

Conservation genetics, evolution and distinct population segments of the Mojave fringe-toed lizard, *Uma scoparia*

R.W. Murphy^{a,*}, T.L. Trépanier^a, D.J. Morafka^{b,✉}

^aCentre for Biodiversity and Conservation Biology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ont., Canada M5S 2C6

^bDepartment of Herpetology, California Academy of Sciences, Golden Gate Park, San Francisco, CA, USA

Available online 14 November 2006

Abstract

Mojave fringe-toed lizards, *Uma scoparia*, occur only on desert sand dunes and associated mosaics of small sand ramps. Consequently, the distribution is naturally discontinuous and geographically complex. Many populations are vulnerable to local extirpation, and some are now gone. We synthesized genealogical and paleoecological data to explain the geographic relationships among populations of *U. scoparia* based on mitochondrial DNA sequence data. The species appears to have arisen from a common ancestor with *U. notata* by a vicariance event, associated with the formation and development of the Lower Colorado River. Within *U. scoparia*, two major maternal lineages are associated with the development of river drainage systems. The northern lineage is from the Amargosa River. The southerly lineage includes the Mojave River basin, Bristol Trough, Clark's Pass, and Colorado River sand transport systems. The northernmost lineage of *U. scoparia*, isolated in the vicinity of Plio-Pleistocene Lake Tecopa, has the greatest amount of DNA sequence divergence. The southern populations exhibit little local genetic differentiation. A small population near Red Pass Lake contains haplotypes from both the northern and southern lineages. We define two distinct population segments (DPSs), one associated with the Amargosa River lineage, and the other with Red Pass Dune.

© 2006 Published by Elsevier Ltd.

Keywords: Mojave desert; Sonoran desert; Biogeography; Genogeography; Phylogeography; MtDNA

*Corresponding author. Tel.: +1 416 586 8099; fax: +1 516 586 5553.

E-mail address: drbob@zoo.utoronto.ca (R.W. Murphy).

✉Deceased.

1. Introduction

Lizards can serve as model organisms in evolutionary studies and be used as flagship species for conservation. They form an important part of the ecosystem, be they large herbivores or fossorial, legless species. The genealogical history of lizards can also be used in the reconstruction of geographic history, especially when their distribution is highly restricted to specific habitats. For example, all species of fringe-toed lizards of the genus *Uma* are associated with paleo-lakes and drainage systems (Norris, 1958; Trépanier and Murphy, 2001). The history of these lizards could reveal much about the development of the hydrologic systems of arid North America. Charismatic *Uma* also have particular adaptations for dune habitats (Pough, 1969; Carothers, 1986). And fringe-toed lizards serve as flagships for the conservation of some dune systems in the American South-west and Mexico.

The Mojave fringe-toed lizard, *Uma scoparia*, is a small heliothermic phrynosomatid and an obligate dune-dweller. It is the northernmost species of *Uma*, ranging in California from extreme southern Inyo County through most of San Bernardino County, barely into the north-eastern corner of Los Angeles County, and southward and eastward through the eastern half of Riverside County to the vicinity of Blythe (Jennings and Hayes, 1994) (Fig. 1). This species also occurs near Parker, La Paz County, Arizona (Elvin, 1960).

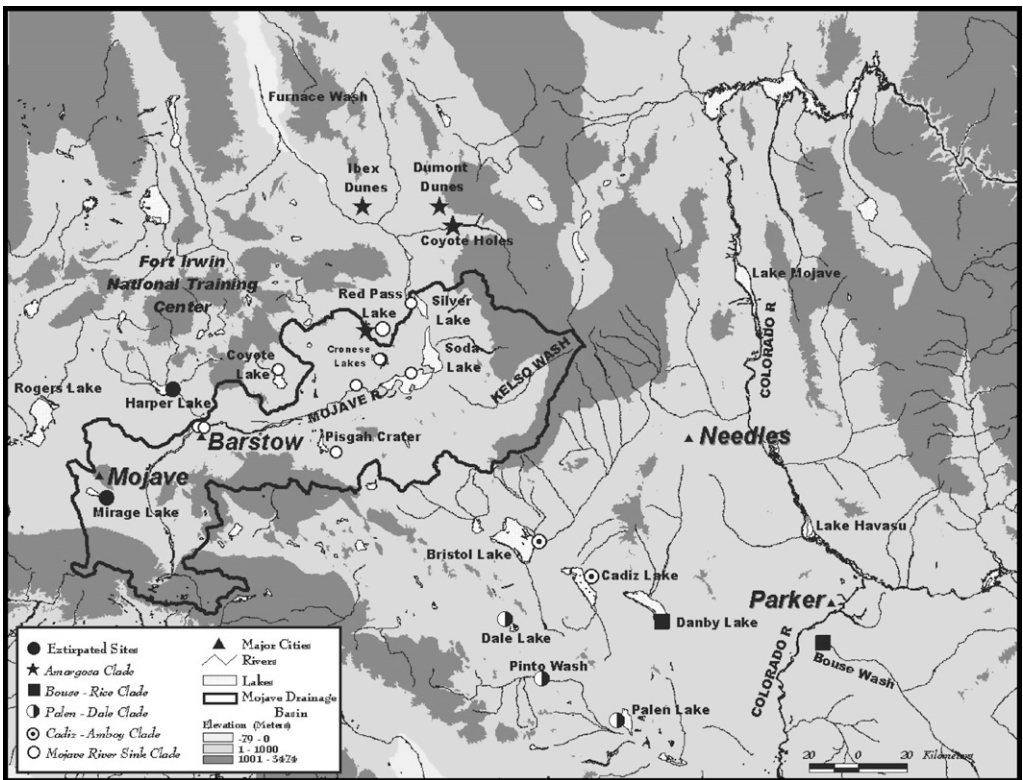


Fig. 1. Distribution of *Uma scoparia* in relation to the modern hydrology of the Mojave Desert and sample sites.

Its common name is a misnomer. About one-third of its distribution occurs in the Lower Colorado River Valley Subdivision of the Sonoran Desert (Brown, 1994; Welsh, Jr., 1994; Ricketts et al., 1999). Within the southern Mojave Desert, the species is confined to the lowest (<600 m) valleys. The Mojave and Colorado ecosystems are both in the Lower Sonoran Life Zone.

The distribution of *U. scoparia* is fragmented because of its obligate habitat specificity to loose sand, even though it is widespread geographically across the Mojave and northern Colorado deserts (Norris, 1958; Pough, 1969). Many local populations of *U. scoparia* are quite small with some having perhaps fewer than 500 adults. Small patches of sand cannot support large populations of lizards. Thus, the species is considered rare according to geographic distribution, population size and habitat specificity (Rabinowitz et al., 1986). Because habitat fragmentation leaves the species vulnerable to local extirpations, the California Department of Fish and Game listed *U. scoparia* as a “species of special concern” (Jennings and Hayes, 1994).

U. scoparia has the potential to yield insights into the development of the Mojave and Sonoran deserts, i.e. the changing Mojave Desert. Because fringe-toed lizards only occur on loose sand and the dunes are isolated from one another, the species’ history will reflect the development of eolian systems. In addition, the restricted habitat potentially allows the identification of conservation units, whether narrowly resolved genetically (Moritz, 1994), more broadly defined as distinct population segments (DPSs) under the provisions of the United States (US) Endangered Species Act (ESA; US Department of the Interior and US Department of Commerce, 1996), or defined by other criteria (e.g. Crandall et al., 2000). Patterns of recent population extirpation have the potential to predict future patterns of anthropogenic habitat modification on dune systems and, thus, focus conservation efforts.

The genealogical relationships of Mojave fringe-toed lizards can be used to test previous biogeographic hypotheses. For example, both Norris (1958) and Banta (1962) proposed that *U. scoparia* was displaced from its northern localities during times of Pleistocene glaciation. They postulated that the lizards reinvaded the northern parts of the Mojave Desert from a refuge in the Bristol Trough after the last pluvial stage. Similarly, because potential habitat for *U. scoparia* occurs north of its current distribution, Norris (1958) believed that these lizards had not reached the northern limits of their potential range.

The scenarios of Norris (1958) and Banta (1962) make several predictions. If a northward dispersal occurred, then little genetic substructuring is expected throughout the range of the Mojave fringe-toed lizard, especially in the northern parts of the distribution. Panmixia and dispersion during pluvial periods would result in greater genetic homogeneity. Dispersal to new areas could be accompanied by reduced genetic variation owing to founder effects. However, if *U. scoparia* persisted in the northern parts of their range throughout the pluvial episode, then substantial genetic variation is expected and a far more interesting question emerges: like the desert tortoise (*Gopherus agassizii*, Morafka and Berry, 2002), is *U. scoparia* adapted to desert environments or exapted (preadapted *sensu* Arnold, 1994)?

Our study assesses genetic diversity and the genealogical history of female lineages of *U. scoparia*. If the dispersal of male fringe-toed lizards parallels that of the females, then a genealogy would also represent the history of the dunes and dune systems. The current analysis provides updates and takes precedence over the study of Trépanier (2002), in which an error in data analysis precludes repeatability. We also examine the need for conservation of some populations of *U. scoparia*.

