Journal of Mammalogy, 90(2):306–320, 2009

PLEISTOCENE IMPACTS ON THE PHYLOGEOGRAPHY OF THE DESERT POCKET MOUSE (*CHAETODIPUS PENICILLATUS*)

TEREZA JEZKOVA,* JEF R. JAEGER, ZANE L. MARSHALL, AND BRETT R. RIDDLE

School of Life Sciences, University of Nevada Las Vegas, 4505 South Maryland Parkway, Las Vegas, NV 89154-4004, USA (TJ, JRJ, BRR)
Public Lands Institute, University of Nevada Las Vegas, 4505 South Maryland Parkway, Las Vegas, NV 89154-2040, USA (JRJ)
Southern Nevada Water Authority, 100 City Parkway, Suite 700, Las Vegas, NV 89106, USA (ZLM)

The desert pocket mouse (*Chaetodipus penicillatus*) comprises 6 nominate subspecies that occupy warm, sandy desert-scrub habitats across the Mojave and Sonoran deserts. The most thorough morphological assessment within the species noted variable levels of distinctiveness, leading to uncertainty regarding the geographic distributions of subspecies. Subsequent genetic assessments using chromosomal, allozymic, and mitochondrial DNA (mtDNA) sequence data detected a general east–west divergence centered on the Colorado River, but few locations were included in these assessments. We investigated phylogeographic structure in *C. penicillatus* by sequencing regions of mtDNA for 220 individuals from 51 locations representing all continental subspecies. We identify 2 major monophyletic mtDNA lineages (clades) roughly centered in the Mojave and Sonoran deserts. These clades broadly overlap along the Lower Colorado River valley and adjacent desert regions across most of the range of *C. p. penicillatus*. Outside this zone of mtDNA clade overlap, Sonoran clade haplotypes occur in populations from across the range of *C. p. pricei* and extend to the northwestern edge of the Sonoran Desert within the southern range of *C. p. angustirostris*. Northern clade haplotypes occur in populations within the ranges of *C. p. sobrinus* and *C. p. stephensi* and in populations from the western Mojave Desert in the northern range of *C. p. angustirostris*. Based on rough estimates for rates of sequence evolution, divergence among the major clades appears to have occurred during the Pleistocene, but well before the latest glacial maximum. The secondary contact among the major clades appears to have some longevity, with little evidence of recent, postglacial range expansion. We develop ecological niche models (EMNs) for the major lineages of *C. penicillatus*, and project these models onto reconstructions of climatic conditions during the latest glacial maximum (LGM; 18,000–21,000 years ago). The ENMs for each clade indicate differences in predicted current geographic distributions as well as distributions during the LGM. Models for the LGM indicate broad retention of potential habitat within the area of contact among the major clades. Furthermore, the ENM for the Mojave clade in particular indicates retention of suitable habitat during the LGM in small isolated patches within northern areas, consistent with the haplotype network that supports the perspective that some populations from the Mojave clade were isolated within northern refugia during the last glacial period.

Key words: *Chaetodipus penicillatus*, desert pocket mouse, ecological niche modeling, mitochondrial DNA, Mojave Desert, phylogeography, Sonoran Desert, subspecies

The desert pocket mouse (*Chaetodipus penicillatus*) inhabits semistabilized and stabilized sandy soils and washes within warm desert-scrub of the Mojave and Sonoran deserts. As originally described (see Hafner and Hafner 1983), this species included populations found throughout the Chihuahuan Desert, but eastern populations, previously recognized as the subspecies *C. p. eremicus* and *C. p. atrodorsalis*, were subsequently elevated to species status as *C. eremicus* (Lee et al. 1996). As currently recognized (see Mantooth and Best 2005), *C. penicillatus* comprises 6 nominate subspecies (Fig. 1A); however, a thorough morphological assessment noted inconsistent levels of variability within subspecies, variable levels of distinctiveness between subspecies, and in some cases uncertainty regarding the geographic borders among subspecies (Hoffmeister and Lee 1967).

Previous genetic assessments of *C. penicillatus* from the Mojave and Sonoran deserts (Fig. 1A) based on chromosome

* *Correspondent: jezkovat@unlv.nevada.edu*

morphology (Patton 1969), allozymes (Patton et al. 1981), and mitochondrial DNA (mtDNA—Lee et al. 1996) documented a difference between populations in the west (from the deserts of southern California and the Lower Colorado River valley extending into northernmost Baja California) and those in the east (from central and southern Arizona and Sonora). Patton et al. (1981) considered the structuring among populations observed in the chromosomal and allozymic data as an east–west divergence and coincident with the morphological trends observed by Hoffmeister and Lee (1967). The western group was identified by Patton et al. (1981) as representing *C. p. angustirostris* and western populations of *C. p. penicillatus*, and the eastern group as *C. p. pricei* and eastern populations of *C. p. penicillatus*. Lee et al. (1996) considered their mtDNA assessment to be congruent with the earlier analyses and regarded the combined data from the western region as sufficient to recognize the samples as representing the subspecies *C. p. angustirostris*. However, these earlier genetic assessments were not intended as systematic analyses of all subspecies and generally included few populations from the western region and lacked samples from the northern subspecies *C. p. sobrinus* and *C. p. stephensi* (Fig. 1A).

In this study, we expanded on these earlier genetic analyses by sequencing portions of mtDNA for samples from across the species range to more thoroughly elucidate and define the geographic distributions of lineages and groups. However, interpreting the derived patterns requires an exploration of underlying causal historical and ecological processes. Presumably, habitat disruptions, contractions, and expansions resulting from climatic shifts during the Quaternary had profound impacts on the evolution of *C. penicillatus* (e.g., Lee et al. 1996; Patton et al. 1981). The current distribution of *C. penicillatus* clearly shows its association with warm-desert habitats; however, within a major portion of the species' distribution, such habitats appear to have been greatly reduced during the latest Pleistocene glacial period (Spaulding 1990; Thompson and Anderson 2000; Van Devender 1990). Paleoenvironmental reconstructions conclude that desert biomes in the Mojave Desert and across broad areas of the northeastern Sonoran Desert were mostly replaced by woodlands during the latest glacial maximum (LGM; 18,000–21,000 years ago—see figures in Betancourt et al. [1990a, 1990b]). A common perspective is that warm-desert organisms in general were extirpated from northern regions of their current ranges during glacial periods, and maintained populations at lower latitudes and elevations in isolated refugia of the Mojave and Sonoran deserts. For example, isolation of *C. penicillatus* within 2 southern desert regions during the last glacial period was hypothesized to explain the genetic differentiation between eastern and western groups (Patton 1969).

One area that appears to have consistently maintained warm-desert conditions, and presumably populations of *C. penicillatus*, is the low-elevation area around the Lower Colorado River valley and the head of the Sea of Cortez (Betancourt et al. 1990a, 1990b; Thompson and Anderson 2000), an area currently occupied by populations of *C. penicillatus*. However, macrofossils of warm-desert plants appear as components of some paleo-Mojave vegetation assemblages, and a treeless desert-scrub may have persisted during the LGM in low-elevation valleys within the northern Mojave Desert (Spaulding 1990). As envisioned, paleodesert-scrub was maintained on southwest-facing slopes and in other xeric sites within low-elevation valleys such as portions of Death Valley and the neighboring Amargosa River drainage (Spaulding 1990). The

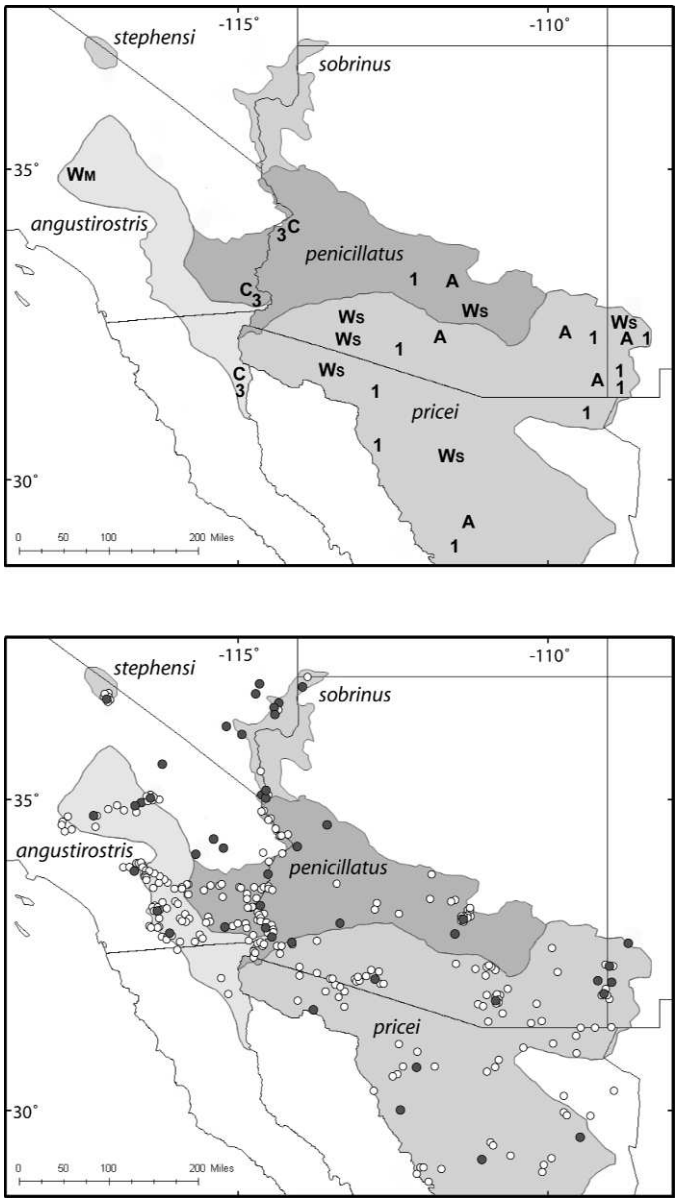

Fig. 1.—A) Depiction of nominate subspecies' distributions (shadings) for *Chaetodipus penicillatus* based on morphological patterns depicted by Hoffmeister and Lee (1967). Previous genetic results using designations as in Lee et al. (1996) are depicted as follows: W_M and W_S represent mtDNA haplotype groups based on sequence data from the Mojave and Sonoran deserts, respectively (Lee et al. 1996); 1 and 3 represent karotypic variants based on chromosome morphology (Patton 1969); A and C represent allozymic groups (Patton et al. 1981). B) Map of localities used in this study. Gray circles represent sample sites for genetic analyses; white circles represent additional sites used for ecological niche modeling.

presence of moderately divergent mtDNA lineages of several warm-desert species within the Mojave Desert has been interpreted as evidence that at least some of these organisms maintained populations within the region through the latest glacial period (e.g., Douglas et al. 2006; Jaeger et al. 2005; Murphy et al. 2006).

Herein, we inferred major mtDNA lineages through phylogenetic analysis using Bayesian inference. We further examined shallow genetic structure using median-joining networks (Bandelt et al. 1999), which better estimate evolutionary relationships among sequences when divergences are recent and ancestral haplotypes are likely to be present (Crandall and Templeton 1996). Inferences of geographic structuring among populations and subspecies were assessed using spatial analysis of molecular variance (SAMOVA—Dupanloup et al. 2002) and tests of isolation by distance (Mantel 1967). As an independent means of evaluating the veracity of the molecular-based scenarios of population histories, we explored scenarios of late Quaternary range shifting and population isolation derived from ecological niche models (ENMs). ENMs predict species distributions (Peterson 2001; Soberon and Peterson 2005) assuming that distributions are mainly determined by climate. Under an assumption of niche conservatism (e.g., Wiens and Graham 2005), these models also have been projected onto reconstructions of climatic conditions during the LGM (Carstens and Richards 2007; Martinez-Meyer et al. 2004; Waltari et al. 2007). Finally, we provide comments on the evolutionary relationships and distinction of recognized subspecies, keeping in mind the subjectivity of the subspecies category (see Cronin 2007 and citations within) and the limitations of our analyses based solely on mtDNA data (Winker et al. 2007).

