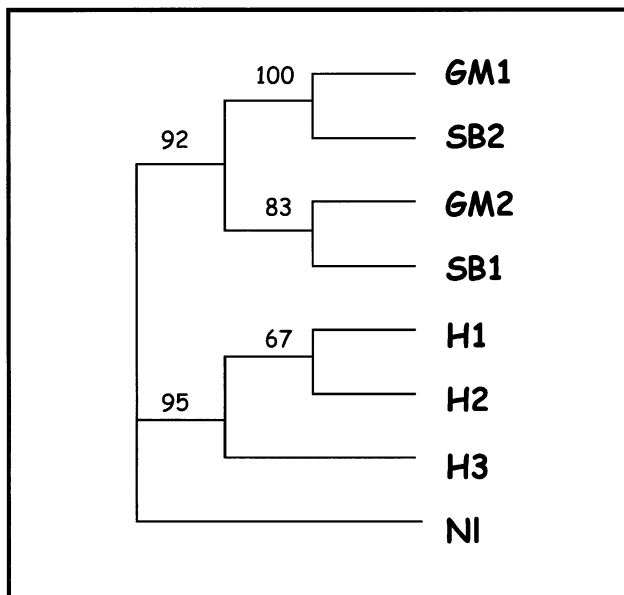


Figure 3 Parsimony tree based on 417 base pairs of D-loop. A bootstrap 50% majority-rule consensus tree yielded an identical topology. The number at the node represents the percentage of trees in which the branch was present. Branch lengths are arbitrary. Legend is as follows: GM1 = MDM182, GM2 = MDM189, SB1 = MDM216, SB2 = MDM217, H1 = MDM1, H2 = JLP16817, H3 = MDM12, NI = MDM22 (Appendix 1).

0.046 (range 0.045–0.066), and the mean distance between *N. lepida* and *N. fuscipes* was 0.119 (range 0.110–0.128; Table 3). Use of only transversions to calculate genetic distances yielded an average within *N. fuscipes* distance of 0.007 (range 0–0.012) and a value for the distance between *N. lepida* and *N. fuscipes* of 0.049 (range 0.0486–0.0514).

While we would anticipate that genetic diversity would be lower for the Granite Mountain animals due to potentially smaller effective population sizes, our relatively small sample sizes ($N = 3$) did not allow us to directly assess the overall level of genetic diversity between and among the various populations. Our analysis did find two unique mtDNA

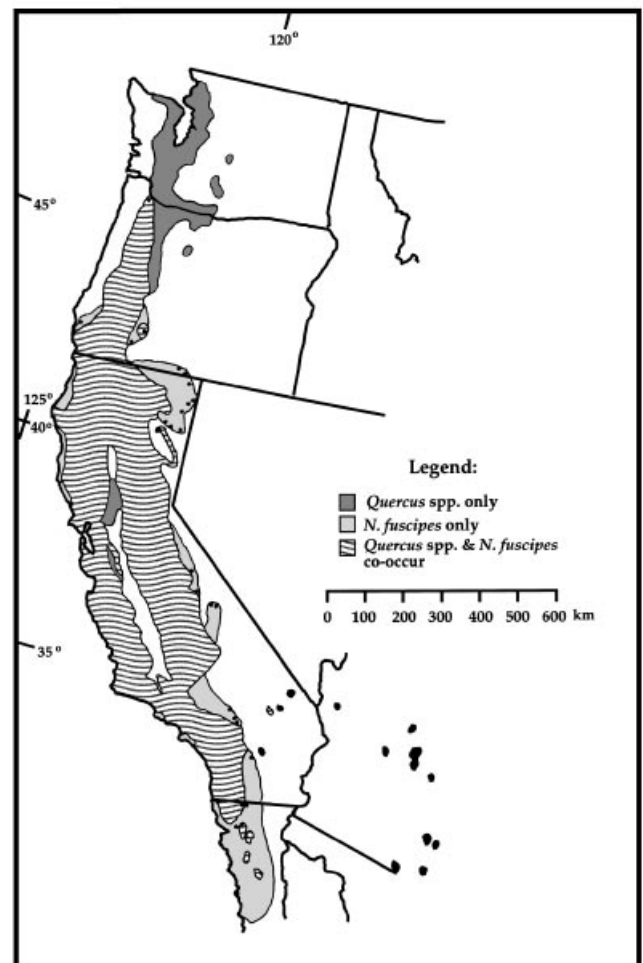


Figure 4 Comparison of the contemporary distributions of *N. fuscipes* and four species of *Quercus*. Three species largely explain the distribution in California: *Quercus agrifolia* (California live oak), *Q. chrysolepis* (Canyon live oak), and *Q. lobata* (Valley oak); the Oregon distribution is explained by the inclusion of *Q. garryana* (Oregon oak). Data for woodrats taken from Linsdale & Tevis (1951) and Hall (1981); *Quercus* distributions are from Little (1971). Dots represent marginal occurrence records of *N. fuscipes*.

haplotypes (2/3) from both the Granites and San Bernardinos; three unique haplotypes were obtained from Hastings (3/3). Using *N. lepida* as the outgroup, a single most parsimonious tree of 86 steps was generated in the PAUP analysis, with a consistency index of 0.884 (Fig. 3). The consistency index was 0.756 with a tree length of 41 steps when only informative characters were included. There was complete concordance among tree topologies; a distance tree and a bootstrap 50% majority-rule consensus tree also found the same relationship among the populations, suggesting that the branching patterns were robust. Again, restricting the analysis to transversions yielded the same topology. The Granite Mountain woodrats form a paraphyletic group with the San Bernardino *N. fuscipes* (Fig. 3). Although our tree is based on a single gene and thus may not reflect an accurate species tree if there has been fairly recent divergence and isolation of the population (e.g. Lyons-Weiler & Milinkovitch, 1997), the topology is consistent with the results of the morphological analysis (Table 2). Our analysis also strongly supports the monophyly of the Hastings *N. fuscipes*. The bootstrap value for this node in the 50% majority rule consensus tree is 95%. Given the uncertainty in the rate of the mtDNA clock, we have not attempted to calculate the timing of molecular divergence.