2. Materials and methods

2.1. Samples

We surveyed populations of Mojave fringe-toed lizards from known or possible sites in Inyo, Kern, Los Angeles, San Bernardino and Riverside counties, California, and La Paz County, Arizona, to obtain tissue samples (Table 1 and Fig. 1). Sampled sites included all major dune systems occupied by *U. scoparia* as verified by collections in the California Academy of Sciences and Los Angeles County Museum of Natural History. Lizards from very small (<100 m diameter), isolated dunes, including some new records, were also sampled. Where they exist, geographic names conform to the US Board on Geographic Names (<http://geonames.usgs.gov/>), but synonyms are also provided in parentheses.

Two- or three-person teams walked at least 1 km during the morning (0800–1100 h PST) when we found the lizards to be most abundant. Occasional afternoon sampling spanned 1500–1930 h, usually in ambient air temperatures greater than 28 °C. Most sampling occurred from mid-March through June.

Lizards were captured by hand or by using fishing poles with nooses. Tail tips were removed at a natural intravertebral break point and placed into a plastic vial filled with 95% ethanol. Tail stumps were treated with a 10% solution of povidone iodine (betadine solution) before the lizards were released at their exact site of capture within 15 min of initial capture. Voucher specimens for most samples were not collected because multiple specimens already existed in museum collections and the species' identity was unambiguous. However, vouchers were taken to document new sites. Voucher specimens were euthanized with an overdose of sodium pentobarbital following approved animal use protocols, fixed in 95% ethanol or 10% formalin, and subsequently maintained in 70% ethanol in the herpetological collections of the Royal Ontario Museum.

2.2. Molecular techniques

The primary outgroup included the other six species of *Uma*. The zebra-tailed lizard, *Callisaurus draconoides*, and the greater earless lizard, *Cophosaurus texanus*, served as secondary outgroup species. Mitochondrial DNA sequences for the outgroup taxa were obtained from GenBank (ATPase 6 = 301958, 301960, 301934, 301914, 301937, 301924, 301922; cytochrome *b* = AF301962, 301970, 301972, 301982, 301985, 302006, 302008), with the exception of *U. exsul* and *U. paraphygas*, which were sampled and sequenced for this study.

Standard chloroform phenol-extraction methods (Hillis et al., 1996; Palumbi, 1996) were used to extract DNA from tail muscle. The mitochondrial gene ATPase 6 was amplified and sequenced using the primers 5' ATG AAC CTA AGC TTC TTC GAC CAA TT 3' (O. Haddrath, pers. comm.) and 5' ACG AAT ACG TAG GCT TGG ATT A 3' (Fu et al., 1999). Amplification and sequencing of cytochrome *b* (cyt *b*) were performed using three primers flanking this region, including 5' CCA TCC AAC ATC TCA GCA TGA TGA AA 3' (Kocher et al., 1989), 5' TGA GGA CAA ATA TCC TTC TGA GG 3' (Fu, 2000) and 5' GTC TTC AGT TTT TGG TTT ACA AGA C 3' (Kocher et al., 1989). Double stranded DNA was prepared for sequencing using the polymerase chain reaction (PCR) (Saiki et al., 1988). Amplification and sequencing protocols follow (Trépanier and Murphy, 2001). The PCR product from the ATPase 6 mtDNA gene was a 599 bp fragment. The PCR product

Table 1

Alphabetical listing of localities, sample sizes, and voucher specimens of sequenced tissue samples of the Mojave fringe-toed lizard, *Uma scoparia*, and outgroup taxa

Species	Locality	Sample size	Voucher
<i>Uma scoparia</i>	Afton Canyon, San Bernardino Co., CA	2	ROM 32201–2
	Amboy Crater, San Bernardino Co., CA	2	ROM 32109–10
	Bitter Spring, San Bernardino Co., CA	5	ROM 00095–99
	Barstow, San Bernardino Co., CA	5	ROM 32095–9
	Bouse Wash, La Paz Co., AZ	3	ROM 2885–7
	Cadiz Lake, San Bernardino Co., CA	3	ROM 3425–7
	Coyote Holes, Kingston Wash, San Bernardino Co., CA	3	ROM 32102–4
	Coyote Lake, San Bernardino Co., CA	5	ROM 3436–40
	Cronese Lakes, San Bernardino Co., CA	3	ROM 32205–7
	Dale Lake, San Bernardino Co., CA	6	ROM 19850–5
	Dumont Dunes, San Bernardino Co., CA	7	ROM 19840–6
	Ibex Dunes, San Bernardino Co., CA	5	ROM 32090–4
	Kelso Dune, San Bernardino Co., CA	1	ROM 4115
	Lenwood Wash, San Bernardino Co., CA	5	ROM 3428–32
	Palen Lake, Riverside Co., CA	5	ROM 3418–22
	Pinto Wash, Riverside Co., CA	2	ROM 32107–8
	Pisgah Crater, San Bernardino Co., CA	3	ROM 4735, 3434–5
	Razor Road, San Bernardino Co., CA	2	ROM 32203–4
	Red Pass Dune, San Bernardino Co., CA	7	ROM 1531, 3406–11
	Rice Valley, Riverside Co., CA	3	ROM 19847–9
Silver Lake, San Bernardino Co., CA	2	ROM 32105–6	
<i>Uma inornata</i>	Coachella Valley Preserve, Riverside Co., CA	1	CAP 1723
<i>Uma notata</i>	Algodones Dunes, Imperial Co., CA	1	ROM 19877
	N of San Felipe, Baja California, MX	1	ROM 34082
<i>Uma rufopunctata</i>	San Pedro, Sonora, MX	1	ROM 4276
Unnamed <i>Uma</i>	Mohawk Dunes, Yuma Co., AZ	1	ROM 19893
<i>Uma exsul</i>	4 km E Gabino Vazques (Bilbao), Coahuila, MX	1	ROM 32001
<i>Uma paraphygas</i>	7 km N of Laboratorio del Desierto, Instituto de Ecología, Chihuahua, MX	1	ROM 32045
<i>Callisaurus draconoides</i>	Ocotillo, Imperial County, CA	1	ROM 4146
<i>Cophosaurus texanus</i>	15 km N of Laboratorio del Desierto, Instituto de Ecología, Chihuahua, MX	1	ROM 32048

ROM = Royal Ontario Museum Field Collection Tag Numbers; CAP = tissue collections of Christopher A. Phillips (Illinois Natural History Survey).

from *cyt b* was a 1031 bp fragment that included a portion of the tRNA^{Thr}. Sequences were aligned by eye using BioEdit (Hall, 1997–1999). Transition and transversion ratios were calculated separately for each gene using the number of events averaged across all most parsimonious reconstructions in MacClade 4.06 (Maddison and Maddison, 2003).

2.3. Cladistic analysis

Lizards with identical haplotypes were merged using MacClade. Thus, all individuals in the analyses had different haplotypes. The two genes were combined for analysis. Unweighted maximum parsimony (MP) analyses were performed on potentially informative characters only using PAUP* 4.0b10 (Swofford, 2002). Most parsimonious trees (MPTs) were obtained by employing the heuristic tree search algorithm with random addition of individuals, 10 000 replicates while retaining minimal trees only and holding two trees at each replicate, tree bisection-reconnection branch swapping with steepest descent, and collapsed zero length branches. All multi-state characters were evaluated as nonadditive (unordered). Nodal consistency was assessed using nonparametric bootstrap proportions (Felsenstein, 1985) and decay analysis (Bremer, 1994) performed in PAUP*, and nodal Templeton tests (nTT) (Lee, 2000) performed in AutoCladeS (Eriksson, 2001). Bootstrapping (BS) used to assess relative support for the nodes was accomplished using 10 000 random pseudo-replicates of the data, with each pseudo-replicate being replicated twice. The selection of preferred trees from among the MPTs used sequential deletions of secondary outgroups taxa (Murphy et al., 2002). Cladogenic patterns were evaluated for their correspondence to geological and hydrological history of the Mojave and Sonoran deserts. The history of the deserts was taken from contributions in Enzel et al. (2003) and literature cited therein.

Bayesian inference was also used to infer matriarchal history (Huelsenbeck and Ronquist, 2001; Buckley et al., 2002; Nylander et al., 2004; Ronquist, 2004) and to obtain nodal support values. The program MrModeltest v2.2 (Nylander, 2004) was used to select an evolutionary model that best fit the data using the Akaike Information Criterion (Akaike, 1974, 1979). Hierarchical likelihood ratio tests (Goldman, 1993) were implemented by comparing log-likelihood scores of 56 models of molecular evolution. Bayesian inference, conducted using MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001), was initiated with random starting trees. Six Markov chains were used, and the dataset was run for 3×10^6 generations. Trees were sampled every 100 generations. Two independent analyses with different starting trees were run to avoid being trapped on local optima, and the fluctuating values of likelihood were graphically monitored (Huelsenbeck and Bollback, 2001). We plotted the log-likelihood scores of sample points against generation time and determined that stationarity was achieved when the log-likelihood values of the sample points reached a stable equilibrium value (Huelsenbeck and Ronquist, 2001). The analysis was a priori required to achieve a split frequency standard deviation of ≤ 0.005 . After discarding 25% of the sampled trees as burnin, the remaining trees were used to generate a 50% majority rule consensus tree.