Materials and Methods

Taxon sampling.—We acquired tissue samples from 220 individuals of *C. penicillatus* from 51 localities (1–15 samples/locality). Animals specifically captured for this study were either ear-clipped and released or euthanized following methods approved by the American Society of Mammalogists (Gannon et al. 2007) and the Animal Care and Use Committee, University of Nevada, Las Vegas. This sampling spanned the range of the species and represented 5 of 6 currently recognized subspecies (Fig. 1B; Appendix I); the exception was *C. p. seri*, a taxon endemic to Tiburon Island in the Sea of Cortez. We included specimens of *C. eremicus* and *C. pernix* as outgroup taxa based on previous phylogenetic studies (Alexander and Riddle 2005; Lee et al. 1996). We also sequenced samples of *C. intermedius* for use in calibration of sequence divergence.

Laboratory methods.—We isolated total genomic DNA from kidney, liver, or ear tissue following the protocol of Longmire et al. (1997) or the protocol for the DNeasy Extraction Kit (Qiagen Inc., Valencia, California). We amplified and sequenced the mitochondrial control region for all samples using the primers H00651 and a slightly modified version of L16007 (Lpen: TCC ACC TCC CAA AGC TGG TAT TC—after Kocher et al. 1989). For the phylogenetic analyses, we also amplified and sequenced a portion of the cytochrome oxidase III (*COIII*) gene for a subset of samples using primers H9323 and L8618 (Riddle 1995). Amplifications were accomplished at a 55°C annealing temperature either using Promega Taq DNA Polymerase in Storage Buffer A (Promega Corp., Madison, Wisconsin) followed by purification using GeneClean (II Kit; Qbiogene, Inc., Montreal, Quebec, Canada) or using Takara *Ex Taq* Polymerase Premix (Takara Mirus Bio, Inc., Madison, Wisconsin) followed by purification using ExoSap-IT (USB Corp., Cleveland, Ohio). We conducted double-stranded cycle sequencing using fluorescence-based chemistry (BigDye Terminator v3.1 Cycle Sequencing Kit; Applied Biosystems, Inc., Foster City, California). Unincorporated dye labels were removed by Sephadex gel separation (e.g., Sambrook et al. 1989) before electrophoresis and visualization on an ABI Prism 3130 automated sequencer (Applied Biosystems, Inc.). Sections of some sequences were confirmed using an earlier version of this chemistry (v1.1) and an ABI Prism 310. We aligned sequences using Sequencher (Gene Codes Corp., Ann Arbor, Michigan) and verified manually.

Phylogenetic analysis.—We conducted a phylogenetic analysis using Bayesian inference on a combined data set of 955 base pairs (bp) of control region and 690 bp of the *COIII* gene for 22 exemplars of *C. penicillatus* and samples of *C. eremicus* and *C. pernix*. Because the evolutionary processes for the *COIII* gene and the noncoding control region appeared to be different, we partitioned our analysis based on these regions. The *COIII* gene was further partitioned based on codon position, with the 1st and 2nd codon positions combined (because of limited variability) and the 3rd position evaluated separately. We identified best-fitting models for each data partition after evaluation using MrModeltest (version 2.2—Nylander et al. 2004) and selected the HKY model for the *COIII* 1st and 2nd codon positions (combined), GTR model for the *COIII* 3rd positions, and HKY+I+ Γ for the control region sequences.

We assessed tree topology and clade support using the program MrBayes (version 3.1.1—Ronquist and Huelsenbeck 2003), and conducted preliminary runs to assess heating values across chains, branch length priors (10, 50), and burn-in. For final analysis, runs were conducted with 4 Monte Carlo Markov chains using a heating value of 0.05 (to increase swapping among chains) and branch lengths set to 10. We derived consensus trees and posterior probabilities from 3 final runs of 10 million generations each, sampled every 100 generations, with the first 2.5 million generations (25,000 trees) discarded as burn-in after visual evaluation (Leaché and Reeder 2002).

Network analysis.—We constructed a median-joining network for 220 control region sequences of *C. penicillatus* (*COIII* data were not included in this analysis) using the program Network (version 4.200; http://www.fluxus-technology.com). The median-joining method uses a maximum parsimony approach to search for all shortest, least complex phylogenetic trees from a given data set (Bandelt et al., 1999). To construct the final network, we weighted transversions twice as high as transitions (transversion to transition ratio in the data set was 1:3), and excluded (i.e., zero weighted) nucleotide positions representing insertions/deletions and 3 hypervariable positions.

We explored various weighting and site exclusion schemes (including equal-weighting and all sites included) but we could discern little difference in the various network topologies (data not shown). After generating the median-joining network, we employed the maximum-parsimony (MP) option (Polzin and Daneschmand 2003) to remove superfluous (nonmaximally parsimonious) links from the network, allowing better visualization for interpretation.

Geographic structure analysis.—We used the program SAMOVA 1.0 (Dupanloup et al. 2002) to assess partitions among populations by maximizing the proportion of total genetic variance due to differences among geographically defined groups (i.e., F_{CT}-values). SAMOVAs were performed using 500 initial conditions and pairwise differences. We explored the partitioning of variance for predefined number of groups (K) with analysis of molecular variance (as implemented by SAMOVA), where we compared maximum indicators of differentiation (F_{CT}-values) for each K (Miller 2005). Because SAMOVA is sensitive to small sample sizes, we pooled samples from sites that were less than 30 km apart without any obvious landscape barriers (i.e., rivers or mountain ranges), and excluded sites with sample sizes smaller than particular thresholds (see ''Results''). We explored the behavior of the SAMOVA algorithm to various threshold sizes for our data (because the number of sites excluded depended on the threshold size selected), but because results were similar in all cases, we report on the most robust sample sizes for analyses (the largest threshold possible without loss of important populations). Although we explored the entire data set, final analyses were conducted separately for the major clades identified in this study.

In the presence of isolation by distance, SAMOVA may identify partitions that fall between the most widely spaced populations or sometimes in the middle of the sampling area (Dupanloup et al. 2002). Consequently, we employed Mantel tests (in the program Alleles In Space—Miller 2005) to assess correlation between population pairwise F_{ST}-values and Euclidean geographical distances, and visually confirmed evaluations by plotting haplotype diversity on geography. We evaluated mismatch distributions using Arlequin (version 3.1—Excoffier et al. 2005) to test for population expansions (Schneider and Excoffier 1999).

Ecological niche modeling.—For each major clade identified in this study, we developed ENMs under current climatic conditions and then projected these models onto reconstructions of climatic conditions during the LGM (Thompson and Anderson 2000) to predict geographical distributions of suitable habitat under these different conditions. Models were generated from occurrence records and digital environmental layers using the software package Maxent (3.0-beta—Phillips et al. 2004, 2006). We compiled species occurrence information from 3 sources: Mammal Networked Information System (MaNIS; http://manisnet.org); Collections Database of the Museum of Vertebrate Zoology, University of California (http://mvzarctos.berkeley.edu); and from collections at the School of Life Sciences, University of Nevada Las Vegas. Distinguishing *C. penicillatus* from related taxa can sometimes be difficult (e.g., Hoffmeister 1986) and we recognize that historical records are likely to contain errors. To mitigate inclusion of potentially mislabeled or misidentified samples from museum records, we included only samples with subspecific identifications and mapped all locations to exclude those that did not appear to be in habitat of *C. penicillatus* (e.g., locations within mountainous terrain). We also excluded localities that lacked geographic coordinates, lacked value for geographic uncertainty, and records with geographic uncertainty greater than 5 km; this level of uncertainty was chosen based on the average resolution of 5 km for environmental layers. The final data included the 51 occurrence records of *C. penicillatus* amassed for this study (all confirmed locations) and 283 additional museum records that met minimum criteria (Fig. 1B). These data were then partitioned by major clade for modeling (see ''Results''). We also developed ENMs for *C. eremicus* using 63 occurrence records (in databases, identified as *C. eremicus*, *C. p. eremicus*, and *C. p. atrodorsalis*) including the 4 sites sampled in this study.

For environmental layers of current climatic conditions, we used altitude and 19 bioclimatic variables from the WorldClim data set (version 1.4) with resolution of 2.5 min (Hijmans et al. 2005). Bioclimatic variables are derived from monthly temperature and precipitation climatic layers and represent biologically meaningful aspects of climate variation (Carstens and Richards 2007; Hijmans et al. 2005; Waltari et al. 2007). For LGM climate, we used data derived from general circulation model simulations using the Model for Interdisciplinary Research on Climate (MIROC), downscaled to the same resolution as the current Worldclim data (for details see Waltari et al. 2007). In Maxent, we used the default convergence threshold and 500 iterations (maximum), with 25% of occurrence records for model training (e.g., Waltari et al. 2007). The final models were visualized in ArcGIS 9.2. (ESRI, Inc., Redlands, California). From continuous probabilities that range from 0 to 100 indicating the relative suitability of the climatic conditions for the species, we set the threshold to 5% as suggested by previous studies (Pearson et al. 2007; Waltari et al. 2007). We used receiver operating characteristic for its area under the curve (AUC) value to evaluate the model performance (Fielding and Bell 1997; Raes and Steege 2007; but see Lobo et al. [2008] for critical review of this method).

Results

Phylogeographic relationships.—Examination of both the *COIII* gene and control region sequence data showed substantial genetic variation among samples of *C. penicillatus*, and between *C. penicillatus* and the samples of *C. eremicus* and *C. pernix* (Table 1). Our assessment of the combined *COIII* gene and control region sequence data using Bayesian inference strongly showed support for the presence of 2 major clades within *C. penicillatus* (Fig. 2). The phylogenetic tree failed to support *C. eremicus* as the sister taxon to *C. penicillatus* in relationship to our *C. pernix* outgroup, as has been indicated in previous studies (Alexander and Riddle 2005). This lack of outgroup resolution may have resulted from the saturation of

TABLE 1.—Sequence divergence (uncorrected *p*-distances) among major clades of *Chaetodipus penicillatus* (Mojave and Sonoran), and among *C. penicillatus*, *C. eremicus*, and *C. pernix* based on mtDNA *COIII* sequence data from exemplars and control region sequence data from the entire data set (net between group means calculated in MEGA version 3.1—Kumar et al. 2004).