Distributional comparisons

The degree of overlap between the contemporary distribution of the four *Quercus* species and *N. fuscipes* is striking. They occur in sympatry in over 69.6% of their combined estimated range of ~404,814 km² (Fig. 4). Virtually all of the oak habitat also contained *N. fuscipes*. The portion that did

not (~12.8%) was largely located in Washington and/or Oregon beyond the current northern distributional limit of *N. fuscipes*. We suspect that *N. fuscipes* may be displaced from preferred habitat at these higher latitudes by the much larger and cold tolerant *N. cinerea* (Smith, 1997).

The degree of overlap is even more striking when methodological differences are considered. Hall (1981) depicts marginal trapping records of *N. fuscipes* as contiguous with the mainland population, when in fact many of these may actually reflect large discontinuities in the distribution (e.g. Figure 4). The *N. fuscipes* population in northern Baja California, for example, is extremely patchy and apparently maps onto pockets of montane habitat (F. A. Smith, pers. obs., Fig. 4). In contrast, Little (1971; the source of our oak distributions) maintained marginal records as disjunct populations. Hence, we have undoubtedly overestimated the nonoak habitats occupied by *N. fuscipes*. When methodological differences are considered, there is almost complete overlap between oak and dusky-footed woodrat ranges within California. In fact, the largest area containing *N. fuscipes* but no oak, was considered outside the dusky-footed woodrat's range prior to 1981 (e.g. Linsdale & Tevis, 1951), and may represent a subsequent range expansion (Murray & Barnes, 1969). If this is the case, we would predict that oaks may now also be present in this area. Note that the vegetation atlas used was compiled in the late 1960s; our work does not reflect changes since that time.

Analysis of the topographic maps for the Mojave Desert suggests that large contiguous areas of woodland habitat existed over much of the late Pleistocene and early Holocene (Fig. 5). We estimate that at ~9000 ybp, over 52% (31,003 km²) of

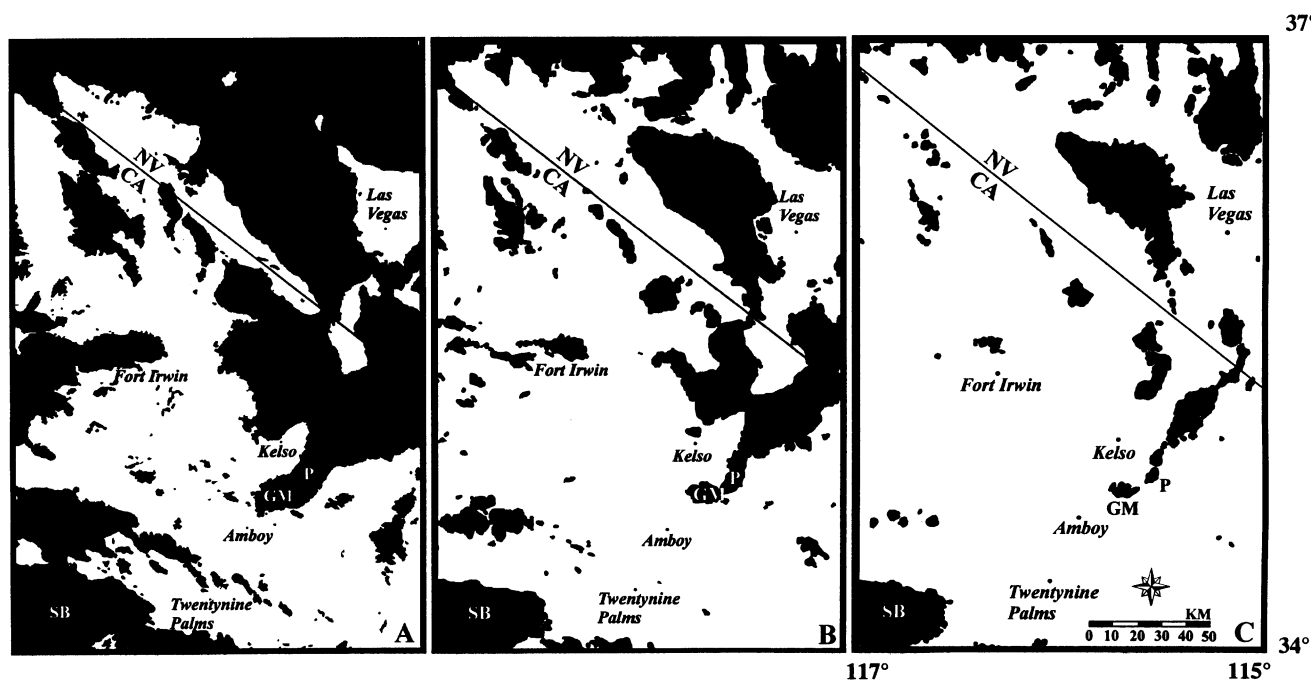


Figure 5 Distribution of Oak-Juniper woodlands in the Mojave Desert over the late Quaternary: (a) Approximately 8000 ybp (elevations > 900 m); (b) Approximately 3500–2000 ybp (elevations > 1200 m); (c) current (elevations > 1400 m). See text for details.

Table 4 Estimated maximum extent of Pinyon-juniper-oak woodlands within a portion (115°–117° longitude by 34°–37° latitude) of the Mojave Desert, over the late Pleistocene and Holocene. Data are derived from USGS topographical maps at 1 : 500,000 scale (see text for details of methodology and assumptions). Habitat islands of less than 25 km² each have been combined under the heading 'Miscellaneous Mountains'.