3. Results

3.1. Field surveys

We sampled 79 *U. scoparia* from 21 localities (Table 1 and Fig. 1). We did not find *U. scoparia* at the following four sites where they are documented to have occurred: Harper Lake (Harper's Dry Lake) and El Mirage (Dry) Lake in San Bernardino Co., and on Lovejoy Buttes (Wilsona Butte) and Piute Butte (Peck's Butte) in Los Angeles Co. The lizards appear to be extirpated from these sites.

3.2. Genetic variability

We sequenced 1630 nucleotide sites from two protein-encoding mitochondrial genes: ATPase 6 (599 bp) and *cyt b* (1031 bp). Among the total of 79 individuals in the ingroup, 52 unique haplotypes were detected. No indels were observed. For ATPase 6, 26 (4.3%) of the 599 nucleotide sites were variable with 14 (2.3%) being potentially phylogenetically informative. For *cyt b*, 88 (8.5%) of the 1031 sites were variable, with 52 (5.0%) being potentially phylogenetically informative. Combined, 114 sites (7.0%) were variable, with 66 (4.0%) potentially phylogenetically informative (ingroup only). Among the variable sites, most changes were silent. Nucleotide substitutions at 20 positions resulted in the coding of alternative amino acids, seven of which occurred in ATPase 6 and 13 in *cyt b*. Sequence divergence among sand dunes ranged from 0.00% to 2.94%. The greatest divergence occurred between the northernmost samples from Coyote Holes, Dumont and Ibex dunes and samples associated with the Mojave River drainage system. Within dune systems, haplotypes differed from 0.00% to 2.15% of resolved sequences. The highest level of divergence occurred at a small patch of sand (<2 km²) on the north-west side of Soda Mountain overlooking Red Pass Lake (= Red Pass Playa). Hereafter, we refer to this site as Red Pass Dune. The second highest divergence within a dune was observed at Cadiz Lake, which had 0.69% divergence. Most of the potentially informative sites also varied among the outgroup taxa. All sequences were deposited in GenBank (ATPase 6 = AF301954, AF384873, AF384898, AF389552; *cyt b* = AF302002, AF384921, AF384954, AF389627).

3.3. Trees

A MP analysis of the combined sequence data was based on 352 potentially informative characters, including variable nucleotide sites in all outgroup taxa. Rooted with the secondary outgroups, the analysis resulted in 451 MPTs, each with a length of 745 steps (CI=0.60, RI=0.80). A strict consensus tree revealed three nodes for the ingroup: a basal node that united dunes associated with the Amargosa River, and two more terminal nodes, one being Red Pass Dune, and the other uniting Dumont and Ibex dunes and Coyote Holes. More southerly populations associated with the Mojave River formed a completely unresolved bush.

Because most of the potentially informative nucleotide sites within *U. scoparia* also varied within the secondary outgroups, we re-defined the outgroup to include the other species of *Uma* only. *C. draconoides* and *C. texanus* were deleted from the next analysis. After excluding the secondary outgroup, a 271 potentially informative nucleotide positions were found. Reevaluation of these data found 886 MPTs (length=453 steps, CI=0.67, RI=0.87). Three additional nodes which united all individuals from Bouse Wash, and most individuals within Dale and Cronese lakes were found.

Many of the potentially informative sites in the ingroup also varied in *U. paraphygas* and *U. exsul*, the more distant species of *Uma*. Thus, a final analysis used the *U. notata* group to root the network for *U. scoparia* because they are sister groups (Wilgenbusch and de Queiroz, 2000; Trépanier and Murphy, 2001). The final evaluation, based on 166 potentially informative characters, obtained 253 MPTs (length=305 steps, CI=0.72, RI=0.92). The cladistic analyses using the other species of *Uma* as the outgroup consistently recovered six lineages, three of which contained multiple haplotypes (Fig. 2)

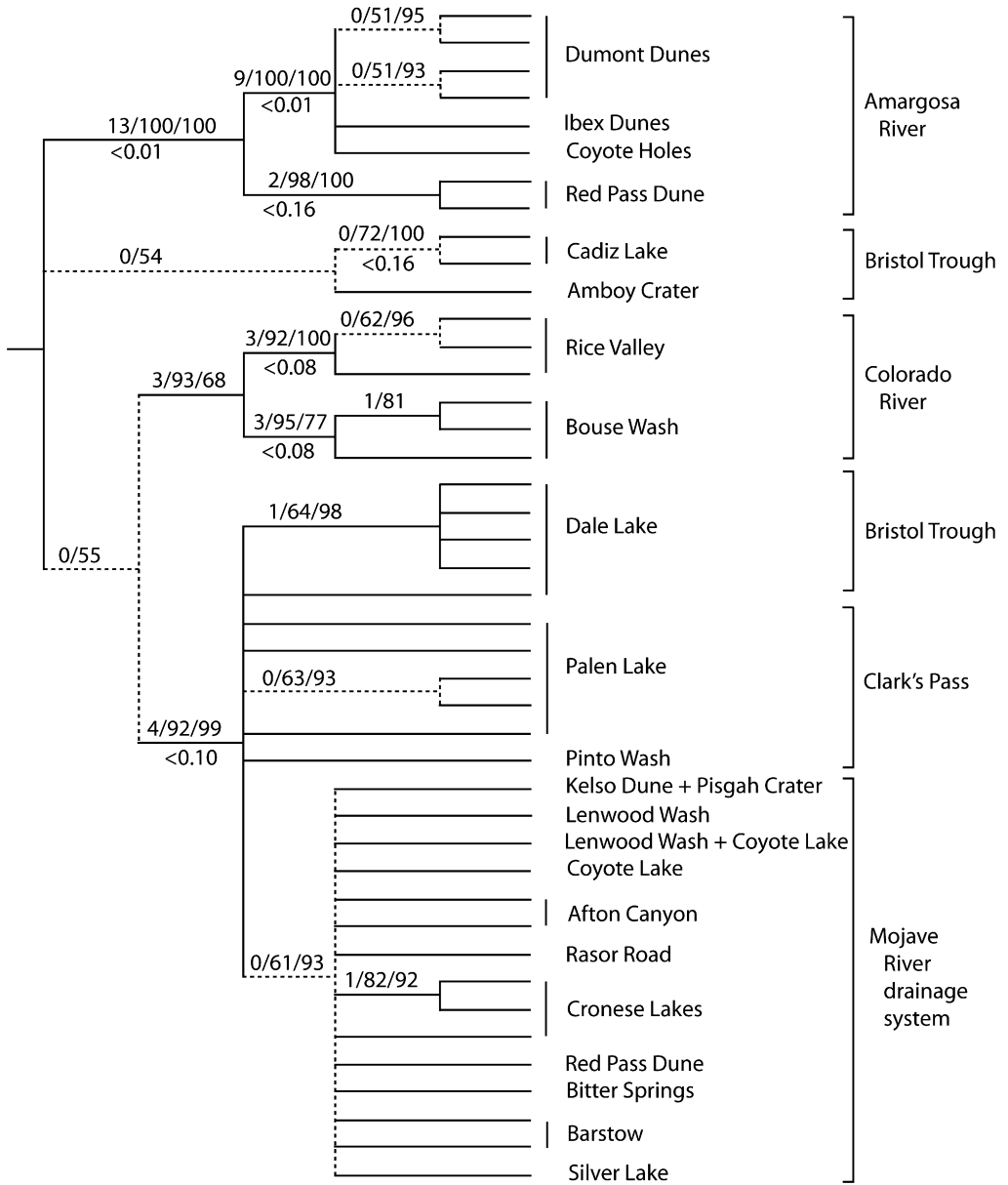


Fig. 2. A 50% majority rule bootstrap consensus tree that possibly reflects the matriarchal genealogy of the Mojave fringe-toed lizard, *Uma scoparia*. The tree is based on a maximum parsimony analysis of partial sequences of the mtDNA genes ATPase 6 and cytochrome *b*. The *U. notata* complex was used as the outgroup. Dashed lines represent nodes that were not resolved in the maximum parsimony analysis. Numbers above the nodes are Bremer decay indices/Bootstrap proportions based on unweighted maximum parsimony (>0.50)/bootstrap proportions based on Bayesian inference, and below nodes, nodal Templeton values ($p < 0.20$). Although fringe-toed lizards from Dale Lake are genetically associated with those from the Mojave River drainage system, Dale Lake is geologically associated with the Bristol Trough.

and three with single haplotypes. The Amargosa River clade included lizards from Dumont, Ibex and Red Pass dunes plus Coyote Holes. The two haplotypes at Red Pass Dune associated with the Amargosa River are united by three synapomorphies, but 14 unambiguous changes separate them from other members of the Amargosa River clade. Another clade contained lizards from Bouse Wash and Rice Valley (= Rice Dunes). This latter clade is geographically associated with the Pleistocene Colorado River. The third clade was associated with the Mojave River drainage system plus the Bristol Trough. Within the former group, only one or two autapomorphies separate *U. scoparia* on Red Pass Dune from the Mojave River drainage system. Within the Bristol Trough and Clark's Pass sand transport pathways, some individuals from Palen, Cronese and Dale lakes clustered together, but others did not. Two haplotypes from Cadiz Lake and the haplotype found at Amboy Crater did not cluster together, although they occur in close geographic proximity to one another. However, the lack of resolution did not preclude the possibility that Cadiz Lake and Amboy Crater formed a single lineage. More significantly, populations in the Bristol Trough did not cluster together because *U. scoparia* at Dale Lake clustered with populations from Clark's Pass and the Mojave River drainage system. In this case, the genealogical patterns did not conform to geological formations and types of sand.