Taxa	*COIII*	Control region
C. penicillatus, Mojave–Sonoran clades	0.024	0.018
C. penicillatus–*C. eremicus*	0.069	0.025
C. penicillatus Mojave Clade–*C. eremicus*	0.074	0.026
C. penicillatus Sonoran Clade–*C. eremicus*	0.077	0.032
C. penicillatus–*C. pernix*	0.075	0.041
C. eremicus–*C. pernix*	0.101	0.039

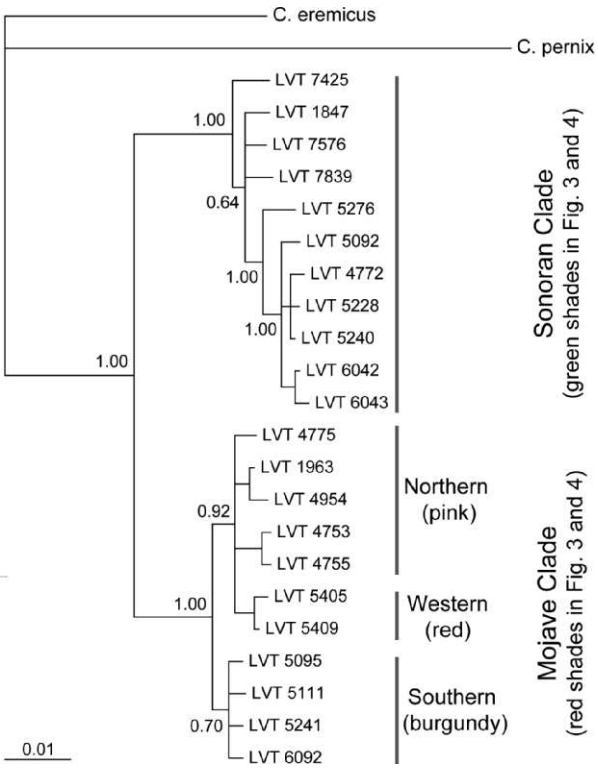

FIG. 2.—Bayesian tree for a subset of 22 samples of *Chaetodipus penicillatus* using 955 bp of the mtDNA control region and 690 bp of the *COIII* gene. *Chaetodipus eremicus* and *C. pernix* were used as outgroup taxa. The number at each node represents the Bayesian posterior probability, indicating strong support for separate ''Mojave'' and ''Sonoran'' clades. Subgroups identified in the network analysis of the control region data (Fig. 4) are indicated although the ''Northern'' and ''Western'' subgroups are not phylogenetically distinct in this analysis based on the combined mtDNA data set.

highly variable base substitution sites within the rapidly evolving mtDNA regions used in this study, masking deeper phylogenetic patterns.

Haplotypes within *C. penicillatus* were generally distributed into major northern and southern clades, but with a broad overlap within the region of the Lower Colorado River valley and western Arizona (Fig. 3). Haplotypes of the southern clade were primarily distributed in populations from the Sonoran Desert and included representation in our samples from the southern desert of California and the Lower Colorado River valley (north to the Nevada boarder; Fig. 3, locations 15 and 16). Hereafter, we referred to this southern clade as the ''Sonoran clade.'' Haplotypes of this clade occupied the range of *C. p. pricei*, southern portions of the range of *C. p. angustirostris* (Fig. 3, locations 32–35), and occurred across most of the range of *C. p. penicillatus*. In the range of *C. p. penicillatus*, however, the Sonoran clade haplotypes occurred in populations predominately mixed with northern clade haplotypes. Haplotypes of the northern clade, referred to hereafter as the ''Mojave clade,'' comprised populations throughout the Mojave Desert, and along areas on both sides of the Lower Colorado River valley extending east into the Sonoran Desert of western Arizona (to Aqua Caliente, Arizona; Fig. 3, location 31). The range of the Mojave clade corresponded to the ranges of *C. p. sobrinus*, *C. p. stephensi*, northern populations of *C. p. angustirostris* (the later; Fig. 3, locations 10–14), and *C. p. penicillatus* in the area of overlap with the Sonoran clade.

Population and geographic relationships.—The median-joining network clearly captured the broad north–south division among the data of *C. penicillatus* identified in the phylogenetic analysis (Fig. 4). We further interpreted the network as providing evidence for 3 Mojave clade subgroups. Although these subgroups were separated by a minimum of only 2 and 3 steps in the network weighting scheme (the actual numbers of nucleotide substitutions were 3 and 4 between the subgroups), these subgroups showed distinct geographic distributions (Fig. 3). The northernmost subgroup (referred to hereafter as the ''Northern Mojave subgroup'') represents haplotypes that occupied the northern reaches of desert pocket mouse range on both sides of the Colorado River in the range of *C. p. sobrinus*, and a population within Death Valley recognized as *C. p. stephensi*. A 2nd subgroup occurred in sites from the western Mojave Desert north of the San Bernardino Mountains within the northern range of *C. p. angustirostris* (referred to hereafter as the ''Western Mojave subgroup''). The 3rd subgroup (referred to hereafter as the ''Southern Mojave subgroup'') occupied the range of *C. p. penicillatus* along the Lower Colorado River valley and adjacent areas of western Arizona (within the predominately mixed populations containing Sonoran clade haplotypes).

We interpreted some support for the Mojave clade subgroups from SAMOVA (Table 2); however, the robustness of this analysis was likely limited because the threshold sample sizes had to be set low to avoid losing too many locations (reported here at $\geq$4 samples per population). Setting the number of partitions (*K*) to 2 groups separated the sites containing Southern Mojave subgroup haplotypes (in populations predominately overlapping with Sonoran clade haplotypes) from other more northern sites, whereas setting partitions to 3 groups essentially recaptured the subgroup structure we identified in the network. Setting partitions to 4 groups resulted in the Northern Mojave subgroup being partitioned, with the Death Valley site representing *C. p. stephensi* (Fig. 3, location 1) grouped with sites from the Las Vegas Valley identified as

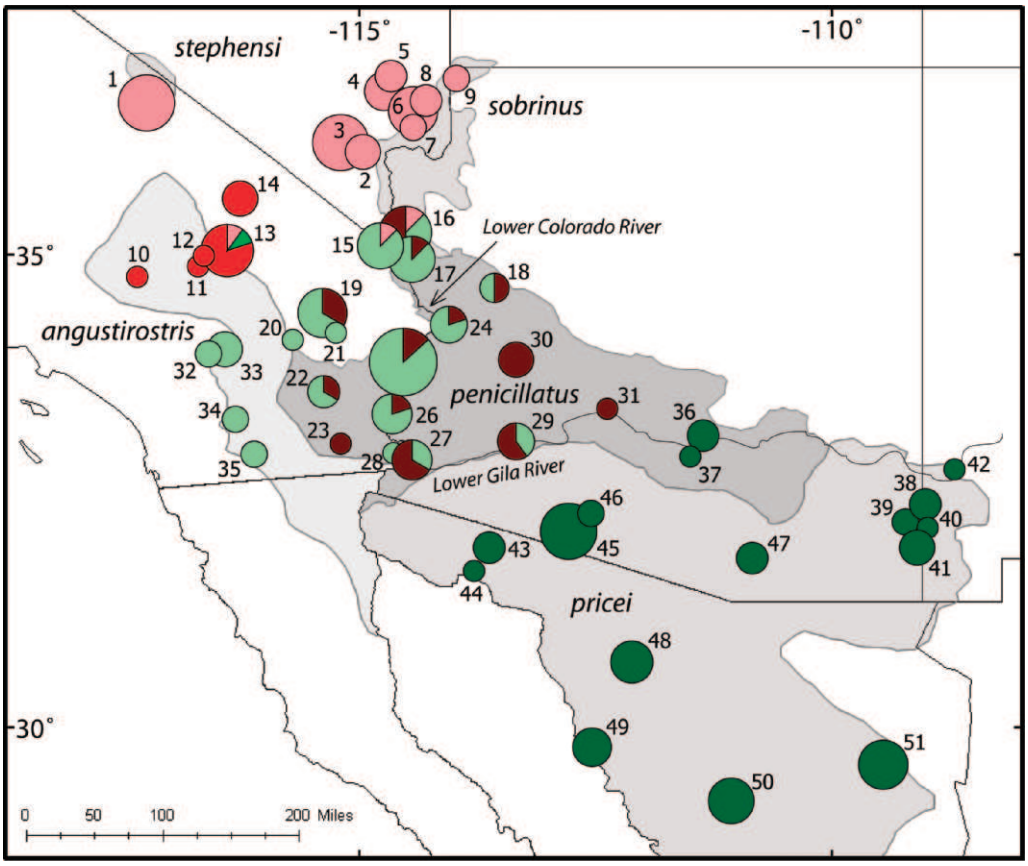

Fig. 3.—Distribution of major clades and subgroups of mtDNA control region sequences for *Chaetodipus penicillatus* identified in the median-joining network (Fig. 4). Sonoran clade indicated in green with shades indicating general north–south haplotype distributions. Mojave clade indicated in red shades with identified subgroups (burgundy = Southern Mojave subgroup, red = Western Mojave subgroup, pink = Northern Mojave subgroup). Pie graph sizes reflect sample size at each location progressing from smallest ($n = 1$) to largest ($n = 15$) and numbers identify sample localities listed in Appendix I. Background shading depicts nominate distributions of subspecies as in Fig. 1.

representing *C. p. sobrinus* (Fig. 3, locations 2 and 3) separately from those representing *C. p. sobrinus* further east (Fig. 3, locations 4 and 5, and 6–8). Although F_{CT}-values for the Mojave clade continued to rise through $K = 6$ groups (the point of asymptote for increasing F_{CT}-values is often used as a measure of the number of meaningful partitions within the data—Dupanloup et al. 2002; Miller et al. 2006), we interpreted further partitions as manifestations of the limited data and sampling peculiarities.

Unlike the Mojave clade, the network depicted the Sonoran clade as a single large cluster of haplotypes separated by 1–14 steps and containing numerous loops (Fig. 4). This cluster contained higher haplotype diversity (Table 3) than that exhibited in the Mojave clade, with many haplotypes being unique or found only at a single site. Mismatch distribution analysis of this clade indicated a good fit of the data to expectations of population expansion (as did our assessment of the Mojave clade and all the other subgroups), but this signal did not appear to us as one expected for recent population or range expansion given the relatively high haplotype and nucleotide diversity (Table 3). Although not obvious, our visual inspection of the network on geography revealed a north–south trend in the clustering of Sonoran clade haplotypes with only a single haplotype shared between populations south of the Gila River (Fig. 3, locations 36–51) and populations north of the Gila River (most of these northern populations mixed with Mojave clade haplotypes). This north–south pattern was supported by SAMOVA when the number of partitions was set to 2. In this analysis, sample size threshold was set at ≥5, and F_{CT}-values asymptote at about 4 groups. The further partitioning resulted in the identification of a site from far southeastern Mexico (Moctezuma site; Fig. 3, location 51) followed by a group represented by the combined sites from the well-known biotic transition zone between Sonoran and Chihuahuan deserts (Fig. 3, locations 38–41).

From Mantel tests, however, we detected significant correlations between pairwise F_{ST}-values and values of Euclidian geographical distances for both the Sonoran clade ($r = 0.3725$, $P < 0.01$) and Mojave clade ($r = 0.5845$, $P < 0.01$), as well as for the entire data set ($r = 0.3218$, $P < 0.01$). The possibility of isolation by distance raised an alternative interpretation for the patterns observed in the SAMOVAs, particularly that for the Sonoran clade. In that analysis, the placement of the partition for $K = 2$ appeared to represent the approximate middle of the sampling area, and with the higher values of K, the partitions identified the more geographically isolated populations, as

would be predicted for the behavior of SAMOVA in the face of isolation by distance (Manni et al. 2004).

Ecological niche models.—Examination of our phylogeographic data indicated a historical separation of *C. penicillatus* into 2 major lineages (Mojave and Sonoran clades), and given environmental differences in the habitats occupied by major segments of these 2 groups, we constructed separate ENMs for each, as well as for *C. eremicus*. We partitioned occurrence records by clade based on geographic location, but the substantial overlap of Mojave and Sonoran clade haplotypes in the range of *C. p. penicillatus* required the incorporation of 109 occurrence records from this region in the generation of models for both lineages; thus, the models generated for each lineage were not fully independent. In total, we assigned 152 records to the Mojave clade within the ranges of *C. p. sobrinus*, *C. p. stephensi*, *C. p. penicillatus*, and *C. p. angustirostris* north of the San Bernardino Mountains, and assigned 291 records to the Sonoran clade in the ranges of *C. p. pricei*, *C. p. penicillatus*, and *C. p. angustirostris* south of the San Bernardino Mountains.