Elevational contour	≥ 900 m			≥ 1200 m			≥ 1400 m		
	Area (km ²)	% total area	Ne ^a	Area (km ²)	% total area	Ne	Area (km ²)	% total area	Ne
Total woodland ^b	31,003	52.9	6,200.6	15,574	26.6	3,114.8	9,072	15.5	1,814.4
Granite Mtns							55	< 0.1	11.0
Providence Mtns									
New York Mtns									
McCullough Mtns							1,005 ^e	1.7	201.0
Ivanpah Mtns							436	0.7	87.2
Spring Mtns				7,075 ^d	12.1	1,415.0	2,136	3.6	427.2
Kingston Mtns				287	4.9	57.4	94	0.2	18.8
Greenwater Mtns				294	5.0	58.8	148	0.3	29.6
Funeral Mtns				123	2.1	24.6	24	< 0.1	4.8
Nellis Sector:									
Spotted Mtns							3,496	6.0	699.2
Mercury Peak							50	< 0.1	10.0
Skull Mtn							33	< 0.1	6.6
Bare Mtn	21,871 ^c	37.3	4,374.2	5,417 ^f	9.2	1,083.4	34	< 0.1	6.8
Nopah Range	157	0.3	31.4	56	< 0.1	11.2	28	< 0.1	5.6
Nth of Nopah	152	0.3	30.4	11	< 0.1	2.2	1	< 0.1	0.2
Arrow Canyon Range	121	0.2	24.2	0	0	0	0	0	0
Mouty Mtns	164	0.3	32.8	0	0	0	0	0	0
Spirit Mtns	156	0.3	31.2	20	< 0.1	4.0	0	0	0
Clipper Mtns	45	< 0.1	9.0	0	0	0	0	0	0
Old Woman Mtns	315	0.5	63.0	90	0.2	18.0	6	< 0.1	1.2
'West' Granite Mtns ^g	1,798	3.1	359.6	220	0.4	44.0	63	0.1	12.6
Teifort Mtn	33	< 0.1	6.6	0	0	0	0	0	0
Cady Mtns	57	< 0.1	11.4	0	0	0	0	0	0
San Bernardino Mtns	6,070	10.3	1,214.0	1,981	3.4	396.2	1,463	2.5	292.6
Miscellaneous Mtns	64	0.1	12.8	0	0	0	0	0	0

^a Potential population size in thousands, based on woodrat density estimate of two individuals/ha (200 individuals/km²) and multiplied by approximate ha of habitat at this contour interval. See text for details.

^b Total area contained within 2 × 3° rectangle is approximately 58,633 km².

^c The Granite, Providence, New York, McCullough, Ivanpah, Spring, Kingston, Greenwater, Funeral and Nellis Sector (including the Spotted Mountains, Mercury Peak, Skull and Bare Mountain) form a single contiguous area at this elevational contour.

^d The Granite, Providence, New York, McCullough, Ivanpah and Spring Mountains form a single contiguous area at this elevational contour.

^e The Providence, New York, and McCullough Mountains form a single contiguous area at this elevational contour.

^f Mercury Peak, Skull, and Bare Mountain all form a single contiguous area within an area we have called the Nellis Sector (other ranges are included) at this elevational contour.

^g At least three different mountain ranges within the Mojave are referred to as the Granite Mountains. Our study refers to the range situated at 24°47' N latitude, 115°43' W longitude.

the area within our rectangle was occupied by juniper/pinyon/oak woodlands (Table 4). At this time, most of the mountains in the northern portion formed a single habitat block of > 21,800 km². The retreat of woodlands to higher elevation (~1200 m) sites resulted in a much more fragmented habitat, but nevertheless several large contiguous areas remained (e.g. Figure 5b). The Granites, Providence, New York, McCullough, Spring and Ivanpah Mountains, for example, still formed a single large area of habitat of ~7075 km². We estimate that this area alone could potentially support a woodrat population of over 1.4×10^6 individuals (Table 4). As woodlands retreated to their current

elevational range, further fragmentation occurred. Yet, even today we estimate that there are approximately 9000 km² of woodlands (15.5% of the total area) within just this portion of the Mojave. Most is probably contained within the San Bernardino, the Providence/New York/McColloughs, the Spring Mountains, and a group of connected ranges we have called the Nellis Sector (Table 4). Surprisingly, the Granite Mountains do not appear to be particularly isolated, but form a more or less continuous range with the Providence, New York, and McCullough Mountains to the north-east (Fig. 5, Table 4). In fact, less than 3 km currently separate the Granites from the Providence Mountains (Fig. 6). With