Using MrModeltest, the general time reversal plus invariant sites and a gamma distribution (GTR+I+G) model was selected for use in the Bayesian inference analysis ($-\ln L = 6502.5288$; $K = 10$; $AIC = 13,025.0576$). Bayesian inference resulted in a tree that was identical to the MP consensus trees except for relationships at the base of the tree, where neither the MP nor Bayesian approaches resolved substantial support for the tree nodes. The Bayesian analysis was not conducted with the sequential deletion of more distant outgroup taxa, as was done with the MP treatment. The Bayesian posterior probabilities (BPPs) were usually higher than the BSPs (Fig. 2).

3.4. Nodal stability

Several nodes were strongly supported according to the three indices of nodal stability (Fig. 2). Curiously, the BS majority rule consensus tree resolved six more nodes than were found in the MP analysis. The most strongly supported nodes were associated with the Amargosa River clade. Samples from Rice Valley and Bouse Wash received relatively high support for their associations. Although geographically nearby, Cadiz Lake and Amboy Crater formed a weakly supported clade in the BS analysis; this node was not resolved in the MP analysis. Surprisingly, the node for two haplotypes from Cadiz Lake received relatively high support (BS = 72 and Templeton nodal support [nTT = 0.16]) and yet the node was not resolved in the MP analysis.

4. Discussion

4.1. Matriarchal genealogy

Some nodes on the tree received little BS support. However, low BSPs may result from a small number of unambiguous (non-homoplastic) synapomorphies and therefore do not indicate a lack of confidence in the node (Felsenstein, 1985). In several cases, the homoplasy owes to an apparent homoplastic autapomorphy. Regardless, validity of the

nodes is empirically supported by the observation that individual lizards from a given dune clustered together, or at least their association with a particular dune was not rejected by the tree. The only exception occurred in Red Pass Dune, which contained haplotypes from two different lineages (Fig. 2).

The cladistic analysis of haplotype lineages of *U. scoparia* (Fig. 2) revealed a strong correspondence with drainage systems in the Mojave and Colorado deserts. Lizards from the Amargosa River clade are associated with Lake Tecopa, Lake Manly (now Death Valley; frequently misspelled “Manley”) and Kingston Wash. The genetically divergent population on Red Pass Dune formed the sister group to the other members of this northern lineage. A relatively longer branch united the populations from Dumont Dunes, Ibex Dune, and Coyote Holes (Fig. 2). This longer branch could have indicated that the Amargosa River clade was evolving at a relatively rapid rate. Regardless, a lack of differentiation among lizards at these three dunes suggested that their isolation from one another has occurred relatively recently.

Populations within the Amargosa River clade had differing percentages of variation. A single haplotype was found in five lizards from Ibex Dune. Similarly, all three lizards from Coyote Holes shared the same haplotype. In contrast, five haplotypes were obtained from seven individuals at Dumont Dunes. Thus, Dumont Dunes could have been the source of variation observed within this clade.

Bouse Wash and Rice Valley occur near the north shore of a Late Tertiary body of water, either the marine Bouse Embayment, or lacustrine and fluvial deposits of the ancestral Colorado River (Axen and Fletcher, 1998; Gross et al., 2001; Lucchitta, 2001; Muhs et al., 2003; Poulson and John, 2003). Individual lizards can be unequivocally associated with their respective dunes (Fig. 2). Genetic isolation appears to have occurred by vicariance, as opposed to dispersal, because both sites have multiple maternal lineages and haplotypes from one dune do not nest within the other, as would be expected with recent dispersal.

The last and most diverse lineage with multiple haplotypes is associated with the Mojave River drainage system. Most of the possible relationships within this lineage cannot be resolved; the node is a hard polytomy (Fig. 2). Nearby populations, such as Red Pass Dune and Bitter Spring, are no more than 2 km away from one another but are separated by the north-west extension of the Soda Mountains. Most individuals from Lenwood Wash, Coyote Lake, Afton Canyon, Cronese Lakes, and Barstow are not united into single clades. This pattern indicates that dispersion of individuals and gene flow occurred recently. The lack of genetic differentiation likely reflects a relatively recent isolation. In turn, the recent isolation suggests that *U. scoparia* was more widely distributed during pluvial times. If true, it seems likely that *U. scoparia* is an exaptive species that would likely thrive in more mesic conditions. This hypothesis is supported by our observations of activity periods. The lizards are active in the morning and late afternoon, but absent during the heat of the day.

The clade associated with the Mojave River drainage system contains three poorly differentiated subclades, including individuals from Dale and Palen lakes, and Cronese Lake. Although possible, monophyly of the haplotypes from these lakes could not be confirmed because of the apparent hard polytomy at the base of the clade. Dale and Palen lakes occur in the Bristol Trough and Clark’s Pass sand transport pathways (Muhs et al., 2003), along with Pinto Wash, and these populations have the southernmost distributions for *U. scoparia* (Fig. 1). Four of five individuals from Dale Lake shared a common

matriarchal lineage. Both specimens sampled from Pinto Wash had identical sequences, and only two of five individuals from Palen Lake were united. There is no clear-cut history of isolation among the dune systems within this major clade.

Amboy Crater and Cadiz Lake (Fig. 2) occur in close proximity within the Bristol Trough. The number of accrued autapomorphic states (Fig. 2) indicates that substantial genetic divergence exists within Cadiz Lake; the two haplotypes differ at 11 nucleotide sites. A larger sampling of individuals from both dunes, as well as an analysis of microsatellite DNA alleles, is required to investigate the potential of gene flow among these sites.

Among all species of *Uma*, only Red Pass Dune has a coalescence of historical lineages that are not sister groups. Red Pass Dune contains two haplotypes, one from the very distinctive Amargosa River clade and the other from the Mojave River drainage system (Fig. 2).

Conservation genetics frequently make use of statistical parsimony and unrooted haplotype networks (e.g. Templeton, 1998, 2004; Posada and Crandall, 2001). However, it has been argued that the maximum explanatory power of the data is that which makes the least assumptions, i.e. unweighted parsimony (e.g. Siddall and Kluge, 1997; Frost et al., 2001). In part, justification for the network approach is also built upon the notion of a persistent ancestor. This concept owes, in part, to the assumption of a traceable intraspecific phylogeny. Unfortunately, this assumption is falsified in sexually reproducing organisms owing to genetic recombination. Mitochondrial DNA gene genealogies only reflect the maternal history of animals and not that of paternal history. Trees derived from mtDNA necessarily reflect female dispersal and dispersion. In stark contrast, nuclear genes segregate and flow independently of the history of movement of particular individuals within demes. As a consequence, within species mtDNA gene trees are predictably at odds with nuclear gene trees (10 examples given in Ballard and Whitlock, 2004), in part because of the role genetic recombination plays in gene flow. Methods of haplotype network building also incorporate haplotypic frequency data. However, Murphy and Doyle (1998) demonstrated numerous problems, violations of assumptions, and common failures with inferring phylogenetic and genealogical relationships from frequency-based data morphological and molecular data. Trees derived from frequency data can reflect random drift, selection or any other mechanism that changes gene frequencies, and not the history of population fragmentation.

4.2. Historical biogeography

Genetic characterizations of individual populations, their matriarchal genealogy, geology and paleoecology of the Mojave Desert region can be synthesized to form an explanatory historical scenario. Two primary events are noted: the origin of the species and the primary intraspecific divergence into northern and central clades.

4.2.1. Interspecific evolution: the origin of *U. scoparia*

Geologic events caused hydrological changes that facilitated vicariance and dispersal of ancestral *Uma*. In the later Miocene (13–12 Ma), fault blocking, subsidence and erosion developed closed basin drainages in and around the preexisting (Oligocene) Colorado Plateau (Eberly and Stanley, 1978; Lucchitta, 1979). Between 10.5 and 6 Ma, these

drainages expanded, coalesced, and ultimately formed new routes of water discharge. One of these new discharge points may have been the Bouse Embayment.