All models were significantly better than random (AUC = 0.5) in receiver operating characteristic analyses (Mojave clade: training AUC = 0.998; test AUC = 0.996; Sonoran clade: training AUC = 0.995; test AUC = 0.993; *C. eremicus*: training AUC = 0.991; test AUC = 0.984). The ENMs for the current distributions of Mojave and Sonoran clades (Figs. 5A and 5C) indicated relatively continuous habitat for *C. penicillatus* across central portions of the Sonoran Desert into the Mojave Desert, but inferred differences in distributions along the fringes of these desert regions. As might be expected, the model for the Mojave clade (Fig. 5A) predicted slightly more suitable habitat and greater connectivity among habitats in northern and western regions of the Mojave Desert than that estimated for the Sonoran clade (Fig. 5C). More strikingly, the model for the Sonoran clade inferred more extensive suitable habitat in the southern and southeastern regions of the Sonoran Desert relative to that estimated for the Mojave clade.

Projections of ENMs for both major clades of *C. penicillatus* onto the paleoclimate reconstruction for the LGM predicted a general loss of suitable habitat within northern and northwestern regions relative to current distributions, particularly that within the Mojave Desert (Figs. 5B and 5D). Within northern regions, both models predicted retention of suitable habitats during the LGM within the lower deserts of California (south of the San Bernardino Mountains) and in the region of the Lower Colorado River valley. Both models also predicted retention of an isolated patch of habitat in Death Valley in the northwestern Mojave Desert. The predicted paleodistribution of suitable habitat for the Mojave clade (Fig. 5B) was markedly restricted to the areas described above and to the low-elevation areas surrounding the head of the Sea of Cortez. However, this model indicated additional small, isolated patches of suitable habitat in low-elevation valleys within the western Mojave Desert. Pluvial lakes occupied some of these valleys at times, but we interpret the model as indicating the potential retention of refugial habitat along sandy shoreline in these areas.

In contrast, the paleodistribution predicted for suitable habitat for the Sonoran clade was substantially broader and

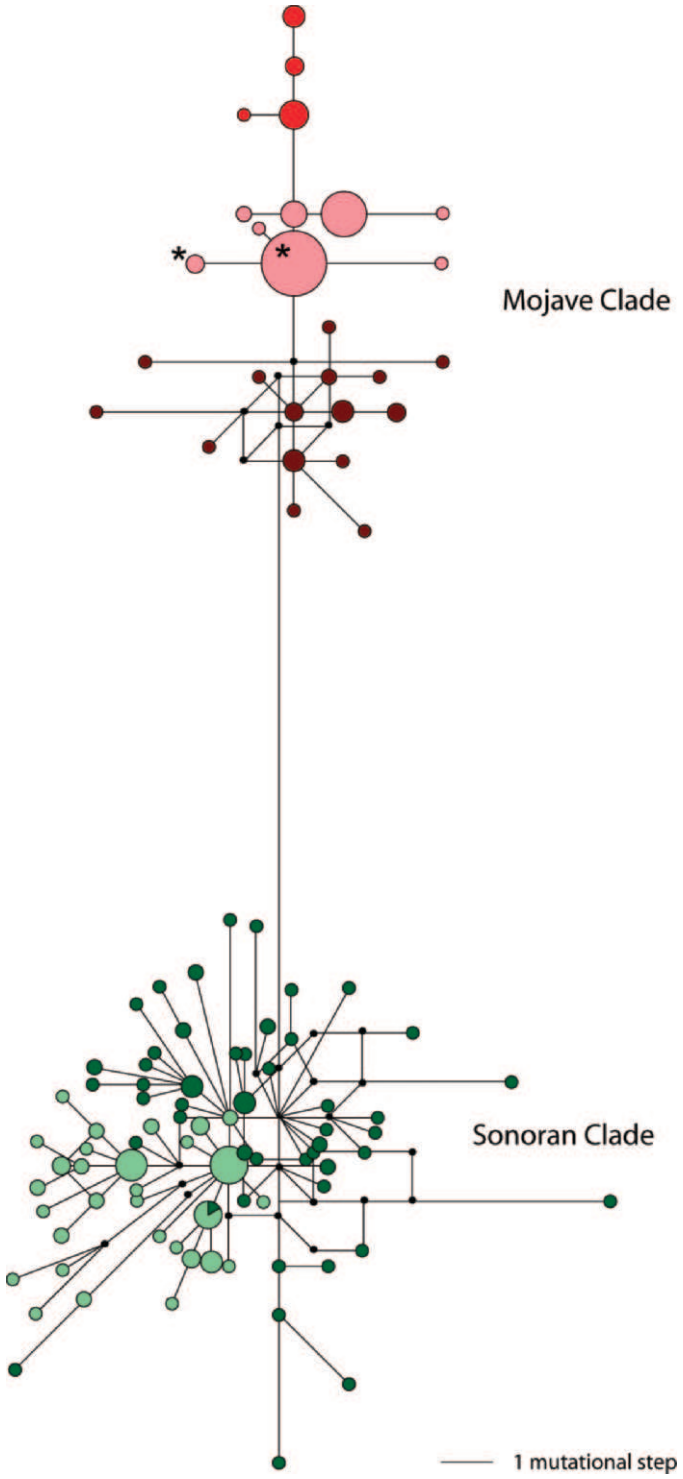

Fig. 4.—Median-joining network of mtDNA control region sequences for *Chaetodipus penicillatus*. Sonoran clade indicated in green with light green indicating northern distribution and dark green indicating southern distribution. Mojave clade indicated in red shades with identified subgroups (burgundy = Southern Mojave subgroup, red = Western Mojave subgroup, pink = Northern Mojave subgroup). The length of connection lines between haplotypes is proportional to number of mutational changes, with the shortest connection line representing 1 mutational change. Black dots indicate median vectors inferred from the data. Circle size reflects number of individuals exhibiting a given haplotype progressing from smallest ($n = 1$) to largest ($n = 8$). The asterisks represent haplotypes found in individuals from Death Valley.

TABLE 2.—Results from SAMOVAs of *Chaetodipus penicillatus* mtDNA control region sequence data by major clade and number of groups (*K*). Presented for each *K*-value are the resulting F_{CT}-value, *P*-value, and identified groups (partitions). Within the partition column, numbers (1–51) refer to sites identified in Fig. 3 and listed in Appendix I, plus signs (+) between numbers indicate sites that were pooled to increase sample sizes, and parentheses enclose groups identified in analyses. Sample size thresholds (haplotypes from each clade per population) were set at ≥4 for the Mojave clade and ≥5 for the Sonoran clade, resulting in the exclusion from analyses of sites: 9, 10, 18, 20, 22–24, 26, 28, 29, 31, 34–37, 42–44, and 47.

Clade	*K*	F_{CT}	*P*-value	Partition
Mojave	2	0.5082	0.00880	(1, 2+3, 4+5, 6+7+8, 11+12+13, 14) (16, 27, 30)
	3	0.5397	0.00000	(1, 2+3,4+5, 6+7+8) (11+12+13, 14) (16, 27, 30)
	4	0.6316	0.00098	(1, 2+3) (4+5, 6+7+8) (11+12+13, 14) (16, 27, 30)
	5	0.6799	0.00098	(1, 2+3) (4+5, 6+7+8) (11+12+13, 14) (16, 30) (27)
	6	0.7085	0.00098	(1, 2+3) (4+5, 6+7+8) (11+12+13) (14) (16, 30) (27)
Sonoran	2	0.2325	0.00098	(15, 17, 19+21, 25, 32+33) (38+39+40+41, 45+46, 48, 49, 50, 51)
	3	0.2578	0.00000	(15, 17, 19+21, 25, 32+33) (38+39+40+41, 45+46, 48, 49, 50) (51)
	4	0.2898	0.00000	(15, 17, 19+21, 25, 32+33) (38+39+40+41) (45+46, 48, 49, 50) (51)
	5	0.2892	0.00098	(15, 17, 19+21, 25) (32+33) (38+39+40+41) (45+46, 48, 49, 50) (51)

included predicted long-term retention of habitats within the low-elevation desert regions of Arizona and in Sonora and Sinaloa (Fig. 5D). This model also predicted retention of habitat in portions of the northeastern Sonoran Desert extending down into paleohabitats in the northwestern Chihuahua Desert. Unlike the Sonoran clade of *C. penicillatus*, the ENMs for *C. eremicus* predicted a substantial retraction of habitat from current distribution during the LGM, with persistence of habitat within a southern core area of the Chihuahuan Desert (Figs. 5E and 5F).

DISCUSSION

General concordance with previous morphological and genetic assessments.—As documented in previous genetic analyses (Lee et al. 1996; Patton 1969; Patton et al. 1981), populations of *C. penicillatus* (outside those now identified as *C. eremicus*—Lee et al. 1996) appear to consist of 2 main genetic lineages, although the patterns revealed in our mtDNA assessment are more complex than the generalized east–west split previously interpreted. We identify 2 divergent mtDNA lineages roughly distributed in the Mojave and Sonoran deserts, with broad geographic overlap of haplotypes within populations along areas of the Lower Colorado River valley and in western Arizona (at least 2 of the 3 western sites previously assessed for chromosomal and allozymic variation came from this zone of secondary contact). Possibly, the overlap of Mojave and Sonoran clades extends farther south along the Colorado River and into the northeastern edge (San Felipe region) of the Baja California Peninsula, but this could not be verified because of sampling limitations.

The distribution of populations showing admixture of the major mtDNA clades roughly corresponds to the distribution described by Hoffmeister and Lee (1967) for the subspecies *C. p. penicillatus* (Fig. 3). These authors noted a narrow zone of morphological character shifts between *C. p. penicillatus* and *C. p. pricei* along the Gila River in southwestern Arizona, and our 2 sample sites along the Gila River corresponded to the southern limit of Mojave clade haplotypes. Tellingly, Hoffmeister and Lee (1967:369) noted that individual morphological variation was high in *C. p. penicillatus*, and these authors speculated that ''Because of this high variability and great variation in extremes, one might think that two or more species are involved . . . .'' However, they went on to reject this perspective. Given these earlier statements on morphology, the mtDNA patterns within the range of *C. p. penicillatus* might reflect introgression of 2 distinct forms of *C. penicillatus* at the organismal level. Alternatively, increased morphological variation might reflect phenotypic adaptation to a greater mosaic of different habitats than elsewhere in the range of the species. Future analyses of nuclear DNA variation will be required to assess congruence between various gene trees and the species tree.

Hoffmeister and Lee (1967:373) also noted ''a considerable degree'' of individual morphological variation in their samples of *C. p. angustirostris*, and stated that ''The zone of contact

TABLE 3.—Diversity statistics for the 2 major clades and 4 subgroups of *Chaetodipus penicillatus* discussed in text and raggedness index from analysis of mismatch distributions. All raggedness *P*-values ≥ 0.2360.