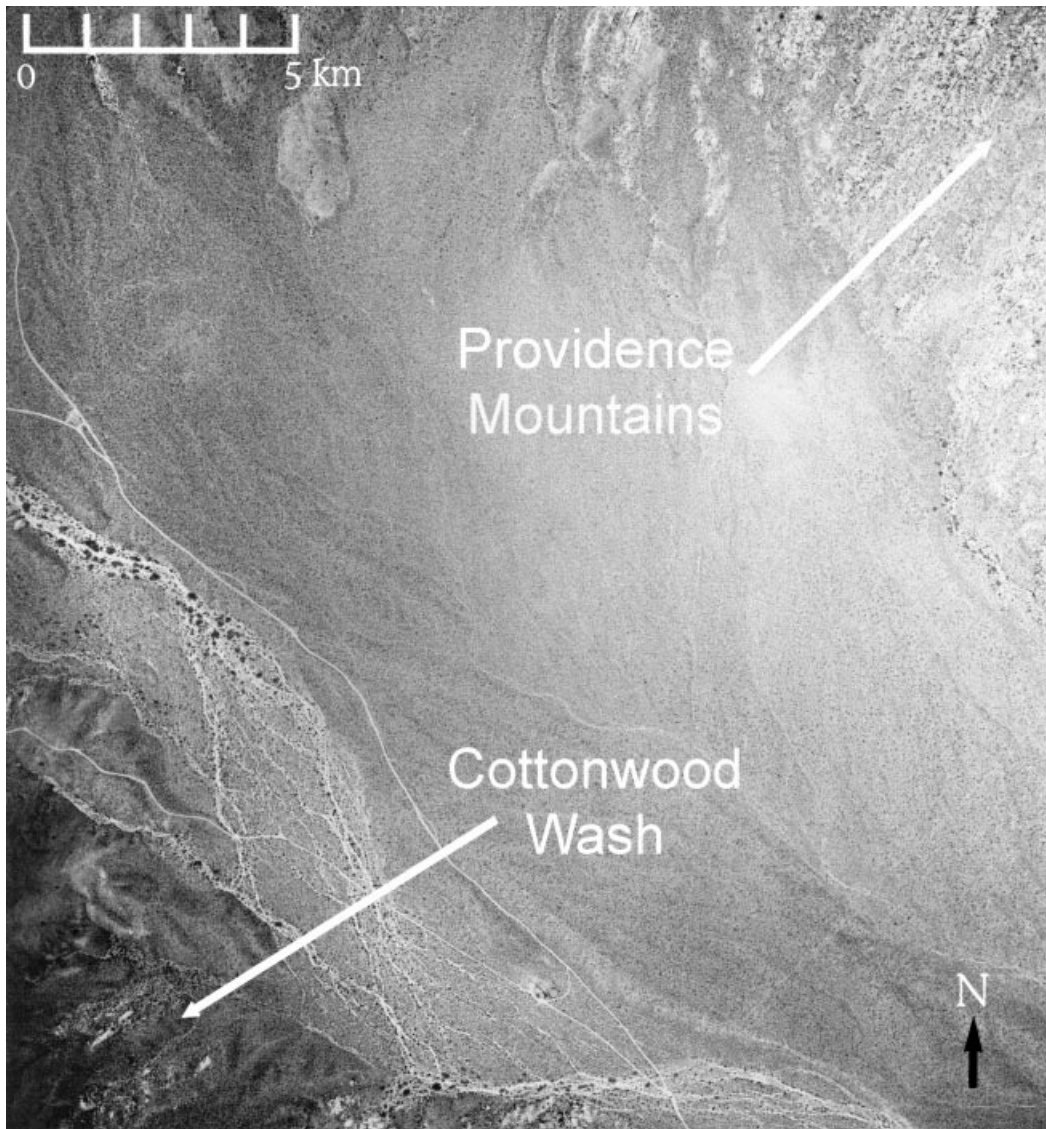


Figure 6 Aerial photograph taken 18 May 1979 of the north-east Granite Mountains and southern portion of the Providence Mountains. Dots indicate individual pinyon, juniper, or oak plants. Scale is 1 : 6000 (1 cm = 1 km). The relict population was discovered at Cottonwood Wash. Note that riparian corridors extend quite a distance into the Bajada. Isolated junipers are found between the two mountain ranges as well, and may facilitate dispersal across the intervening area. Photograph courtesy of C. Luke, co-Director of Granite Mountain Desert Research Center.

the exception of the present study and a population at Joshua Tree National Park (Cameron, 1971), *N. fuscipes* has not been reported from any area within the Mojave; given the large amount of potential habitat we suspect this is due to a paucity of sampling rather than to low or nonexistent woodrat populations.

Another interesting point that arises from our analysis is that the Granite Mountains are likely to be a fairly marginal site for *N. fuscipes*. We estimate that the Providence Mountains, for example, are likely to contain an order of magnitude more potential habitat than the Granites (~1005 vs. 55 km²;

Table 4). Consequently, some 200,000 animals could be present within the Providence/New York/McCollough Mountains, compared to the 11,000 or so we estimate currently inhabit the Granite Mountain range. It should be remembered, however, that large uncertainties surround these values. We could be under- or over-estimating population density by an order of magnitude.

DISCUSSION

The genetic and morphometric analyses clearly demonstrate

that the animals found in Upper Cottonwood Wash are a relict population of *N. fuscipes* (Fig. 3; Tables 3 and 4). This concurs with our preliminary assessment based on their large body size, distinctly marked dusky hind feet and unique den construction (Fig. 2a). Although we did expect some degree of sympatry between the distribution of oak trees and dusky-footed woodrats, we were overwhelmed by the almost complete overlap found (Fig. 4). We feel sure that this result is more than a correlated response to similar environmental requirements, but instead reflects a close obligate or functional relationship (e.g. Linsdale & Tevis, 1951; Murray & Barnes, 1969; Cameron, 1971; Atsatt & Ingram, 1983; Kelly, 1989). Dusky-footed woodrats depend on oak trees for food, shelter and as a building substrate (e.g. Linsdale & Tevis, 1951; Kelly, 1989, 1991). In fact, dens are often constructed at the base of and even within the branches of oaks (Linsdale & Tevis, 1951), and reproduction has been demonstrated to be highly correlated with the production of acorn mast crop (Kelly, 1989). Studies have demonstrated a strong preference for *Quercus*, even when other food resources are abundant, despite the high phenolic content (Linsdale & Tevis, 1951; Chew & Woodman, 1974; Atsatt & Ingram, 1983; Kelly, 1989). Such a tightly linked habitat specificity has apparently existed since at least the Rancholabrean (e.g. Harris, 1985; Jefferson, 1991; Fig. 1). Within *Neotoma*, at least, such a high degree of habitat specificity is not unique. Stephens' woodrat is known to have developed a close obligate relationship with juniper foliage (Vaughan & Czaplewski, 1985).

A consistent result arising from both our morphological and genetic analyses is that the Granite Mountain *N. fuscipes* form a paraphyletic group with the woodrats from the San Bernardino population (Fig. 3). We had hypothesized that the ~10,000 years that had presumably elapsed since they formed a contiguous group with other *N. fuscipes*, combined with what we assumed was a fairly small effective population size, would have led to some degree of evolutionary divergence. A number of studies have demonstrated evolutionary changes over much shorter periods of time (e.g. Thomas et al., 1990; Sullivan, 1994). Using allozyme data, for example, Sullivan (1994) concluded that vicariance processes associated with discontinuities in Pleistocene vegetation were a major factor structuring the pattern of differentiation seen among allopatric populations of *N. mexicana* in the Southwest. The paraphyly we find between the Granite Mountain and San Bernardino *N. fuscipes* suggests that there has been a much more recent isolation, and/or a much larger effective population size than originally suspected.

Given the tight and arguably obligate relationship found between dusky-footed woodrats and several oak species, and the ubiquity of oak within the Mojave Desert during the Pleistocene and early Holocene, it seems reasonable to assume that *N. fuscipes* must have been fairly widely distributed across the region. We suspect that *N. fuscipes* may still inhabit many of these larger woodland patches. In particular, we predict this will prove true of the Providence/New York and Ivanpah Mountains (e.g. Fig. 5). These relatively undisturbed ranges contain about 16% of the total woodland habitat in this area (Table 4). It is also possible that sev-

eral large ranges such as the Spring Mountains in western Nevada may harbour animals; fossil evidence certainly suggests that *N. fuscipes* ranged this far east during the Pleistocene (Harris, 1985; Jefferson, 1991). Although we have no direct evidence that *N. fuscipes* currently are found within the Providence Mountains, we think it is highly likely. The available habitat currently found within the Granites ($\approx 55 \text{ km}^2$; Table 4) does not appear to be sufficient to buffer against the frequent local extinctions that woodrats experience (e.g. Smith, 1996). Woodrats typically do not reproduce until their second year, and mean survivorship is less than 6 months (Linsdale & Tevis, 1951; Escherich, 1981; Vaughan & Czaplewski, 1985; Kelly, 1989; Carraway & Verts, 1991; Smith, 1996). Further, females generally produce only a single litter per year, and mean litter size is only 2.6 young (range 1–4; Linsdale & Tevis, 1951; Carraway & Verts, 1991). Consequently, most individuals do not live long enough to reproduce, and smaller and/or marginal populations are subject to frequent extinctions. Normal mortality combined with seasonally dependent fecundity can thus lead to considerable volatility in local population dynamics. A four year study of the desert woodrat (*N. lepida*) at the Granite Mountains, for example, clearly demonstrated such sink/source population dynamics (Smith, 1996). We estimate that perhaps 11,000 dusky-footed woodrats may exist in the Granite Mountains (Table 4). Yet, the Granite Mountain *N. fuscipes* population is clearly viable. Young of the year and/or individuals in reproductive conditions were caught in both 1990 and 1998 (Appendix 1).