The current, southern limit of *U. scoparia* conforms roughly to the junction of the Colorado River and Proto-Gulf of California. The geological events may have isolated populations of several species, including the desert tortoise (Lamb et al., 1989; McLuckie et al., 1999), collared lizards, *Crotaphytus bicinctores* and *C. collaris* (McGuire, 1996), and toads, *Anaxyrus* (formerly *Bufo*) *californicus* and *A. microscaphus*, although the middle Pleistocene uplift of the Mojave Desert ranges may have separated the toads (Hunt, 1983; Gergus, 1998).

4.2.2. Intraspecific evolution of *U. scoparia*

U. scoparia occurs only within 45 m of its typical sand-dwelling habitat (Norris, 1958). This restriction to sand dunes facilitates biogeographic analyses because the history of isolation of the populations is associated with the history of the playas and dunes themselves. Given that sand forms from hydrological processes, the distribution of Mojave fringe-toed lizards can be expected to parallel that of the developing riverine and sand transport systems (Lancaster and Tchakerian, 2003; Muhs et al., 2003). Although evidence suggests that populations of fringe-toed lizards can only disperse as fast as their sand substrates advance, one Chihuahuan fringe-toed lizard, *U. paraphygas*, dispersed at least 200 m from one dune to another (Trépanier, 2002).

4.2.3. The north–south split in *U. scoparia*

Historical biogeography typically correlates branching patterns of genealogical trees with evolving landforms. The most basal split in the matriarchal gene tree of *U. scoparia* forms northern and southern lineages (Fig. 2). This pattern best reflects the isolation of the Amargosa and Mojave rivers.

Death Valley was well-defined by the Pliocene, and it became the very large, ancient Lake Manly. This lake was an occasional terminus for the Amargosa and Mojave rivers (McKenna and Hodges, 1990; Sharp and Glazner, 1997; Cox et al., 2003; Enzel et al., 2003). Simultaneously, Lake Tecopa dominated the landscape of the Mojave Desert lowlands from the Late Pliocene (>3 Ma) through the middle Pleistocene (<500 Ka), particularly when it was joined by Lake Manly to its west (Sharp and Glazner, 1997). At times of pluvial activity, and frequently in a more mesic environment (Van Devender, 1977, 1990; Spaulding, 1990), it is likely that the interconnected network of streams and channels connected populations of fringe-toed lizards.

The distribution of *U. scoparia* follows river courses, and these courses changed about 500 Ka because of mountain building events (Sharp and Glazner, 1997). In particular, the northern lineage associated with the Amargosa River was likely isolated from more southerly populations aligned with the Mojave River.

The extent of sequence divergence in related taxa provides some evidence for this time frame. Zebra-tailed lizards, *C. draconoides*, in the mid-peninsula of Baja California have an mtDNA divergence of about 9% (Lindell et al., 2005). The mid-peninsula discontinuity in mtDNA sequences has been observed in most species of animals on the peninsula and a divergence of 9–11% is common for other species of lizards (Murphy and Aguirre-Léon, 2002). This break has been attributed to a hypothetical vicariance event, mid-peninsular seaway (Upton and Murphy, 1997; Riddle et al., 2000; Murphy and Aguirre-Léon, 2002; Lindell et al., 2006), which is now dated at >3 Ma (Rodríguez-Robles and de

Jesús-Escobar, 2000; Lindell et al., 2005, 2006). Thus, for zebra-tailed and other lizards, divergence appears to be occurring at about 4% nucleotide sequence change per 10^7 yr. If this rate of change also occurred in fringe-toed lizards, then the northern and southern lineages of *U. scoparia* were isolated in the mid-Pleistocene, about 500 Ka, likely as a consequence of orogenic events that changed the courses of rivers (Sharp and Glazner, 1997), as opposed to pluvial stages. The initial north–south division of *U. scoparia* may have occurred near Red Pass Lake, as suggested by the southernmost occurrence of members of Amargosa River clade.

4.2.4. Late Pleistocene divergence in the lineages

The distribution of *U. scoparia* also reflects glacial history. The Quaternary in southwestern North America was dominated by glacial and interglacial cycles (Imbrie and Imbrie, 1979). About 94% of the Quaternary was dominated by glaciopluvial events (Van Devender and Burgess, 1985). Climates in the Mojave Desert region were frequently, if intermittently, more mesic and cooler than present, particularly during the glaciations (Spaulding, 1991; Enzel et al., 1992, 2003). The cooler and more-moist times include the “Little Ice Age” that occurred 390 yr bp and an earlier episode at 3.6 Ka (Wells et al., 2003). In these two episodes, most major playas of the Mojave River drainage sustained standing water for periods of up to 40 yr.

Glaciation had predictable impacts on the environment in terms of the formation of sand dunes (Enzel et al., 2003) and the distribution of their associated organisms. During glacial events, the climate was wet. Mountains were eroded by chemical weathering and soil formed. Alluvial fans and sand dune fields were stabilized and eroded. During the onset of dry, interglacial periods, lakes turned into marshes. As aridity continued, the climate became warmer, the ranges of mesophilic species contracted and the distribution of xerophilic species expanded. Mountains underwent mechanical weathering and erosion dominated. Alluvial fans and sand dunes expanded and built up.

The northernmost maternal lineage of *U. scoparia*, including populations from south-eastern Death Valley (Ibex and Dumont dunes) and the Silurian Valley (Coyote Holes) is united by distinct haplotypes. The absence of substantial genetic differentiation among individuals from these three locations suggests that populations from the northernmost clade were contiguous. Flooding along the Amargosa River (Brown et al., 1990; Enzel et al., 1992) would have facilitated repeated Holocene dispersion of *U. scoparia*. Habitat suitable for *U. scoparia* persisted at times of maximum glaciation, likely in xerothermic lakeshore dune microhabitats. Spaulding (1990) noted persistence of lowland vegetation in the glacial Mojave Desert prior to the beginning of the xerothermic post-glacial period 7.8 Ka. In Death Valley, a speciose and succulent semi-desert vegetation occurred at 425–775 m along its lateral slopes during full glacial times, 19–17 Ka (Woodcock, 1986; Spaulding, 1999). Typical warm desert plants, like *Ambrosia dumosa*, appeared by 10.2 Ka, and the dominant *Larrea tridentata* emerged between 9.1 and 8.2 Ka.

All habitats currently occupied by the northern clade of *U. scoparia* are below 200 m except for Red Pass Dune (>500 m). Despite the downward displacement of desert vegetation, the doubly faulted deep grabens of the Silurian and Death valleys were probably sufficiently low to shelter populations of *Uma* throughout the Pleistocene Epoch, either as desert lowlands during interglacial episodes, or more likely along the lowland lakeshore dunes, perhaps near Dumont Dunes and Salt Spring. Given that

Mojave fringe-toed lizards could have persisted in the Mojave Desert during glacial periods, how did they become isolated?

In the Pleistocene, the lineage of *U. scoparia* associated with Amargosa River may have become isolated in Silurian Valley between Lake Tecopa at its northern end and by Silver Lake (now a playa) to the south. Populations of *U. scoparia* at Dumont Dunes and Coyote Holes occur between these sites. Intermittent spillways over the south-western sill of Lake Tecopa might have established the population on Ibex Dunes, the only population to reach, or remain as a remnant in, Death Valley proper and the northernmost occurrence of the genus. Hydrological evidence is consistent with this interpretation. The high shorelines of Lake Manly have been estimated at 90 m above the lakebed, both at 12 Ka and at an earlier maximum fill at 125–86 Ka (Machette et al., 2001; Anderson and Wells, 2003). Both Ibex and Dumont dunes occur above the highest shoreline.

The extent of genetic divergence within the southern lineage suggests that most populations were contiguous during times of maximum glaciation. The possible exceptions include populations on dune systems in the Bristol Trough, and especially those in Rice Valley and Bouse Wash. These populations appear to have been derived from a single maternal lineage.

4.2.5. Comparison to previous hypotheses

Norris (1958) believed that the northernmost populations of *U. scoparia* from Death and Silurian valleys arrived relatively recently by dispersal. However, his scenario conflicts with the matriarchal history. Norris recognized a north-western group consisting of lizards from Silver Lake, Sperry Canyon, Saratoga Springs (= Ibex Dunes), East Cronese Lake, Alvord Mountains, Newberry Dunes, Daggett, Harper's (Dry) Lake, El Mirage (Dry) Lake, Wilsona Butte and Peck's Butte. These lizards had (1) posteriorly occluded postmental scales; (2) a high incidence of lacking pre-cloacal spots; and (3) a low number of scales separating the interparietal and post-parietal scales. Norris assumed that the anatomical similarity owed to a common westerly dispersal along stream routes. However, the morphological data unite some populations in two major maternal lineages that cannot be exclusive sister groups, i.e. the morphological data would be homoplastic if they represented apomorphic (derived) character states. However, the morphological similarity presents no problem or homoplasy when considered to be the plesiomorphic condition. Regardless, Norris' morphological data have the potential to phenotypically diagnose the genetically identified northernmost lineage.