Clade, and subgroup or region	Samples (haplotypes)	Polymorphic sites (s)	Mean no. pairwise differences	Haplotype diversity	Nucleotide diversity (× 100)	Raggedness
Mojave Clade	92 (30)	43	4.7279 ± 2.3347	0.9310 ± 0.0127	0.4977 ± 0.2722	0.00472
Northern Subgroup	49 (8)	10	1.8946 ± 1.0997	0.7993 ± 0.0307	0.2003 ± 0.1290	0.05370
Western Subgroup	16 (5)	9	1.8583 ± 1.1227	0.7500 ± 0.0775	0.1964 ± 0.1329	0.07722
Southern Subgroup	27 (17)	31	3.6011 ± 1.8853	0.9544 ± 0.0217	0.3791 ± 0.2210	0.03243
Sonoran Clade	128 (93)	83	6.8762 ± 3.2570	0.9894 ± 0.0037	0.7208 ± 0.3780	0.00971
Northern distribution	57 (31)	35	4.7450 ± 2.3552	0.9568 ± 0.0158	0. 4989 ± 0.2747	0.01109
Southern distribution	71 (62)	71	7.4266 ± 3.5126	0.9960 ± 0.0032	0. 7809 ± 0.4094	0.01006

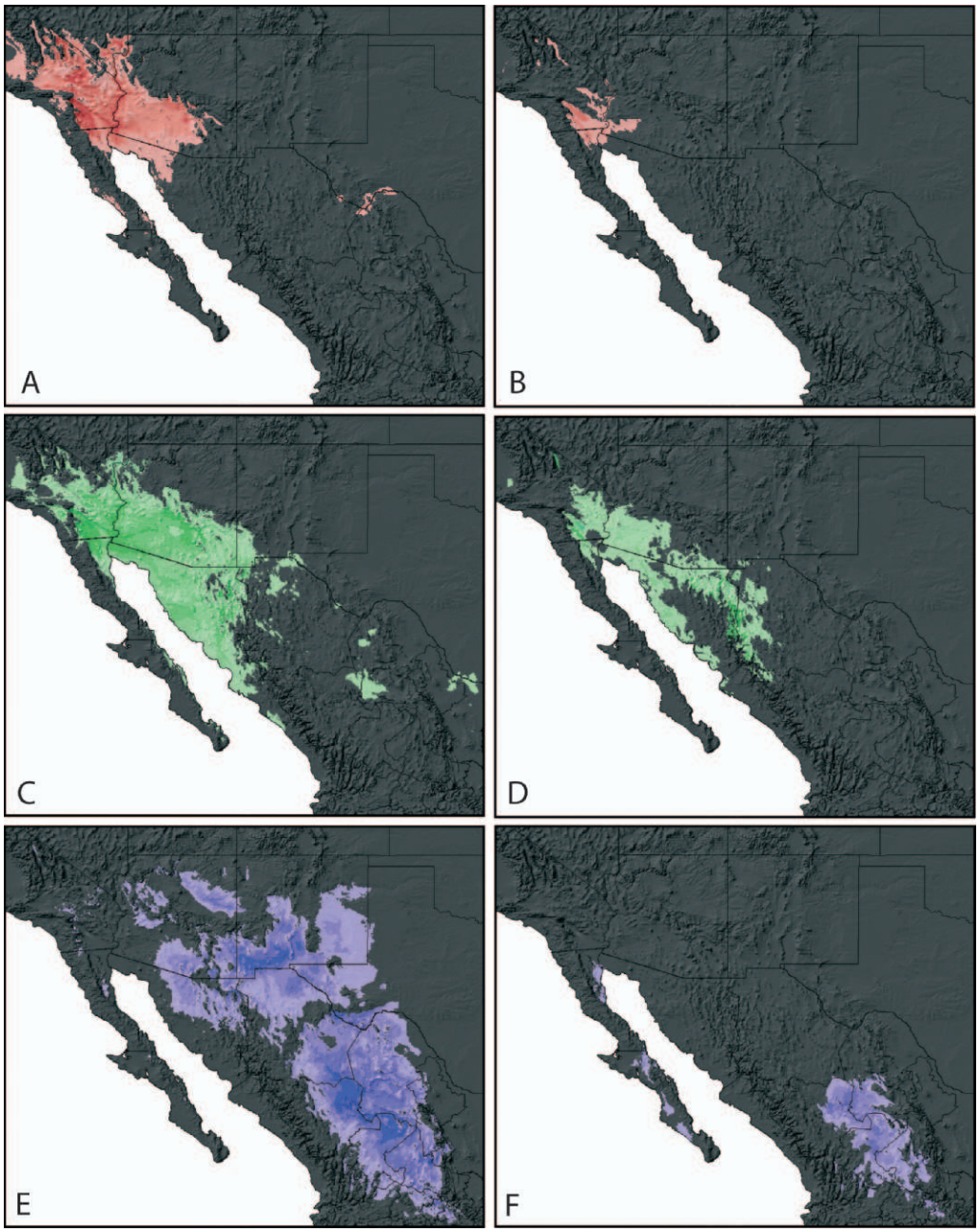

Fig. 5.—Ecological niche models based on current climatic conditions for A) Mojave clade and C) Sonoran clade of *Chaetodipus penicillatus*, and E) *C. eremicus*. Ecological niche models of latest glacial maximum climatic condition for B) Mojave clade, D) Sonoran clade, and F) *C. eremicus*. The color shading represents probability of occurrence, with darkest shading being most suitable and lightest shading least suitable. The probability of occurrence less than 5% is depicted by gray-shaded relief and represents unsuitable habitat (see Methods for modeling details).

between *angustirostris* and *penicillatus* is not sharply delimited . . . .'' As depicted by Hoffmeister and Lee (1967), the distribution of *C. p. penicillatus* extends well west of the Lower Colorado River valley (Figs. 1 and 3) into the southern deserts of California; this distribution was not represented in later range maps purportedly based on that analysis (i.e., Hall 1981; Mantooth and Best 2005). Hoffmeister and Lee (1967) expressed reservations about the boundaries they depicted between ranges for *C. p. angustirostris* and *C. p. penicillatus* and indicated that more information may result in the ''east or west'' shifting of the boundaries. Our samples from the western edge of the low desert of southern California (Fig. 3; locations 32–35) revealed only Sonoran clade haplotypes ($n = 10$), which was unlikely if these populations consisted of mixed haplotype lineages in the approximate ratio of 2 (Sonoran) to 1 (Mojavian) as observed in the mixed populations. Therefore, we suspect that our data indicate a real shift in haplotype frequencies in favor of the Sonoran clade within these more western populations.

Within the range currently depicted for the subspecies *C. p. angustirostris*, examination of our data further shows a distinct north–south separation in mtDNA haplotypes. Populations in

the south (from areas near the type location—see Hoffmeister and Lee 1967) contain Sonoran clade haplotypes (as noted above) that are not much distinguishable from those in the mixed populations within the range of *C. p. penicillatus*. However, the northern populations in the western Mojave Desert predominately contain very different and unique Mojave clade haplotypes, although a Sonoran clade haplotype was identified from this region (Fig. 3, location 13). These patterns indicate that *C. p. angustirostris* as currently recognized may comprise 2 relatively distinct populations.

The San Bernardino Mountains and a purported gap in the species distribution over much of the adjacent southeastern Mojave Desert (as depicted in range maps) may limit direct dispersal between the western Mojave Desert and areas farther south. However, the distribution gap in the Mojave Desert is not as broad as previously reported, in that we found *C. penicillatus* within the semistabilized dunes around the Cadiz and Danby dry lakes (Fig. 3, locations 19 and 21). These dry lakes are part of a series of low-elevation valleys, containing playas (i.e., Danby, Cadiz, Bristol, Troy, and Soda Lakes) that extend across the eastern Mojave Desert to the Lower Colorado River. Our ENMs (Figs. 5A and 5C) indicate potential suitable habitat throughout this region. This set of valleys has been hypothesized as a potential Pleistocene drainage extending to the Colorado River (see figure and reference in Enzel et al. [2003]), and patches of habitat in these valleys may at times provide a feasible pathway between southern populations and those in the western Mojave Desert.

Within the northern portions of the Mojave Desert, in the ranges of *C. p. sobrinus* and *C. p. stephensi*, populations contain unique Mojave clade haplotypes. We interpret this Northern Mojave subgroup as representing *C. p. sobrinus*, with the distinction that our mtDNA data provides little support for *C. p. stephensi* within the Death Valley region. Our sample from Death Valley (Fig. 3, location 1) revealed 2 unique haplotypes (3 mutational steps apart), 1 of which is only 1 bp different from 2 common haplotypes of *C. p. sobrinus*, but this limited uniqueness collapsed under the weighting scheme used in the network analysis. Hoffmeister and Lee (1967) thought that the type and paratype specimens of *C. p. stephensi* were physically most unique in being much smaller than nearby specimens of other subspecies; however, these authors also noted several later specimens of *C. p. stephensi* as not being much different from *C. p. angustirostris*. The geographical ranges of *C. p. stephensi* and *C. p. sobrinus* were thought to be isolated by unsuitable habitat. Examination of our data supports this contention in that the ENMs predict no direct east–west habitat connections between the regions, and we captured no *C. penicillatus* during limited sampling in some intervening valleys. Nevertheless, a sample site south of Death Valley (Fig. 3, location 13) contained a haplotype from the Northern Mojave subgroup potentially representing gene flow, although this relatively unique haplotype may instead represent an example of incomplete lineage sorting.

What caused the divergence between Mojave and Sonoran clades?—The Colorado River was once argued as an important barrier to dispersal within chaetodipine rodents, with the purported east–west divergence of genetic lineages interpreted by Lee et al. (1996) as preliminary evidence of the impact of this river on *C. penicillatus* (Riddle et al. 2000). However, the distribution of major mtDNA lineages in *C. penicillatus* transcends the Lower Colorado River valley, with common haplotypes of both the Sonoran and Mojave clades found on both sides of the river. Along the river, *C. penicillatus* currently occupies sandy habitats on the banks where the river follows a relatively shallow gradient and large flooding events and channel changes occurred before modern controls. Hoffmeister and Lee (1967) suggested that the lack of substantial genetic divergence in *C. penicillatus* associated with the river probably reflected a history of periodic avulsions that transferred entire patches of habitat and their associated animals across the river. Within Pleistocene times, the entire Colorado River temporarily shifted northwestward to drain into a low-lying desert area in southern California (i.e., within the Salton Trough), allowing potential biotic connections across areas of desert previously separated by the original river course (see similar discussion in Mulcahy et al. [2006] and citations within). Although the Colorado River undoubtedly limits current gene flow in many desert organisms at the population level, a history of avulsions may explain why many codistributed desert taxa show little genetic structure associated with the lower portions of this river (e.g., Lamb et al. 1992; Mulcahy et al. 2006; Smith and Patton 1980), or potentially why other groups show complex patterns of intrataxa introgression within the region (McGuire et al. 2007).

The Colorado River and Gila River basins were inundated by estuarine or lacustrine waters during the late Pliocene (called the Bouse Embayment; see recent review in Mulcahy et al. [2006]). In a recent phylogeographic assessment, Mulcahy et al. (2006) noted the ''compelling'' pattern that horned lizards (genus *Phrynosoma*) show little genetic structure associated with the Lower Colorado River but much greater genetic structure associated with the Gila River, a pattern previously attributed in *Phrynosoma platyrhinos* (desert horned lizards) to vicariance caused by the Bouse Embayment (Jones 1995). Tantalizingly, Hoffmeister and Lee (1967) found the Gila River to be a strong zone of morphological character shifts in *C. penicillatus*, indicating some type of barrier to gene flow but noting that the Gila River in its current condition was not a likely obstruction. Although our sampling in this region was coarse, the river roughly corresponds to the southern limit of Mojave clade haplotypes, as well as to the point of general divergence (north–south) in haplotypes noted within the Sonoran clade (Fig. 3).