Analysis of the topographic maps suggests that the Granites/Providence/New York/McCollough/Ivanpah and Spring Mountains may actually function as a single metapopulation (Figs 5, 6; Table 4). Despite the apparently fragmented environment, a dynamic equilibrium may be maintained throughout this region by occasional migration of individuals between patches and recolonization after local extinction events (e.g. Kozakiewicz, 1993). In this context, the Granite Mountains are probably a sink population, and are maintained by frequent immigration from the much larger woodland habitat found within the Providence Mountains (Fig. 6). There is some evidence that unexpectedly long distances can be traversed by small mammals in a relatively short time span (Kozakiewicz, 1993). Certainly several population studies conducted on *N. fuscipes* and on other woodrat species (e.g. *N. cinerea*) have noted long distance dispersal (Smith, 1965; Escherich, 1981). Distances of 1.6 km have been crossed in as few as 5 nights (Smith, 1965). Other researchers routinely report movements of > 0.6 km in dispersing *N. fuscipes*, particularly males (Linsdale & Tevis, 1951; Kelly, 1989). A somewhat larger woodrat species, *N. cinerea*, has been documented dispersing over 6–8 km (Escherich, 1981). Currently, less than 3 km separates the 1400 m contour intervals between the Granite and Providence mountain ranges, discounting mesic corridors that probably more closely connect the two (Fig. 6). Movement between the ranges would certainly have been far easier in the past, when woodlands occupied lower elevational levels. Less than 1 km separated them between 3000 and

2000 years ago (Table 4), for example, thus they effectively functioned as a single habitat until fairly recently.

The monophyly of the Hastings *N. fuscipes* also suggests some degree of subdivision among the mainland woodrat population. Whether this is due to the uniqueness of the San Bernardino woodrats (an uniqueness shared by those at the Granite Mountains), or to isolation and/or restricted dispersal of the Hastings animals remains to be seen. Given the rapid urbanization occurring along the coastal regions of California, the Hastings population may be experiencing severe habitat fragmentation. As early as 1938, Hooper noted that there was no longer any contiguous habitat between the location where the type specimen of *N. fuscipes* was collected (in Kern County) and the rest of the population. He attributed this to 'extensive cultivation of the San Joaquin Valley and the denudation of the foothills.' (Hooper, 1938; pg. 224). Given that dispersal may be limited to the south, our results suggest that the Central Valley is a more persistent and rigorous barrier to dispersal than is the Mojave desert.

In many ways our study raises more issues than it explains. Do other Pleistocene refugia exist, as we predict, throughout the Mojave Desert (e.g. Figure 5)? What type of dispersal and/or movement patterns connect these various putative populations? How does the overall level of genetic diversity vary with the refugia size and distance from the mainland? Will further analysis of mainland woodrats reveal similar discontinuities among populations fragmented by increased urbanization along the coast of California? Do the patterns we report here for woodrats apply to other montane woodland organisms that also inhabit these refugia? Detailed study of the genetics, distribution and dispersal of woodrats and other montane mammals within the Granite and Providence Mountain ranges would be very illuminating, and could lead to unique insights into the late Quaternary biogeography of the southwest. We hope these and other issues can be resolved in future studies.

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REFERENCES

- Axelrod, D. I. (1977) Outline history of California vegetation. *Terrestrial vegetation of California* (ed. by M. G. Barbour and J. Major), pp. 139–194. John Wiley and Sons, New York.
- Atsatt, P. A. & Ingram, T. (1983) Adaptations to oak and other fibrous phenolic-rich foliage by a small mammal, *Neotoma fuscipes*. *Oecologia*, **60**, 135–142.
- Barbour, M. G. & Major, J. (1977) *Terrestrial vegetation of California*, 1002 pp. John Wiley and Sons, New York.
- Bender, G. L. (1982) *Reference handbook on the deserts of North America*, 594 pp. Greenwood Press, Westport.
- Betancourt, J. L., Van Devender, T. R. & Martin, P. S. (1990) Synthesis and prospectus. *Packrat middens: the last 40,000 years of biotic change* (ed. by J. L. Betancourt, T. R. Van Devender and P. S. Martin), pp. 435–445. University of Arizona Press, Tucson.
- Brown, J. H. (1971) Mammals of mountaintops: Nonequilibrium insular biogeography. *American Naturalist*, **105**, 563–574.
- Brown, J. H. (1978) The theory of insular biogeography and the distribution of boreal birds and mammals. *Great Basin Naturalist*, **38**, 209–227.
- Brown, J. H. (1995) *Macroecology*, 263 pp. University of Chicago Press, Chicago.
- Brown, J. H. & Lomolino, M. V. (1998) *Biogeography*, 691 pp. Sinauer Associates, Sunderland.
- Cameron, G. N. (1971) Niche overlap and competition in woodrats. *Journal of Mammalogy*, **52**, 288–296.
- Carraway, L. N. & Verts, B. J. (1991) *Neotoma fuscipes*. *Mammalian Species*, **386**, 1–10.
- Chaney, R. W., Condit, C. & Axelrod, D. I. (1944) *Pliocene floras of California and Oregon*. Carnegie Institution Publishers no. 553.
- Chew, R. M. & Woodman, J. C. (1974) Nutritive value of three common chaparral plants for woodrats, *Neotoma fuscipes* and *Neotoma lepida*. *Bulletin of the Southern California Academy of Sciences*, **73**, 115–116.
- Cranford, J. A. (1977) Home range and habitat utilization by *Neotoma fuscipes* as determined by radiotelemetry. *Journal of Mammalogy*, **58**, 165–172.
- Escherich, P. C. (1981) Social biology of the bushy-tailed woodrat, *Neotoma cinerea*. *University of California Publications in Zoology*, **110**, 1–132.
- Fumagalli, L., Pope, L. C., Taberlet, P. & Moritz, C. (1997) Versatile primers for the amplification of the mitochondrial DNA control region in marsupials. *Molecular Ecology*, **6**, 1199–1201.
- Graham, R. W. (1986) Response of mammalian communities to environmental changes during the late Quaternary. *Community ecology* (ed. by J. Diamond and T. J. Case), pp. 300–313. Harper & Row, New York.
- Hall, E. R. (1981) *The mammals of North America*, 767 pp. John Wiley & Sons, New York.
- Harris, A. H. (1985) *Late Pleistocene vertebrate paleoecology of the west*, 293 pp. University of Texas Press, Austin.