The sympatric occurrence of endemic taxa suggests antiquity for many lineages in the northern Mojave Desert. Counter to Norris' (1958) hypothesis, many species might not have been forced southward during times of glaciation, and its cooler, more moist climates. A few examples of endemic taxa in the northern Mojave include vascular plants (> 50 taxa), fish (*Cyprinodon*, *Gila*, *Rhinoichthys* [Miller, 1946]), toads (*Anaxyrus* (formerly *Bufo*) *nelsoni* and *A. exsul*), snakes (*Crotalus mitchellii stephensi*), salamanders (*Batrachoseps campii*), montane lizards (*Elgaria panamintina*) and a new species in the *Plestiodon* (formerly *Eumeces*) *gilberti* complex (Richmond and Reeder, 2002). Many of these endemics are confined to relict montane woodlands and parklands and to intervening valley springs of the Pleistocene Owens River drainage, which may have terminated in Lake Manly.

4.2.6. Intraspecific evolution: sympatric maternal lineages

The occurrence of sympatric maternal lineages at Red Pass Dune may be associated with the formation of Afton Canyon. By the last full glacial episode, the increased precipitation

generated greater water flow into a dammed Mojave River. While the terminus of this closed-basin river oscillated between Harper and Manix lakes, hydrological force eventually became sufficient to cut through Afton Canyon (between the Cave and Cady Mountains), perhaps episodically starting at 18 Ka (Anderson and Wells, 2003; Jefferson, 2003), but certainly flow was continuous by 14–11 Ka (Meek, 1989; Anderson and Wells, 2003). Flow of the river east of Afton Canyon ended into a new series of low valleys including Cronese, Silver and Soda lakes (Wells et al., 2003). These hydrogeologic systems and their associated playas provided a dispersal route and new habitat for *U. scoparia*. Not surprisingly, the maternal relationships among the haplotypes are poorly resolved (Fig. 2).

Red Pass Dune is the only location for *Uma* that contains haplotypes from two non-sister lineages. Secondary contact occurred between lineages from the Mojave River drainage system and the Amargosa River. The lineage from the Amargosa River must have arrived first, because it is well differentiated from other members of Amargosa River clade. The two haplotypes at Red Pass Dune are united by three synapomorphies, but 14 unambiguous changes separate them from other members of the Amargosa River clade. Regarding *U. scoparia* from the Mojave River drainage system, only one or two autapomorphies separate them from other members of their lineage.

Red Pass Lake and Red Pass Dune occur north of Afton Canyon and the Cronese Lakes. Animals from the edges of the Mojave River drainage system and the fringes of Lake Manix probably dispersed northward to Red Pass Lake and the Red Pass Dune making secondary contact with *U. scoparia* from the Amargosa River clade. Climatic and ecological conditions that favored colonization by the desert tortoise, about 9 Ka (Douglas et al., 1988) also may have facilitated the northward dispersal of *U. scoparia* into the Bitter Spring by the early Holocene Epoch. The paleoecology of Bitter Spring, which included perennial water an open pinyon woodland-grassland with a mosaic of vegetation and habitats, is well documented from 15 to 6 Ka (Reynolds, 1991; Reynolds and Reynolds, 1994; Spaulding et al., 1994).

5. Conclusion: distinct population segments and conservation

Inevitably, law accomplishes the conservation and protection of species and populations (Berry et al., 2002). In the US, under the ESA, any species, subspecies or vertebrate “distinct population segment” (DPS) can be listed as “threatened” or “endangered” and receive legal protection if it meets certain statutory criteria. Under current policy established by the US Fish and Wildlife Service and the National Marine Fisheries Service, a population may be protected under the ESA as a DPS following an analysis of: (1) the discreteness of the population segment in relation to the remainder of the species to which it belongs; (2) the significance of the population segment to the species to which it belongs; and (3) the conservation status of the population in relation to the ESA standard for listing. Designations of DPSs should be used “sparingly” and “be well justified biologically” (US Senate, 1979). Discreteness can be satisfied by several criteria (US Department of the Interior and US Department of Commerce, 1996): marked separation from other conspecific populations as a consequence of physiological, ecological or behavioral factors, or physical separation. Physical separation can include natural geographical isolation or by international boundaries where “discreteness” was created by differential protection/exploitation of populations on each side of the border.

Four criteria can be used to measure “significance of the DPS” (US Department of the Interior and US Department of Commerce, 1996): (1) A population can be a DPS if it persists in an unusual or unique ecological setting for that species. (2) If extirpation of the population creates a gap in the range of the species, then it could qualify as being a DPS. (3) A population that is the only remnant of the species’ former range could qualify for designation as a DPS, even if introduced populations are more common elsewhere. (4) Genetic distinctiveness can also be used to qualify a population as being a DPS. The conservation status of each DPS is then determined separately using criteria set out in the ESA.

Two historical units of *U. scoparia* unambiguously qualify for designations as DPSs on the basis of several criteria. Natural geographic barriers, including the absence of sand and presence of mountains, separate populations from one another. Each dune is a discrete entity and it is extremely unlikely that gene flow is occurring among the isolated dunes, and especially among dune systems not connected by a recent hydrogeologic system. Ecologically, dispersal is virtually impossible because of the absence of intervening sand dunes. Within some dune systems, the presence of a single “monophyletic” maternal lineage provides evidence that dispersal has not occurred; if dispersal was common we would expect to see haplotypes from different lineages scattered among the dune systems, as observed on Red Pass Dune (Fig. 2). The Amargosa River lineage is genetically distinct. The presence of unique haplotypes gives credence to the possibility of regional adaptations and incipient speciation. The Amargosa River lineage represents a significant historical component and it deserves recognition as a DPS. In addition, Red Pass Dune is special in being the only population of *Uma* that contains two distinctive maternal lineages. Accordingly, we propose the recognition of two primary DPSs as follows:

1. Amargosa River DPS: Dumont and Ibex dunes and Coyote Holes.
2. Red Pass Dune DPS.

Designation of the primary DPSs does not adequately represent the significance and extent of isolation of the dune-restricted populations. Our concept of DPSs for *U. scoparia* is similar to the current management of the desert tortoise, i.e. a precedence exists for making further subdivisions. The “Mojave Population” of *G. agassizii* is listed as a DPS, and the Recovery Plan (US Fish and Wildlife Service, 1994) describes six smaller units as both DPSs and ESUs each of which is designated as a named “Recovery Unit.”

An individual *U. scoparia* from Bouse Wash and Rice Valley can be associated unambiguously with its particular dune. It is quite likely that individuals from Amboy Crater and Cadiz Lake can also be associated with their respective dunes. A phylogenetic analysis of the sequence data can associate some lizards from the Mojave River drainage system with their respective dunes, but not most. However, it is likely that additional sequence data, particularly from more rapidly evolving genes, will further resolve the historical associations. Until these data are available, it is preferable not to recognize additional subdivisions or DPSs.

Many populations represent isolated historical units that could represent incipient species. They could be locally adaptive and have unique behavioral and physiological attributes. Consider, for example, *U. scoparia* at Dumont Dunes. Within the Amargosa River DPS, Dumont Dunes is the only population documented to have variation in its mtDNA; four different haplotypes were found among the seven individuals sequenced.

Among five individuals from Ibex Dune, only one haplotype was observed. Similarly, all three individuals from Coyote Holes shared a haplotype. Thus, the population of *U. scoparia* at Dumont Dunes deserves designation as a DPS because it is the only location where a “pure” lineage from the Amargosa River DPS is documented to harbor variation in its mtDNA; the only other variable population within this lineage occurs at the very small Red Pass Dune.

Red Pass Dune is deserving of status as a DPS. It contains a unique maternal lineage associated with the Amargosa River DPS as well as haplotypes from the Mojave River drainage system. In addition, Red Pass Dune is the only location where, among all species of *Uma*, divergent maternal lineages occur in sympatry.

Unfortunately, *U. scoparia* is now extirpated from at least two historical localities within the Mojave Desert in San Bernardino Co., at Harper and El Mirage lakes (dry). Further west in Los Angeles Co. populations at Lovejoy Buttes and Piute Butte have also been extirpated, thus reducing the geographic range in the west. Recent searches of the Desert dunes failed to locate a single individual.

Having defined DPSs, it is possible to evaluate the conservation status of each and, where appropriate, obtain protection through application of the ESA. A full review of the conservation status of each DPS, as well the attainment of protection, is beyond the scope of this paper, because conservation necessarily involves law. Regardless, the isolated nature of the populations leaves them vulnerable to local extirpations—extinctions of incipient species. Dune systems are very fragile, as reflected in part by protection currently afforded to other species of fringe-toed lizards. The Coachella Valley fringe-toed lizard, *U. inornata*, is a federally threatened species (US Department of the Interior, 1980). *U. scoparia* and the Colorado Desert fringe-toed lizard, *U. notata* are listed as species of special concern in California (Jennings and Hayes, 1994). In Mexico, *U. notata*, is listed as threatened, the Chihuahuan fringe-toed lizard, *U. paraphygas*, is considered endangered, and the Coahuila fringe-toed lizard, *U. exsul*, is listed as rare (SEMARNAP, 2000).