To investigate the general timeframe for the observed divergence, we required calculation of mutation rates and therefore times to common ancestry of mtDNA haplotypes within *C. penicillatus*. However, fossils of chaetodipine species that could be used to calibrate molecular divergence are difficult to diagnose. For example, the fossil record in perognathine heteromyids does not currently differentiate between *Chaetodipus* and *Perognathus* (Wahlert 1993), which we now know to be 2 deeply divergent lineages within the subfamily Perognathinae (Alexander and Riddle 2005; Hafner et al. 2007). In the face of these limitations, we use estimates of mutation rates derived from a previous study of heteromyid rodents (Hafner

et al. 2007) to estimate a general timeframe for mtDNA coalescence within *C. penicillatus*. That previous study estimated divergence times across a mtDNA phylogeny for the Heteromyidae by employing a parametric Bayesian analysis using MULTIDIVTIME (Thorne and Kishino 2002), anchored with fossil calibration points, 1st between *Dipodomys* and *Perognathus*, and 2nd at the base of the Perognathinae. A direct extrapolation from that analysis produces a mean divergence date between *C. intermedius* and *C. eremicus* of 3.0 (2.09–4.07) million years ago (mya) and between *C. eremicus* and *C. penicillatus* of 1.3 (0.93–1.81) mya at 95% credibility (J. Hafner, Occidental College, pers. comm.).

Equating the timing of divergence between these species pairs to sequence divergence in the control region of *Chaetodipus*, we estimated a mutation rate of 2.87% (2.11–4.11%) per million years. Accordingly, the divergence between the Sonoran and Mojave clades of *C. penicillatus* corresponds to 0.63 (0.44–0.85) mya. The same assessment generates a mutation rate for the *COIII* gene of 5.7% (4.18–8.13%) per million years and a divergence estimate between the major clades dating to 0.42 (0.30–0.57) mya. We must interpret these estimates guardedly, given that the assessment was intended for family-level divergences, and given that levels of mtDNA divergence among taxa in our study were not consistent across the control region and *COIII* gene (Table 1). Nevertheless, extremely conservative, and hence unlikely, mutation rates for these genes approaching 1% between lineages per million years would be required for the timing of the divergence between major clades of *C. penicillatus* to be consistent with divergence preceding the Pleistocene. Therefore, as estimated herein, the split between the Sonoran and Mojave clades appears to have occurred during Pleistocene times, but clearly before the latest glacial cycle. Numerous scenarios are possible, but the climatic oscillations of the Pleistocene could have repeatedly fragmented habitat of *C. penicillatus* and facilitated divergence, as evidenced, for example, by distribution gaps in potential suitable paleohabitat for the Sonoran clade during the LGM (Fig. 5D).

The differences in the ENMs among the major clades are not surprising given that the distribution of each group is centered in different desert ecoregions that vary considerably in the amount and timing of precipitation and in the duration of freezing temperatures (Smith et al. 1997). Provokingly, these models implicate the potential for ecological or ecophysiological differences, or both, that may have evolved in the major lineages of *C. penicillatus* in isolation and that may now play an important role in limiting northward expansion of the Sonoran clade or southward expansion of the Mojave clade, or both. This assumes that either mtDNA alone or in linkage with nuclear genes are under selection across the ecological gradients.

Population expansion was detected for both the Sonoran and Mojave clades based on mismatch distributions (Table 3); however, these clades do not show signatures of recent (post-Pleistocene) range expansion (e.g., Hewitt 1996, 2000), either from southern populations expanding northward, as might be expected, or from northern populations expanding southward. As noted above, within northern areas, the Sonoran clade haplotypes are not generally those found farther south (with 1 exception), and haplotype and nucleotide diversity within these northern populations is relatively high. A reciprocal pattern is observed in the Mojave clade in that the Southern Mojave subgroup contains relatively high genetic diversity and is composed of unique haplotypes from those found to the north. Although the mtDNA in heteromyid rodents appears to be evolving fast relative to other rodent lineages (Spradling et al. 2001), the level of diversity observed in the northern populations of the Sonoran clade and southern populations of the Mojave clade appears to indicate some longevity within their shared range, and consequently longevity of the secondary contact zone.

Evidence of refugial populations during the latest glacial period within the Mojave Desert.—Our network provides evidence for 3 Mojave clade subgroups (Fig. 4), the levels and patterns of divergence among which indicate the potential for relatively recent population isolation within northern regions. Assuming the rates of mtDNA evolution we estimated above, the divergence among these subgroups dates to the latest glacial period, or possibly earlier. During the LGM, suitable habitat for *C. penicillatus* within the Mojave Desert appears to have become fragmented into small patches, as indicated by the paleo-ENM (Fig. 5B) and paleoreconstructions (Spaulding 1990). Small regional populations in northern areas may have become isolated from one another. Patterns of genetic structure and reduced genetic diversity within the Northern and Western Mojave subgroups support this perspective. The apparent retention of suitable habitat within the Death Valley region might have supported persistence and isolation of the Northern Mojave subgroup (Fig. 6A). The greater diversity within the Southern Mojave subgroup indicates likely persistence of populations during the latest glacial period within more continuous habitat in low-elevation areas of the northern Sonoran Desert (Fig. 6A), perhaps together in mixed populations with the more northern haplotypes from the Sonoran clade (Fig. 6B).

We interpret the mtDNA patterns in *C. penicillatus* as generally congruent with refugia hypotheses for warm-desert species within northern areas of the Mojave Desert, as suggested for the Death Valley region (e.g., Douglas et al. 2006; Murphy et al. 2006). However, we are a bit perplexed by the unexpected similarity between haplotypes from Death Valley (in the range of *C. p. stephensi*; Fig. 3, location 1) and those from the northeastern fringe of the Mojave Desert (in the range of *C. p. sobrinus*; Fig. 3, locations 2–9). This similarity may reflect gene flow among these areas (but see discussion above), postglacial expansion from one area to the other (a signal of which does not readily appear in the data), or more simply incomplete lineage sorting among these regions. We also interpret the Western Mojave subgroup (in the currently recognized northern range of *C. p. angustirostris*) as representing evidence for an additional isolated population somewhere within the western Mojave Desert (Fig. 3, locations 10–14).

Conclusions.—We show the presence of 2 monophyletic mtDNA lineages within *C. penicillatus* that are roughly centered in the Mojave and Sonoran deserts. Levels of sequence divergence and rough expectations of molecular evolution for mtDNA indicate Pleistocene origin for this divergence but

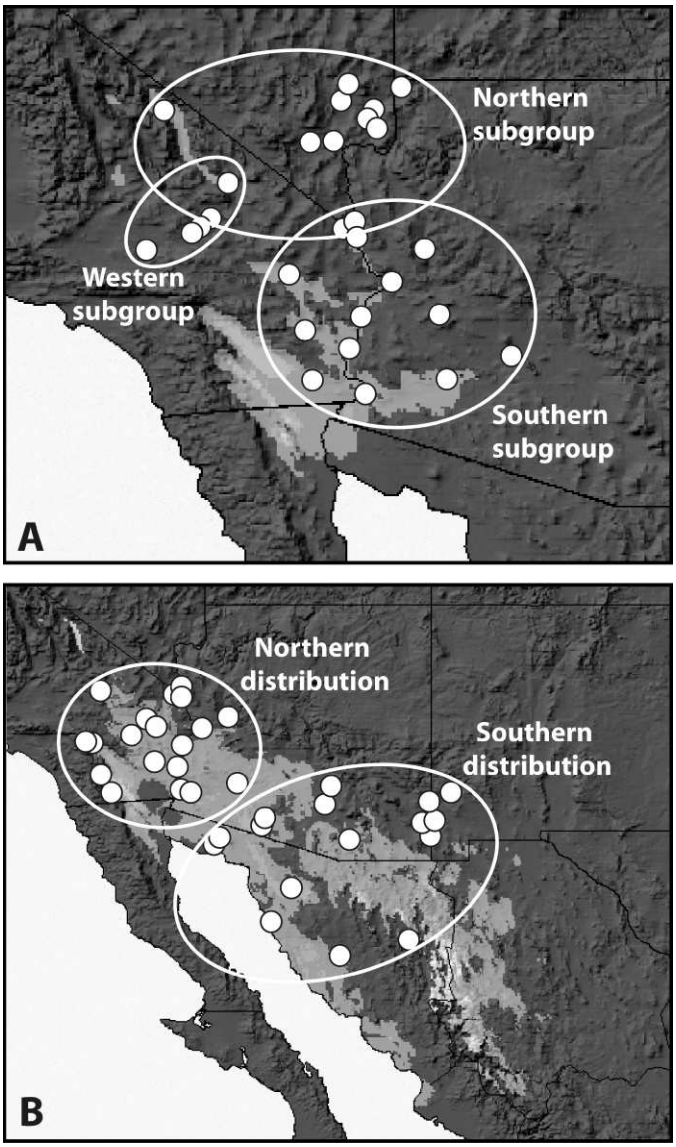

Fig. 6.—Enlarged views of ecological niche models of latest glacial maximum climatic condition for A) Mojave clade and B) Sonoran clade with overlays of sample localities where each clade was identified. The 3 subclades of the Mojave clade (A) and the 2 regional distributions of haplotypes from the Sonoran clade (B) are indicated (note that 1 haplotype was shared between the 2 regions).

before the latest glacial period. A broad area of secondary contact between these lineages exists within the range of the subspecies *C. p. penicillatus*. This mtDNA pattern, along with reservations expressed by Hoffmeister and Lee (1967) regarding their interpretations of morphological patterns, indicates that this currently recognized subspecies is likely of mixed origin derived from the secondary contact between 2 previously isolated groups. Haplotype diversity appears to indicate persistence of both major clades in the area of contact through at least the last glacial period, potentially in mixed populations. Within the northwestern Sonoran Desert within the southern range of *C. p. angustirostris* (as tentatively recognized by Hoffmeister and Lee [1967]), we found only Sonoran clade haplotypes. Sonoran clade haplotypes farther to the south likely represent the subspecies *C. p. pricei.*

Mojave clade haplotypes show some phylogeographic structure that is consistent with expectations of population isolation and divergence into refugia during the last glacial period. In these northern ranges, we identify shallow mtDNA lineages defining a group within the morphologically identified ranges of *C. p. sobrinus* and *C. p. stephensi*, and a separate group within the western Mojave within areas historically described by morphological pattern as populations of *C. p. angustirostris*. Although we find little support for differentiation between populations within the ranges of *C. p. stephensi* and *C. p. sobrinus*, interpretations based on mtDNA alone do not necessarily mean a lack of divergence caused by selection on other characters (e.g., Winker et al. 2007). In general, phylogeographic patterns within *C. penicillatus* are consistent with an interpretation that favorable habitat conditions were retained over much of the low-elevation areas of the Sonoran Desert throughout the last glacial period, and likely through earlier climatic cycles, whereas habitat in the Mojave Desert was more affected by climatic changes, resulting in greatly reduced and fragmented habitat for *C. penicillatus*.