- Hayes, J. P. & Harrison, R. G. (1992) Variation in mitochondrial DNA and the biogeographic history of the woodrat (*Neotoma*) in the Eastern United States. *Systematic Biology*, **41**, 331–334.
- Hayes, J. P. & Richmond, M. E. (1993) Clinal variation and morphology of woodrats (*Neotoma*) of the eastern United States. *Journal of Mammalogy* **74**, 204–216.
- Hooper, E. T. (1938) Geographical variation in woodrats of the species *Neotoma fuscipes*. *University of California Publications in Zoology*, **42**, 213–246.
- Jefferson, G. T. (1991) A catalogue of late Quaternary vertebrates from California: Part two, mammals. *Natural History Museum of Los Angeles County Technical Report*, **7**, 1–129.
- Kelly, P. A. (1989) Population ecology and social organization of dusky-footed woodrats, *Neotoma fuscipes*. PhD Dissertation, University of California Berkeley, p. 191.
- Kelly, P. A. (1991) The dusky-footed woodrat. *Oaks of California* (ed. by B. M. Pavlik, P. C. Muick, S. Johnson and M. Popper), 90 pp. Cachuma Press, Los Olivos.
- Kimura, M. (1980) A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, **16**, 111–120.
- King, T. J. Jr (1976) Late Pleistocene-early Holocene history of coniferous woodland in the Lucerne Valley region, Mojave Desert, California. *Great Basin Naturalist*, **36**, 227–238.
- Kozakiewicz, M. (1993) Habitat isolation and ecological barriers — the effect on small mammal populations and communities. *Acta Theriologica*, **38**, 1–30.
- Leskinen, P. H. (1975) Occurrence of oaks in late Pleistocene vegetation in the Mojave desert of Nevada. *Madroño*, **23**, 234–235.
- Little, E. L. (1971) *Atlas of US trees, Vol. 1: conifers and important hardwoods* US Department of Agriculture Miscellaneous Publications. no. 1146, Washington D. C.
- Linsdale, J. M. & Tevis, L. P. (1951) *The dusky-footed woodrat*, 664 pp. University of California Press, Berkeley.
- Lyons-Weiler, J. & Milinkovitch, M. C. (1997) A phylogenetic approach to the problem of differential lineage sorting. *Molecular Biology and Evolution*, **14**, 968–975.
- Lomolino, M. V., Brown, J. H. & Davis, R. (1989) Island biogeography of montane forest mammals in the American Southwest. *Ecology*, **70**, 180–194.
- Medrano, J. F., Aasen, E. & Sharrow, L. (1990) DNA extraction from nucleated red blood cells. *Biotechniques*, **8**, 43.
- Munz, P. A. (1974) *A flora of southern California*, 1086 pp. University of California Press, Berkeley.
- Murray, K. F. & Barnes, A. M. (1969) Distribution and habitat of the woodrat, *Neotoma fuscipes*, in northeastern California. *Journal of Mammalogy*, **50**, 43–48.
- Patterson, B. D. (1982) Pleistocene vicariance, montane islands, and the evolutionary divergence of some chipmunks (genus *Eutamias*). *Journal of Mammalogy*, **63**, 378–398.
- Riddle, B. R. & Honeycutt, R. L. (1990) Historical biogeography in North-American arid regions; an approach using mitochondrial-dna phylogeny in grasshopper mice (genus *Onychomys*). *Evolution*, **44**, 1–15.
- Rowlands, P., Johnson, H., Ritter, E. & Endo, A. (1982) The Mojave desert. *Reference handbook of the deserts of North America* (ed. by G. L. Bender), pp. 103–162. Greenwood Press, Westport.
- Smith, F. A. (1996) Den characteristics and survivorship of woodrats (*Neotoma lepida*) in the eastern Mojave Desert. *Southwestern Naturalist*, **40**, 366–372.
- Smith, F. A. (1997) *Neotoma cinerea*. *Mammalian Species*, **564**, 1–8.
- Smith, M. H. (1965) Dispersal capacity of the dusky-footed woodrat, *Neotoma fuscipes*. *American Midland Naturalist*, **74**, 457–463.
- Spaulding, W. G. (1977) Late Quaternary vegetational change in the Sheep Range, southern Nevada. *Journal of Ariz Academy of Science*, **12**, 3–8.
- Spaulding, W. G. (1981) *The late Quaternary vegetation of a southern Nevada mountain range*. PhD Thesis, University of Arizona, Tucson.
- Spaulding, W. G. (1990) Vegetational and climate development of the Mojave Desert: the last glacial maximum to the present. *Packrat mddens: the last 40,000 years of biotic change* (ed. by J. L. Betancourt, T. R. Van Devender and P. S. Martin), pp. 166–199. University of Arizona Press, Tucson.
- Spevak, T. A. (1983) Population changes in a Mediterranean scrub rodent assembly during drought. *Southwestern Naturalist*, **28**, 47–52.
- Stein, B. A. & Warrick, S. F. (1979) *Granite mountains resource survey*. University of California at Santa Cruz Environmental Field Program. Publication no. 1.
- Sullivan, R. M. (1994) Microevolutionary differentiation and biogeographic structure among coniferous forest populations of the Mexican woodrat (*Neotoma mexicana*) in the American Southwest: a test of the vicariance hypothesis. *Journal of Biogeography*, **21**, 369–389.
- Swofford, D. L. (1993) *Phylogenetic analysis using parsimony (PAUP)*, Version 3.1.1. Illinois Natural History Survey, Champaign.
- Thomas, W. K., Paabo, S., Villablanca, F. X. & Wilson, A. C. (1990) Spatial and temporal continuity of kangaroo rat populations shown by sequencing mitochondrial DNA from museum specimens. *Journal of Molecular Evolution*, **31**, 101–112.
- Van Devender, T. R. (1977) Holocene woodlands in the Southwestern deserts. *Science*, **198**, 189–192.
- Van Devender, T. R. & Spaulding, W. G. (1979) The development of vegetation and climate in the southwestern United States. *Science* **204**, 701–710.
- Vasek, F. C. & Barbour, M. G. (1977) Mojave desert scrub vegetation. *Terrestrial vegetation of California* (ed. by M. G. Barbour and J. Major), pp. 835–868. John Wiley and Sons, New York.
- Vasek, F. C. & Thorne, R. F. (1977) Transmontane coniferous vegetation. *Terrestrial vegetation of California* (ed. by M. G. Barbour and J. Major), pp. 797–834. John Wiley and Sons, New York.
- Vaughan, T. A. & Czaplewski, N. J. (1985) Reproduction in Stephens' woodrat: the wages of folivory. *Journal of Mammalogy*, **66**, 429–443.
- Wells, P. V. & Berger, R. (1967) Late Pleistocene history of coniferous woodland in the Mohave Desert. *Science*, **155**, 1640–1647.
- Wells, P. V. & Jorgensen, C. D. (1964) Pleistocene wood rat middens and climatic change in the Mohave desert: a record of juniper woodlands. *Science*, **143**, 1171–1174.
- Wright, S. (1978) *Evolution and the genetics of populations: variability within and among natural populations*, 580 pp. University of Chicago Press, Chicago.