Habitat destruction, habitat loss and disruption of eolian sand transport pathways threaten the survival of *U. scoparia*. Disruption of dune ecosystems by off-highway vehicles poses a major threat. Habitat loss due to agriculture and development contribute to loss of habitat. Fringe-toed lizard densities are negatively affected by sand depletion and surface stabilization (Turner et al., 1984). Sand compaction and sand patch size adversely affect the abundance of fringe-toed lizards (Barrows, 1997). Off-road vehicles can severely compact sands and destroy vegetation at dune sites (Luckenbach and Bury, 1983). This loss of native vegetation results in the elimination of cover, which is used for thermoregulation and predator avoidance (Pough, 1969). Vegetation, presumably native, is also required for food sources for fringe-toed lizards (Luckenbach and Bury, 1983). A high incidence of *U. notata* that were missing tails, or dead, was observed on the heavily frequented off-road vehicle area at Algodones Dunes (Luckenbach and Bury, 1983). Further compounding the effects of human disruption of desert vegetation are the extraordinary time intervals estimated for recovery of plant species through secondary succession. Lovich and Bainbridge (1999) estimate that 50–300 yr may be required for recovery to predisturbance plant cover and biomass, and over 3000 yr for complete recovery of the desert ecosystem. Anthropogenic threats continue to severely impact populations of fringe-toed lizard and the threats must be addressed to ensure the perpetuation of these species. These factors should be taken into consideration when and if the ESA is used to provide protection for one or more DPSs of *U. scoparia*.

Acknowledgements

L.E. Bell, L. Cunningham, K. Emmerich, I. Girard, S. Hillard, R. Hirsh, A. Leaché, M. Marolda and D. Turner assisted in collecting *U. scoparia* in the US. Collecting in Mexico was assisted by H. Gadsden-Esparza, H. López-Corrujedo, J.-L. Estrada-Rodríguez, U. Romero-Méndez, A. Orona-Espino and A. Herrera. S. Papadakos-Morafka assisted throughout the study. This project is a product of research contracts (#5278 and #5376) between the Directorate of Public Works of the US Army, the National Training Center (NTC) at Fort Irwin, and California State University Dominguez Hills (CSUDH) Foundation to DJM. We are particularly indebted to W. Quillman of the NTC. Genomic research was conducted under a subcontract from CSUDH Foundation and the Natural Sciences and Engineering Research Council of Canada Discovery Grant A3148 to RWM. All collecting used approved Animal Use Protocols, Death Valley National Park Service Scientific Research and Collecting Permit (DJM), and California Department of Fish and Game (CDFG) Permits (8001062-03 to DJM). Fieldwork in Mexico was conducted using permits from the Secretaría de Desarrollo Urbano y Ecología (SEDUE) to H. Gadsden-Esparza, and Federal Permit #DOO.02-2802 issued to RWM; tissues were imported into Canada on SEDUE export permit DOO 750-1268 issued to RWM. Collecting in Arizona used Permit #HK081491 (to D. Turner). We are particularly indebted to R. Jones and S. Parmenter of the CDFG for advice and suggestions. We also thank T. Egan and E. La Rue of the US Bureau of Land Management and K.H. Berry of the US Geological Survey for directing us to previously unsampled localities. K.H. Berry, J. Calzia, J.P. Galloway, N. Lancaster, T. Reeder, B.R. Riddle, J. Weigand and one anonymous reviewer provided valuable comments on the manuscript. A. Ngo assisted with analyses of the data. Fig. 1 was prepared by K. Keith and Fig. 2 by A. Lathrop.

References

- Akaike, H., 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19, 716–723.
- Akaike, H., 1979. A Bayesian extension of the minimum AIC procedure of autoregressive model fitting. *Biometrika* 66, 237–242.
- Anderson, K.C., Wells, S.G., 2003. Latest Quaternary paleohydrology of Silurian Lake and Salt Spring basin, Silurian Valley, California. In: Reynolds, R.E., Wells, S.G., Brady, R.H.I. (Eds.), *At the End of the Mojave: Quaternary Studies in the Eastern Mojave Desert*. Special Publications of the San Bernardino County Museum Association, San Bernardino, pp. 129–141.
- Arnold, E.N., 1994. Investigating the origin of performance advantage, adaptation, exaptation, and lineage effects. In: Eggleton, P., Van-Wright, R. (Eds.), *Phylogenetics and Ecology*. Academic Press, London, UK, pp. 123–168.
- Axen, G.J., Fletcher, J.M., 1998. Late Miocene–Pleistocene extensional faulting, northern Gulf of California, Mexico and Salton Trough, California. *International Geology Review* 40, 217–244.
- Ballard, J.W.O., Whitlock, M.C., 2004. The incomplete natural history of mitochondria. *Molecular Ecology* 13, 729–744.
- Banta, B.H., 1962. Preliminary remarks upon the zoogeography of the lizards inhabiting the Great Basin of the western United States. *Wasmann Journal of Biology* 20, 253–287.
- Barrows, C.W., 1997. Habitat relationships of the Coachella Valley fringe-toed lizard *Uma inornata*. *Southwestern Naturalist* 42, 218–223.
- Berry, K.H., Morafka, D.J., Murphy, R.W., 2002. Defining the desert tortoise(s): our first priority for a coherent conservation strategy. *Chelonian Conservation Biology* 4, 249–262.
- Bremer, K., 1994. Branch support and tree stability. *Cladistics* 10, 295–304.

- Brown, D.E., 1994. Biotic Communities: Southwestern United States and Northwestern Mexico. University of Utah Press, Salt Lake City.
- Brown, W.J., Wells, S.G., Enzel, Y., Anderson, R.Y., McFadden, L.D., 1990. The late Quaternary history of pluvial Lake Mojave-Silver Lake and Soda Lake basins, California. In: Reynolds, R.E., Wells, S.G., Brady, R.H.I. (Eds.), *At the End of the Mojave: Quaternary Studies in the Eastern Mojave Desert*. Special Publications of the San Bernardino County Museum Association, San Bernardino, pp. 55–72.
- Buckley, T.R., Arensburg, P., Simon, C., Chambers, G.K., 2002. Combined data, Bayesian phylogenetics, and the origin of the New Zealand cicada genera. *Systematic Entomology* 51, 4–18.
- Carothers, J.H., 1986. An experimental confirmation of morphological adaptation: toe fringes in the sand-dwelling lizard *Uma scoparia*. *Evolution* 40, 871–874.
- Cox, B.F., Hillhouse, J.W., Owen, L.A., 2003. Pliocene and Pleistocene evolution of the Mojave River, and associated tectonic development of the Transverse Ranges and Mojave Desert, based on borehole stratigraphy studies and mapping of landforms and sediments near Victorville, California. In: Enzel, Y., Wells, S.G., Lancaster, N. (Eds.), *Paleoenvironments and Paleohydrology of the Mojave and Southern Great Basin Deserts*. Geological Society of America Special Paper 368, pp. 1–42.
- Crandall, K.A., Bininda-Emonds, O.R.P., Mace, G.M., Wayne, R.K., 2000. Considering evolutionary processes in conservation biology. *Trends in Ecology & Evolution* 15, 290–295.
- Douglas, C.L., Jenkins, D.L., Warren, C.N., 1988. Spatial and temporal variability in faunal remains in Fort Lake Mojave-Pinto period sites in the Mojave Desert. In: Willig, J.A., Aikens, C.M., Fagan, J.L. (Eds.), *Early Human Occupations in Far Western-Western North America: The Clovis–Archaic Interface*. Nevada State Museum Anthropology Paper, Carson City, pp. 131–144.
- Eberly, L.D., Stanley Jr., T.B., 1978. Cenozoic stratigraphy and geologic history of southwestern Arizona. *Geological Society of America Bulletin* 89, 921–940.
- Elvin, D.W., 1960. Range extension for *Uma scoparia* Cope. *Herpetologica* 16, 31.
- Enzel, Y., Brown, W.J., Anderson, R.Y., McFadden, L.D., Wells, S.G., 1992. Short-duration Holocene lakes in the Mojave River drainage basin, Southern California. *Quaternary Research* 38, 60–73.
- Enzel, Y., Wells, S.G., Lancaster, N. (Eds.), 2003. *Paleoenvironments and Paleohydrology of the Mojave and Southern Great Basin Deserts*. Geological Society of America Special Paper 368.
- Eriksson, T., 2001. AutoCladeS, Swedish Academy of Sciences.
- Felsenstein, J., 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39, 783–791.
- Frost, D.R., Rodriguez, M.T., Grant, T., Titus, T.A., 2001. Phylogenetics of the lizard genus *Tropidophorus* (Squamata: Tropicuridae: Tropicurinae): Direct optimization, descriptive efficiency, and sensitivity analysis of congruence between molecular data and morphology. *Molecular Phylogenetics and Evolution* 21, 352–371.
- Fu, J., 2000. Toward the phylogeny of the family Lacertidae—why 4708 base pairs of mtDNA sequences cannot draw the picture. *Biological Journal of the Linnean Society* 71, 203–217.
- Fu, J., Murphy, R.W., Darevsky, I.S., 1999. Limited genetic variation in *Lacerta mixta* and its parthenogenetic daughter species: Evidence from cytochrome *b* and ATPase 6 gene DNA sequences. *Genetica* 105, 227–231.
- Gergus, E.W.A., 1998. Systematics of the *Bufo microscaphus* complex: allozyme evidence. *Herpetologica* 54, 317–325.
- Goldman, N., 1993. Statistical tests of models of DNA substitution. *Journal of Molecular Evolution* 36, 182–198.
- Gross, E.A., Patchett, P.J., Dallegge, T.A., Spencer, J.E., 2001. The Colorado River system and Neogene sedimentary formations along its course: Apparent Sr isotopic connections. *Journal of Geology* 109, 449–461.
- Hall, T., 1997–1999. BioEdit Sequence Alignment Editor. Department of Microbiology, North Carolina State University.
- Hillis, D.M., Mable, B.K., Moritz, C., 1996. Applications of molecular systematics. In: Hillis, D.M., Moritz, C., Mable, B.K. (Eds.), *Molecular Systematics*. Sinauer, Sunderland, MA, pp. 515–543.
- Huelsenbeck, J.P., Bollback, J.P., 2001. Application of the likelihood function in phylogenetic analysis. In: Balding, D.J., Bishop, M., Cannings, C. (Eds.), *Handbook of Statistical Genetics*. Wiley, New York, pp. 415–439.
- Huelsenbeck, J.P., Ronquist, F.R., 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17, 754–755.
- Hunt, C.B., 1983. Physiographic overview of our arid lands in the western US. In: Wells, S.G., Haragan, D.R. (Eds.), *Origin and Evolution of Deserts*. University of New Mexico Press, Albuquerque, pp. 7–64.
- Imbrie, J., Imbrie, K.P., 1979. *Ice Ages, Solving the Mystery*. Enslow, Short Hills, NJ.
- Jefferson, G.T., 2003. Stratigraphy and paleontology of the middle to late Pleistocene Manix Formation, and paleoenvironments of the central Mojave River, southern California. In: Enzel, Y., Wells, S.G., Lancaster, N.