Resumen

El Ratón de Desierto o de Abazones (*Chaetodipus penicillatus*) comprende seis subespecies que ocupan hábitats de desierto arbustivo arenoso cálido a través de los desiertos de Sonora y Mojave. La evaluación morfológica más detallada de esta especie determinó niveles variables de distinción entre especímenes, lo que conlleva a un nivel de incertidumbre acerca de la distribución geográfica de las subespecies. Las evaluaciones genéticas hechas posteriormente utilizaron datos de cromosomas, aloenzimas y secuencias de ADN mitocondrial (ADNmt) y detectaron una divergencia general de este a oeste centrada en el Río Colorado; sin embargo, estas evaluaciones incluyeron pocas localidades. Investigamos la estructura filogeográfica de *C. penicillatus* secuenciando regiones de ADNmt de 220 individuos provenientes de 51 localidades, los cuales representan todas las subespecies continentales. Identificamos dos linajes monofiléticos (clados) principales de ADNmt centrados más o menos en los desiertos de Sonora y Mojave. Estos clados se superponen a lo largo del Valle Bajo del Río Colorado y en zonas desérticas adyacentes a través de la mayor parte del alcance geográfico de *C. p. penicillatus*. Fuera de esta zona de sobre posición de los clados de ADNmt, los haplotipos del Clado de Sonora ocurren en poblaciones a través del rango de *C. p. pricei* y se extienden hasta el límite noroeste del Desierto de Sonora, dentro de la distribución sureña de *C. p. angustirostris*. Los haplotipos del Clado del Norte ocurren en poblaciones dentro de la distibución geográfica de *C. p. sobrinus* y *C. p. stephensi*, así como en poblaciones del oeste del Desierto de Mojave, en la parte norte de la distribución de *C. p. angustirostris*. Basado en las estimaciones aproximadas de tasas de evolución de secuencias, la divergencia entre los clados principales parece haber ocurrido durante el Pleistoceno, pero bastante previo al Último Máximo Glacial (UMG). El contacto secundario entre los dos clados principales parece tener mayor tiempo de existencia, con

poca evidencia de expansiones recientes post-glaciales de las distribuciones geográficas. Desarrollamos Modelos de Nicho Ecológico (MNE) para los principales linajes de *C. penicillatus* y proyectamos estos modelos sobre las reconstrucciones de las condiciones climáticas durante el UMG (18,000-21,000 años antes del presente). Los MNE para cada clado indican diferencias en las distribuciones geográficas predichas, así como en las distribuciones durante el UMG. Los modelos para el UMG indican un amplio mantenimiento del hábitat potencial dentro del área de contacto entre los clados principales. Además, el MNE para el Clado Mojave en particular, indica un mantenimiento de hábitat adecuado durante el UMG en pequeños parches aislados dentro de las áreas norteñas, un hallazgo que es consistente con la red de haplotipos que respalda la perspectiva de que algunas poblaciones del Clado de Mojave estuvieron aisladas dentro de refugios norteþos durante el último periodo glacial.

Acknowledgments

We thank L. Alexander, D. Hafner, and J. Hafner for their assistance with this research, and the numerous students, both graduate and undergraduate, for assistance with field efforts. Samples from some locations were graciously provided by the Museum of Vertebrate Zoology, University of California Berkeley, and the Los Angeles County Museum. Work in the southern Nevada region was supported by the Las Vegas Valley Water District and the Clark County Desert Conservation Program under project 1999-UNLV-102 to further implement or develop the Clark County Multiple Species Habitat Conservation Plan. Support for the broader research was provided by the National Science Foundation in grant DEB-0237166 to BRR, Experimental Program to Stimulate Competitive Research Advanced Computing in Environmental Science Program grant SFFA UCCSN 02-123 to TJ, and Major Research Instrumentation grant DBI-0421519 to the University of Nevada, Las Vegas. Spanish translation of the abstract was provided by J. González-Maya and J. Rodríguez.

Literature Cited

Alexander, L. F., and B. R. Riddle. 2005. Phylogenetics of the New World rodent family Heteromyidae. Journal of Mammalogy 86:366–379.

Bandelt, H. J., P. Forster, and A. Rohl. 1999. Median-joining networks for inferring intraspecific phylogenies. Molecular Biology and Evolution 16:37–48.

Bentancourt, J. L., T. R. Van Devender, and P. S. Martin. 1990a. Introduction. Pp. 2–11 in Packrat middens: the last 40,000 years of biotic change (J. L. Bentancourt, T. R. Van Devender, and P. S. Martin, eds.). University of Arizona Press, Tucson.

Bentancourt, J. L., T. R. Van Devender, and P. S. Martin. 1990b. Synthesis and Prospectus. Pp. 435–447 in Packrat middens: the last 40,000 years of biotic change (J. L. Bentancourt, T. R. Van Devender, and P. S. Martin, eds.). University of Arizona Press, Tucson.

Carstens, B. C., and C. L. Richards. 2007. Integrating coalescent and ecological niche modeling in comparative phylogeography. Evolution 61:1439–1454.

Crandall, K. A., and A. R. Templeton. 1996. Applications of intraspecific phylogenetics. Pp. 81–99 in New uses for new phylogenies (P. H. Harvey, A. J. Leigh Brown, J. Maynard Smith, and S. Nee, eds.). Oxford University Press, Oxford, United Kingdom.

Cronin, M. A. 2007. The Preble's meadow jumping mouse: subjective subspecies, advocacy, and management. Animal Conservation 10:159–161.

Douglas, M. E., M. R. Douglas, G. W. Schuett, and L. W. Porras. 2006. Evolution of rattlesnakes (Viperidae; *Crotalus*) in the warm deserts of western North America shaped by Neogene vicariance and Quaternary climate change. Molecular Ecology 15:3353–3374.

Dupanloup, I., S. Schneider, and L. Excoffier. 2002. A simulated annealing approach to define the genetic structure of populations. Molecular Ecology 11:2571–2581.

Enzel, Y., S. G. Wells, and N. Lancaster. 2003. Late Pleistocene lakes along the Mojave River, southeastern California. Pp. 61–77 in Paleoenvironments and paleohydrology of the Mojave and southern Great Basin deserts (Y. Enzel, S. G. Wells, and N. Lancaster, eds.). Special Paper 368, The Geological Society of America, Boulder, Colorado.

Excoffier, L., G. Laval, and S. Schneider. 2005. Arlequin (version 3.0): an integrated software package for population genetics data analysis. Evolutionary Bioinformatics Online 1:47–50.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38–49.

Gannon, W. L., R. S. Sikes, and the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809–823.

Hafner, J. C., and M. S. Hafner. 1983. Evolutionary relationships in heteromyid rodents. Great Basin Naturalist Memoirs 7:3–29.

Hafner, J. C., et al. 2007. Basal clades and molecular systematics of heteromyid rodents. Journal of Mammalogy 88:1129–1145.

Hall, E. R. 1981. The mammals of North America. Vol. I. 2nd ed. John Wiley & Sons, Inc., New York.

Hewitt, G. M. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. Biological Journal of the Linnean Society 58:247–276.

Hewitt, G. M. 2000. The genetic legacy of the Quaternary ice ages. Nature 405:907–913.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965–1978.

Hoffmeister, D. F. 1986. Mammals of Arizona. University of Arizona Press, Tucson.

Hoffmeister, D. F., and M. R. Lee. 1967. Revision of pocket mice *Perognathus penicillatus*. Journal of Mammalogy 48:361–380.

Jaeger, J. R., B. R. Riddle, and D. F. Bradford. 2005. Cryptic Neogene vicariance and Quaternary dispersal of the red-spotted toad (*Bufo punctatus*): insights on the evolution of North American warm desert biotas. Molecular Ecology 14:3033–3048.

Jones, K. B. 1995. Phylogeography of the desert horned lizard (*Phrynosoma platyrhinos*) and the short-horned lizard (*Phrynosoma douglassi*): patterns of divergence and diversity. Ph.D. dissertation, University of Nevada, Las Vegas.

Kocher, T. D., et al. 1989. Dynamics of mitochondrial-DNA evolution in animals—amplification and sequencing with conserved primers. Proceedings of the National Academy of Sciences 86:6196–6200.

Kumar, S., K. Tamura, and M. Nei. 2004. MEGA3: integrated software for molecular evolutionary genetics analysis and sequence alignment. Brief Bioinformatics 5:150–163.

Lamb, T., T. R. Jones, and J. C. Avise. 1992. Phylogeographic histories of representative herpetofauna of the southwestern

United States—mitochondrial-DNA variation in the desert iguana (*Dipsosaurus dorsalis*) and the chuckwalla (*Sauromalus obesus*). Journal of Evolutionary Biology 5:465–480.

Leaché, A. D., and T. W. Reeder. 2002. Molecular systematics of the eastern fence lizard (*Sceloporus undulatus*): a comparison of parsimony, likelihood, and Bayesian approaches. Systematic Biology 51:44–68.

Lee, T. E., B. R. Riddle, and P. L. Lee. 1996. Speciation in the desert pocket mouse (*Chaetodipus penicillatus* Woodhouse). Journal of Mammalogy 77:58–68.

Lobo, J. M., A. Jiménez-Valverde, and R. Real. 2008. AUC: a misleading measure of the performance of predictive distribution models. Global Ecology and Biogeography 17:145–151.

Longmire, J. L., M. Maltbie, and R. J. Baker. 1997. Use of lysis buffer in DNA isolation and its implication for museum collections. Occasional Papers, The Museum, Texas Tech University 163:1–3.

Manni, F., E. Guerard, and E. Heyer. 2004. Geographic patterns of (genetic, morphologic, linguistic) variation: how barriers can be detected by using Monmonier's algorithm. Human Biology 76: 173–190.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research 27:209–220.

Mantooth, S. L., and T. L. Best. 2005. *Chaetodipus penicillatus*. Mammalian Species 767:1–7.

Martinez-Meyer, E., A. T. Peterson, and W. W. Hargrove. 2004. Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. Global Ecology and Biogeography 13:305–314.

McGuire, J. A., et al. 2007. Mitochondrial introgression and incomplete lineage sorting through space and time: phylogenetics of crotaphytid lizards. Evolution 61:2879–2897.

Miller, M. P. 2005. Alleles In Space (AIS): computer software for the joint analysis of interindividual spatial and genetic information. Journal of Heredity 96:722–724.

Miller, M. P., M. R. Bellinger, E. D. Forsman, and S. M. Haig. 2006. Effects of historical climate change, habitat connectivity, and vicariance on genetic structure and diversity across the range of the red tree vole (*Phenacomys longicaudus*) in the Pacific Northwestern United States. Molecular Ecology 15:145–159.

Mulcahy, D. G., A. W. Spaulding, J. R. Mendelson III, and E. D. Brodie, Jr. 2006. Phylogeography of the flat-tailed horned lizard (*Phrynosoma mcallii*) and systematics of the *P. mcallii–platyrhinos* mtDNA complex. Molecular Ecology 15:1807–1826.

Murphy, R. W., T. L. Trepanier, and D. J. Morafka. 2006. Conservation genetics, evolution and distinct population segments of the Mojave fringe-toed lizard, *Uma scoparia*. Journal of Arid Environments 67:226–247.

Nylander, J. A. A., F. Ronquist, J. P. Huelsenbeck, and J. L. Nieves-Aldrey. 2004. Bayesian phylogenetic analysis of combined data. Systematic Biology 53:47–67.

Patton, J. L. 1969. Karyotypic variation in the pocket mouse, *Perognathus penicillatus* Woodhouse (Rodentia–Heteromyidae). Caryologia 22:351–358.

Patton, J. L., S. W. Sherwood, and S. Y. Yang. 1981. Biochemical systematics of chaetodipine pocket mice, genus *Perognathus*. Journal of Mammalogy 62:477–492.

Pearson, R. G., C. Raxworthy, M. Nakamura, and A. T. Peterson. 2007. Predicting species' distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography 34:102–117.

Peterson, A. T. 2001. Predicting species' geographic distributions based on ecological niche modeling. Condor 103:599–605.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190:231–259.

Phillips, S. J., M. Dudík, and R. E. Schapire. 2004. A maximum entropy approach to species distribution modeling. Pp. 655–662 in Proceedings of the Twenty-First International Conference on Machine Learning. Association for Computing Machinery, New York.

Polzin, T., and S. V. Daneschmand. 2003. On Steiner trees and minimum spanning trees in hypergraphs. Operations Research Letters 31:12–20.

Raes, N., and H. Ter Steege. 2007. A null-model for significance testing of presence-only species distribution models. Ecography 30:727–736.

Riddle, B. R. 1995. Molecular biogeography in the pocket mice (*Perognathus* and *Chaetodipus*) and grasshopper mice (*Onychomys*): the late Cenozoic development of a North American aridlands rodent guild. Journal of Mammalogy 76:283–301.