BIOSKETCHES

Felisa Smith is a Research Associate Professor at the University of New Mexico. Her research investigates the ecological and evolutionary effects of temperature perturbations on mammals, particularly in terms of body size response to temperature fluctuations during the late Quaternary. Felisa is the leader of a National Center for Ecological Analysis and Synthesis (NCEAS) working group on 'Body size in ecology and paleoecology: linking pattern and process across spatial, temporal and taxonomic scales'.

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Karla Menendez is a Ph. D. student at the University of New Mexico studying the causes of breast cancer. Her undergraduate honors thesis investigated morphological variation in *Neotoma fuscipes*.

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Appendix I Woodrats used in morphological and genetic analyses.

Location	County	Elev. (m)	Museum or Collector ID*	Sex	Year of Capture	Length (mm)				Body Mass (g)	Pregn. Lact. or scrotal?
						Body	Tail	Hind foot	Ear		
<i>N. lepida lepida</i>											
Cottonwood Basin	San Bernardino	1300	MDM 185	F	1998	140	135	34	28	125	yes
Cottonwood Basin	San Bernardino	1300	MDM 329	F	1998	145	135	30	27	115	yes
Cottonwood Basin	San Bernardino	1300	MDM 336	F	1998	145	140	29	28	121	yes
Cottonwood Basin	San Bernardino	1300	MDM 343	F	1998	135	135	29	26	105	no
Cottonwood Wash	San Bernardino	1354	LACM 75701	F	1976	169	112	28	29		
N. Granite Pass	San Bernardino	1046	LACM 75700	F	1976	163	130	27	31		
Cottonwood Basin	San Bernardino	1300	MDM 320	M	1998	145	130	30	27	140	yes
Cottonwood Basin	San Bernardino	1300	MDM 321	M	1998	160	135	30	27	140	yes
Cottonwood Basin	San Bernardino	1300	MDM 328	M	1998	145	130	30	27	130	yes
Cottonwood Basin	San Bernardino	1300	MDM 341	M	1998	150	135	30	30	150	yes
Cottonwood Basin	San Bernardino	1300	MDM 342	M	1998	150	140	31	30	150	yes
Cottonwood Wash	San Bernardino	1354	LACM 75703	M	1976	175	114	30	29		
Cottonwood Wash	San Bernardino	1477	LACM 75704	M	1976	190	121	29	30		
Coyote Springs	San Bernardino	985	LACM 75697	M	1976	171	130	28	30		
N. Granite Pass	San Bernardino	1046	LACM 75699	M	1976	181	125	29	31		
Arroyo Seco Rd	Monterey	300	MDM 22* AF091260	F	1997	165	145	32	30	155	yes
<i>N. fuscipes simplex</i>											
Cactus Flats	San Bernardino		MVZ 6249	F	1905	180	175	35			
Cushenberry	San Bernardino	1650	MDM 216* AF091255	F	1998	155	175	32	31	140	
Cushenberry	San Bernardino	1650	MDM 218	F	1998	170	170	35	33	155	
Doble	San Bernardino		MVZ 6204	F	1905	180	170	35			
Dry Lake	San Bernardino		MVZ 6171	F	1905	178	166	37			
Morongo Valley	San Bernardino	1169	LACM 1981	F	1930		158	35			
Morongo Valley	San Bernardino	1169	LACM 1983	F	1930	160	155	35			
Morongo Valley	San Bernardino	1169	LACM 1984	F	1930	193	112	37			
	San Bernardino		1903	F		212	198	40			
Cushenberry	San Bernardino	1650	MDM 217* AF091256	M	1998	175	180	34	34	180	
Doble	San Bernardino		MVZ 6223	M	1905	186	169	35			
Fish Creek	San Bernardino		MVZ 6206	M	1905	205	172	37			
Fish Creek	San Bernardino		MVZ 6199	M	1905		165	35			
Fish Creek	San Bernardino		MVZ 6201	M	1905		160	35			
Fish Creek	San Bernardino		MVZ 6196	M	1905	198	172	36			
Fish Creek	San Bernardino		MVZ 6220	M	1905	215	179	38			
	San Bernardino		1900	M		203	172	38			
Morongo Valley	San Bernardino	1169	LACM 1974	U	1930	172	148	36			
<i>N. fuscipes luciana</i>											
Hastings	Monterey	750	MDM 1* AF091257	F	1997	190	219	41	33	219	yes
Hastings	Monterey	750	MVZ 149742	F	1975	181	181	40	31	182	yes
Hastings	Monterey	750	MVZ 138902	F	1967	202	193	33	27	221	yes
Hastings	Monterey	750	MVZ 181499	F	1988	192	202	40	32	224	yes
Hastings	Monterey	750	MVZ 181505	F	1988	192	218	42	33	222	yes