Riddle, B. R., D. J. Hafner, and L. F. Alexander. 2000. Comparative phylogeography of Bailey's pocket mouse (*Chaetodipus baileyi*) and *Peromyscus eremicus* species group: historical vicariance of the Baja California Peninsular Desert. Molecular Phylogenetics and Evolution 17:161–172.

Ronquist, F., and J. P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572–1574.

Sambrook, J., E. F. Fritsch, and T. Maniatis. 1989. Molecular cloning: a laboratory manual. Cold Spring Harbor Laboratory Press, Plainview, New York.

Schneider, S., and L. Excoffier. 1999. Estimation of demographic parameters from the distribution of pairwise differences when the mutation rates vary among sites: application to human mitochondrial DNA. Genetics 152:1079–1089.

Smith, S. D., R. K. Monson, and J. E. Anderson. 1997. Physiological ecology of North American desert plants. Springer-Verlag, Berlin, Germany.

Smith, M. F., and J. L. Patton. 1980. Relationships of pocket gopher (*Thomomys bottae*) populations of the Lower Colorado River. Journal of Mammalogy 61:681–696.

Soberon, J., and A. T. Peterson. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. Biodiversity Informatics 2:1–10.

Spaulding, W. G. 1990. Vegetational and climatic development of the Mojave Desert: the last glacial maximum to the present. Pp. 166–199 in Packrat middens: the last 40,000 years of biotic change (J. L. Bentancourt, T. R. Van Devender, and P. S. Martin, eds.). University of Arizona Press, Tucson.

Spradling, T. A., M. S. Hafner, and J. W. Demastes. 2001. Differences in rate of cytochrome-I evolution among species of rodents. Journal of Mammalogy 82:65–80.

Thompson, R. S., and K. H. Anderson. 2000. Biomes of western North America at 18,000, 6000 and 0 14C yr BP reconstructed from pollen and packrat midden data. Journal of Biogeography 27: 555–584.

Thorne, J. L., and H. Kishino. 2002. Divergence time and evolutionary rate estimation with multilocus data. Systematic Biology 51:689–702.

Van Devender, T. R. 1990. Late Quaternary vegetation and climate of the Chihuahuan Desert, United States and Mexico. Pp. 104–133 in Packrat middens: the last 40,000 years of biotic change (J. L.

Bentancourt, T. R. Van Devender, and P. S. Martin, eds.). University of Arizona Press, Tucson.

WAHLERT, J. H. 1993. The fossil record. Pp. 1–37 in Biology of the Heteromyidae (H. H. Genoways and J. H. Brown, eds.). Special Publication 10, The American Society of Mammalogists.

WALTARI, E., R. J. HIJMANS, A. T. PETERSON, A. S. NYA'RI, S. L. PERKINS, AND R. P. GURALNICK. 2007. Locating Pleistocene refugia: comparing phylogeographic and ecological niche model predictions. PLoS ONE 2:e563.

WIENS, J. J., AND C. H. GRAHAM. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology and Systematics 36:519–539.

WINKER, K., D. A. ROCQUE, T. M. BRAILE, AND C. L. PRUETT. 2007. Vainly beating the air: species-concept debates need not impede progress in science or conservation. Ornithological Monographs 63:30–44.

Submitted 28 July 2008. Accepted 6 September 2008.

Associate Editor was Carey Krajewski.

APPENDIX I

Descriptions of sample locations in the United States and Mexico by species. Samples for *Chaetodipus penicillatus* are listed by location identification number (referencing Fig. 3). Provided are locality descriptions, latitude and longitude, and sample identification in parentheses (LVT = School of Life Sciences, University of Nevada, Las Vegas; MVZ = Museum of Vertebrate Zoology, University of California Berkeley; LACM = Los Angeles County Museum). Sequences are referenced in GenBank under accession numbers AB456272–AB456529.

Chaetodipus penicillatus.—1) Inyo Co., California, Stovepipe Wells, 36.60967, −117.10654 (LVT 6032–6041); 2) Clark Co., Nevada, Las Vegas Wash, 2 miles W Lake Las Vegas, 36.09831, −114.95085 (LVT 4951–4954); 3) Clark Co., Nevada, Las Vegas Valley Water District, North Well, 36.17313, −115.19120 (LVT 1963–1972); 4) Clark Co., Nevada, 2.8 miles NW Moapa Valley National Wildlife Refuge, 36.72140, −114.72628 (LVT 4939–4943); 5) Clark Co., Nevada, 15 miles NNW Glendale, 36.88433, −114.66861 (LVT 4818–4820); 6) Clark Co., Nevada, Overton Wildlife Management Area, 36.51838, −114.42219 (LVT 4753-4756, 4767-4770); 7) Clark Co., Nevada, Lake Mead National Recreation Area, Bluepoint Spring, 36.38956, −114.42457 (LVT 4955, 4956); 8) Clark Co., Nevada, 8 miles NE Overton, Virgin River, 36.57481, −114.33834 (LVT 4813–4815); 9) Mohave Co., Arizona, 5 miles SW Littlefield, 36.84390, −113.97818 (LVT 1961, 1962); 10) San Bernardino Co., California, Silver Lakes, 34.74000, −117.33670 (LVT 8716); 11) San Bernardino Co., California, 3 miles SSW Harvard, Mohave River, 34.92250, −116.64503 (LVT 7815); 12) San Bernardino Co., California, 30 miles E Barstow on I15, 34.97546, −116.56729 (LVT 1304); 13) San Bernardino Co., California, 1 miles W, 0.5 miles N Afton, 35.04261, −116.39960 (LVT 5409-5418); 14) San Bernardino Co., California, 1 miles W, 16 miles S Tecopa, 35.60436, −116.23364 (LVT 5405-5408); 15) Clark Co., Nevada, 6 miles S of Laughlin, 35.08958, −114.63502 (LVT 4772-4781); 16) Mohave Co., Arizona, 1 miles S, 1 miles W Bullhead City, 35.13411, −114.56955 (LVT 5231–5238); 17) Mohave Co., Arizona, 2 miles N, 3 miles E Fort Mohave, 35.05666, −114.60070 (LVT 5223–5230); 18) Mohave Co., Arizona, Wikieup, 34.63463, −113.56629 (LVT 5239, 5240); 19) San Bernardino Co., California, SE of Cadiz, 34.37897, −115.36884 (LVT 6092-6100); 20) San Bernardino Co., California, 29 Palms, 34.10910, −115.68350 (LVT 8810); 21) San Bernardino Co., Sablon, Danby Dry Lake, 34.25993, −115.27249 (LVT 6030); 22) Riverside Co., California, Corn Spring, 33.62610, −115.32470 (LACM 96076, 96077, 96085); 23) Imperial Co., California, 1.5 miles S, 6.5 miles W Glamis, 32.98574, −115.18065 (LVT 1016); 24) La Paz Co., Arizona, Bill Williams National Wildlife Refuge, 34.27863, −114.05312 (LVT 5273, 5274, 5276–5278); 25) Riverside Co., California, N of Blythe–Colorado River, 33.83539, −114.53333 (LVT 6042–6050, 6085–6090); 26) La Paz Co., Arizona, 2.5 miles S Cibola, 33.31527, −114.65040 (LVT 5092–5096); 27) Yuma Co., Arizona, E shore Mittry Lake, 32.82722, −114.44911 (LVT 5241–5245, 5802); 28) Imperial Co., California, 1 miles W, 0.75 S Imperial Dam, 32.87817, −114.49792 (LVT 5803); 29) Yuma Co., Arizona, 2 miles N Agua Caliente, 33.01321, −113.32639 (LVT 5107–5111); 30) Maricopa Co., Arizona, 15 miles S Salome, 33.64476, −113.42178 (LVT 9243–9245, 9248); 31) Maricopa Co., Arizona, 4 miles S, 3 miles W Rainbow Valley, 33.18883, −112.40089 (LVT 9233); 32) Riverside Co., California, 1 miles S, 2.5 miles E Cabazon, 33.90694, −116.71703 (LVT 5402, 5403); 33) Riverside Co., California, 0.5 miles S, 0.8 miles W Whitewater, 33.91660, −116.65252 (MVZ 206781–206784); 34) San Diego Co., California, 0.5 miles S, 4.5 miles E Borrego Springs, 33.24525, −116.30155 (LVT 1021, 1022); 35) San Diego Co., California, 5 miles W, 2 miles S Canebrake, 32.88195, −116.11328 (LVT 5216, 5217); 36) Pinal Co., Arizona, 6 miles N, 6 miles E Florence, 33.07160, −111.35000 (LVT 7838–7840); 37) Pinal Co., Arizona, 7 miles S, 1 miles E La Palma, 32.83530, −111.49790 (LVT 7723); 38) Hidalgo Co., New Mexico, 8 miles N, 2 miles W Steins, Doubtful Canyon, 32.34667, −109.02900 (LVT 6160), 8 miles N, 1 miles W Steins, 32.34667, −109.01583 (LVT 6164), 8 miles N Steins, 32.34556, −109.00111 (LVT 6175); 39) Cochise Co., Arizona, 10 miles S San Simon, 32.13023, −109.22175 (LVT 1846, 1847, 1849); 40) Hidalgo Co., New Mexico, 1 miles E Granite Gap, Hwy 80, 32.08860, −108.97310 (LVT 0387); 41) Cochise Co., Arizona, 4 miles SE Portal, 31.89361, −109.08667 (LVT 6133–6136); 42) Grant Co., New Mexico, 2.3 miles N, 1.5 miles E Redrock, 32.72111, −108.71056 (LVT 6127); 43) Sonora, Tanque de Los Papagos, Pinacate, 31.91752, −113.60520 (MVZ 200851–200853); 44) Sonora, 27 miles NW Puerto Penasco, 31.62417, −113.78369 (LVT 0609); 45) Pima Co., Arizona, Organ Pipe Cactus National Monument, 32.14446, −112.78016 (LVT 0393, 0396), 0.5 miles N Organ Pipe Cactus National Monument, 32.14446, −112.78016 (LVT 0411, 0412, 0414–0419); 46) Pima Co., Arizona, 2 miles S Why, 32.24381, −112.75935 (LVT 9222, 9223); 47) Pima Co., Arizona, 5 miles S, 7 miles E Continental, 31.78222, −110.85083 (LVT 5816, 5819), 5 miles S, 6.5 miles E Continental, 31.78389, −110.85861 (LVT 5830); 48) Sonora, 2 miles E Caborca, Cerro Cañedo, 30.69139, −112.13417 (LVT 7568, 7569, 7576–7579); 49) Sonora, 1.5 km E Puerto de la Libertad, 29.88464, −112.64839 (LVT 1236–1240); 50) Sonora, 10 km W Carbon, 29.20000, −111.06667 (LVT 3909–3913, 3917, 3918); 51) Sonora, 21 miles SE Moctezuma, 29.58806, −109.49444 (LVT 7423–7426, 7434–7437).

Chaetodipus eremicus.—Chihuahua, 38 km N Jiminez, 29.19831, −100.79358 (LVT 1201); Cohuila, 1 miles SE Hundido, 26.05284, −101.94655 (LVT 1161); Durango, 5 miles SW Lerdo, 23.89875, −104.62851 (LVT 1133); San Luis, 3 miles S Matehuala, 22.69881, −101.78498 (LVT 1187, 1188).

Chaetodipus pernix.—Sonora, 15 km S Navajoa, 26.96463, −109.43330 (LVT 1294); Sonora, 4 km N Navojoa, 27.13333, −107.43330 (LVT 1262); Sonora, 1 miles E Guasimas, 29.89611, −110.57583 (LVT 6742).

Chaetodipus intermedius.—Pinal Co., Arizona, Picacho State Park, 32.62259, −111.41057 (LVT 0327, 0337).