Hastings	Monterey	750	L&T 643	F	1942	205	212	43	32	232	
Hastings	Monterey	750	L&T 645	F	1942	236	203	42	34	235	
Hastings	Monterey	750	L&T 647	F	1942	216	205	42	33	220	
Hastings	Monterey	750	L&T 650	F	1942	217	204	43	33	279	
Hastings	Monterey	750	L&T 657	F	1942	225	177	40	32	212	
Hastings	Monterey	750	L&T 664	F	1942	222	182	43	32	357	
Hastings	Monterey	750	L&T 685	F	1942	216	179	39	31	247	
Hastings	Monterey	750	L&T 694	F	1942	220	208	42	32	233	
Hastings	Monterey	750	L&T 707	F	1942	214	198	41	32	206	
Hastings	Monterey	750	L&T 708	F	1942	219	198	41	33	259	
Hastings	Monterey	750	L&T 723	F	1942	215	211	43	34	220	
Hastings	Monterey	750	L&T 727	F	1942	227	212	41	32	240	
Hastings	Monterey	750	L&T 738	F	1942	208	204	40	31	184	
Hastings	Monterey	750	L&T 741	F	1942	222	200	41	31	207	
Hastings	Monterey	750	L&T 743	F	1942	217	196	41	32	196	
Hastings	Monterey	750	L&T 619	F	1942	215	184	40	32	269	
Hastings	Monterey	750	L&T 616	F	1942	214	191	38	32	222	
Hastings	Monterey	750	L&T 577	F	1942	212	202	41	34	272	
Hastings	Monterey	750	L&T 563	F	1942	213	181	44	34	259	
Hastings	Monterey	750	L&T 96	F	1942	205	179	39	31	228	
Hastings	Monterey	750	MVZ 177489	M	1987	210	168	46	33	220	yes
Hastings	Monterey	750	MVZ 177485	M	1987	203	188	41	29	269	yes
Hastings	Monterey	750	MVZ 149745	M	1975	199	228	41	27	315	yes
Hastings	Monterey	750	MVZ 149740	M	1988	193	198	42	32	202	yes
Hastings	Monterey	750	MVZ 181502	M	1988	209	192	41	32	310	yes
Hastings	Monterey	750	L&T 646	M	1942	223	210	43	32	262	
Hastings	Monterey	750	L&T 648	M	1942	228	200	42	33	248	
Hastings	Monterey	750	L&T 651	M	1942	223	197	41	33	280	
Hastings	Monterey	750	L&T 653	M	1942	226	204	42	32	251	
Hastings	Monterey	750	L&T 663	M	1942	223	205	41	31	257	
Hastings	Monterey	750	L&T 719	M	1942	214	181	40	33	230	
Hastings	Monterey	750	L&T 720	M	1942	230	130	42	32	302	
Hastings	Monterey	750	L&T 721	M	1942	215	180	42	32	205	
Hastings	Monterey	750	L&T 724	M	1942	230	194	41	32	240	
Hastings	Monterey	750	L&T 737	M	1942	217	191	42	31	258	
Hastings	Monterey	750	L&T 744	M	1942	224	195	41	31	248	
Hastings	Monterey	750	L&T 751	M	1942	225	180	42	32	247	
Hastings	Monterey	750	L&T 621	M	1942	228	174	41	32	265	
Hastings	Monterey	750	L&T 618	M	1942	200	171	37	31	226	
Hastings	Monterey	750	L&T 615	M	1942	219	196	40	31	264	
Hastings	Monterey	750	L&T 614	M	1942	214	188	38	31	236	
Hastings	Monterey	750	L&T 578	M	1942	219	182	40	31	282	
Hastings	Monterey	750	L&T 564	M	1942	203	188	39	32	206	
Hastings	Monterey	750	L&T 555	M	1942	212	203	41	33	268	
Hastings	Monterey	750	L&T 589	M	1942	225	190	39	33	280	
Hastings	Monterey	750	JDM 12* AF091259	F	1997					237	
Hastings	Monterey	750	JLP 16817* AF091258	F	1997	217	200	40	35	262	

Appendix I continued.

Location	County	Elev. (m)	Museum or Collector ID*	Sex	Year of Capture	Length (mm)				Body Mass (g)	Pregn. Lact. or scrotal?
						Body	Tail	Hind foot	Ear		
<i>Granite Mountain Relict population</i>											
Cottonwood Wash	San Bernardino	1477	LACM 75328	F	1976	170	164	32	29		
Cottonwood Wash	San Bernardino	1480	S & K 2048	F	1990		149	31	29	97	no
Cottonwood Wash	San Bernardino	1450	MDM 182* AF091253	F	1998	160	185	32	32	175	yes
Cottonwood Wash	San Bernardino	1450	MDM 186*	F	1998	162	173	31	30	155	yes
Cottonwood Wash	San Bernardino	1450	MDM 183	F	1998	160	185	32	33	200	yes
Cottonwood Wash	San Bernardino	1450	MDM 184	F	1998	145	185	32	32	155	yes
Cottonwood Wash	San Bernardino	1450	MDM 190	F	1998	165	180	32	32	185	yes
Cottonwood Wash	San Bernardino	1477	LACM 75329	M	1976	179	176	34	32		
Cottonwood Wash	San Bernardino	1480	S & K 2050	M	1990		183	34	29	173	yes
Cottonwood Wash	San Bernardino	1480	S & K 2026	M	1990		178	33	26	130	no
Cottonwood Wash	San Bernardino	1480	S & K 2027	M	1990		163	32	29	103	no
Cottonwood Wash	San Bernardino	1450	MDM 189* AF091254	M	1998	155	175	33	32	170	yes
Cottonwood Wash	San Bernardino	1450	MDM 197	M	1998	175	180	32	31	200	yes
Cottonwood Wash	San Bernardino	1450	MDM 201	M	1998	175	180	33	31	175	yes
Cottonwood Wash	San Bernardino	1450	MDM 210	M	1998	155	185	33	33	190	yes
Cottonwood Wash	San Bernardino	1450	MDM 199	M	1998	170	185	34	32	220	yes

*Specimens used in genetic analysis (see methods); GenBank accession numbers are indicated.

¹Legend: LACM = Los Angeles County Museum, MVZ = Museum of Vertebrate Zoology, University of California Berkeley, S & K = F. A. Smith and P. A. Kelly, MDM = M. D. Matocq, L & T = Linsdale and Tevis (1951).

²These animals were caught the same night in close proximity to *N. fuscipes* at the upper head of Cottonwood Wash.