- (Eds.), *Paleoenvironments and Paleohydrology of the Mojave and Southern Great Basin Deserts*. Geological Society of America Special Paper 368, pp. 43–60.
- Jennings, M.R., Hayes, M.P., 1994. Amphibian and Reptile Species of Special Concern in California, California Department of Fish and Game, Rancho Cordova. <http://www.dfg.ca.gov/hcpb/info/herp_ssc.pdf>.
- Kocher, T.D., Thomas, W.K., Meyer, A., Edwards, S.V., Paabo, S., Villablanca, F.X., Wilson, A.C., 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proceedings of the National Academy of Sciences of the United States of America* 86, 6196–6200.
- Lamb, T., Avise, J.C., Gibbons, J.W., 1989. Phylogeographic patterns in mitochondrial DNA of the desert tortoise (*Xerobates agassizi*), and evolutionary relationships among the North American gopher tortoises. *Evolution* 43, 76–87.
- Lancaster, N., Tchakerian, V.P., 2003. Late Quaternary aeolian dynamics, Mojave Desert, California. In: Enzel, Y., Wells, S.G., Lancaster, N. (Eds.), *Paleoenvironments and Paleohydrology of the Mojave and Southern Great Basin Deserts*. Geological Society of America Special Paper 368, pp. 231–249.
- Lee, M.S.Y., 2000. Tree robustness and clade significance. *Systematic Biology* 49, 829–836.
- Lindell, J., Mendez de la Cruz, F., Murphy, R.W., 2005. Deep genealogical history without population differentiation: Discrepancy between mtDNA and allozyme divergence in the zebra-tailed lizard (*Callisaurus draconoides*). *Molecular Phylogenetics and Evolution* 36, 682–694.
- Lindell, J., Ngo, A., Murphy, R.W., 2006. Deep genealogies and the mid-peninsular seaway of Baja California. *Journal of Biogeography* 33, 1327–1331.
- Lovich, J.E., Bainbridge, D., 1999. Anthropogenic degradation of the southern California desert ecosystem and prospects for natural recovery and restoration. *Environmental Management* 24, 309–326.
- Lucchitta, I., 1979. Late Cenozoic uplift of the southwestern Colorado Plateau and adjacent lower Colorado River region. *Tectonophysics* 61, 63–95.
- Lucchitta, I., 2001. The Bouse formation and post-Miocene uplift of the Colorado Plateau. In: Young, R.A., Spamer, E.E. (Eds.), *The Colorado River: Origin and Evolution*. Grand Canyon Association, Grand Canyon, AZ, pp. 173–178.
- Luckenbach, R.A., Bury, R.B., 1983. Effects of off-road vehicles on the biota of the Algodones Dunes, Imperial County, California. *Journal of Applied Ecology* 20, 265–286.
- Machette, M.N., Klinger, R.E., Knott, J.R., 2001. Questions about Lake Manley's age, extent and sources. In: Machette, M.N., Johnson, M.L., Slate, J.L. (Eds.), *Quaternary and Late Pliocene Geology of the Death Valley Region. Recent Observations of Tectonics, Stratigraphy and Lake Cycles (Guidebook for the 2001 Pacific Cell—Friends of the Pleistocene Field Trip)*. USGS Open-file Report 01–51, pp. 143–149.
- Maddison, W., Maddison, D., 2003. *MacClade: Analysis of Phylogeny and Character Evolution*. Sinauer Associates Inc., Sunderland, MA.
- McGuire, J.A., 1996. Phylogenetic systematics of crotaphytid lizards (Reptilia: Iguania: Crotaphytidae). *Bulletin of the Carnegie Museum Natural History* 32, 1–143.
- McKenna, L.W., Hodges, K.V., 1990. Constraints on the kinematics and timing of late Miocene–recent extension between the Panamint and Black mountains, southeastern California. In: Wernicke, B.P. (Ed.), *Basin and Range Extension Tectonics near the Latitude of Las Vegas, Nevada*. Geological Society of America Memoirs 176, 363–376.
- McLuckie, A.M., Lamb, T., Schwalbe, C.R., McCord, R.D., 1999. Genetic and morphometric assessment of an unusual tortoise (*Gopherus agassizii*) population in the Black Mountains of Arizona. *Journal of Herpetology* 33, 36–44.
- Meek, N., 1989. Geomorphic and hydrologic implications of the rapid incision of Afton Canyon, Mojave Desert, California. *Geology* 17, 7–10.
- Miller, R.R., 1946. Correlation between fish distribution and Pleistocene hydrology in eastern California and southwestern Nevada, with a map of Pleistocene waters. *Journal of Geology* 54, 43–53.
- Morafka, D.J., Berry, K.H., 2002. Is *Gopherus agassizii* a desert-adapted tortoise, or an exaptive opportunist? Implications for tortoise conservation. *Chelonian Conservation Biology* 4, 263–287.
- Moritz, C., 1994. Defining 'evolutionarily significant units' for conservation. *Trends in Ecology & Evolution* 9, 373–375.
- Muhs, D.R., Reynolds, R.L., Been, J., Skipp, G., 2003. Eolian sand transport pathways in the southwestern United States: importance of the Colorado River and local sources. *Quaternary International* 104, 3–18.
- Murphy, R.W., Aguirre-Léon, G., 2002. The non-avian reptiles: origins and evolution. In: Case, T.J., Cody, M.L., Ezcurra, E. (Eds.), *A New Island Biogeography of the Sea of Cortés*. Oxford University Press, New York, pp. 181–220.

- Murphy, R.W., Doyle, K.D., 1998. Phylogenetics: frequencies and polymorphic characters in genealogical estimation. *Systematic Biology* 47, 737–761.
- Murphy, R.W., Fu, J., Lathrop, A., Feltham, J.V., Kovac, V., 2002. Phylogeny of the rattlesnakes (*Crotalus and Sistrurus*) inferred from sequences of five mitochondrial DNA genes. In: Schuett, G.W., Höggren, M., Douglas, M.E., Green, H.W. (Eds.), *Biology of Vipers*. Eagle Mountain Publishing, Eagle Mountain, UT, pp. 71–92.
- Norris, K.S., 1958. The evolution and systematics of the iguanid genus *Uma* and its relation to the evolution of other North American desert reptiles. *Bulletin of the American Museum of Natural History* 114, 247–326.
- Nylander, J.A.A., 2004. MrModeltest v2. Program distributed by author. Evolutionary Biology Centre, Uppsala University.
- Nylander, J.A.A., Ronquist, F., Huelsenbeck, J.P., Nieves-Aldrey, J.L., 2004. Bayesian phylogenetic analysis of combined data. *Systematic Biology* 53, 47–67.
- Palumbi, S.R., 1996. Nucleic acids II: the polymerase chain reaction. In: Hillis, D.M., Moritz, C., Mable, B.K. (Eds.), *Molecular Systematics*. Sinauer, Sunderland, MA, pp. 205–247.
- Posada, D., Crandall, K.A., 2001. Intraspecific gene genealogies: trees grafting into networks. *Trends in Ecology & Evolution* 16, 37–45.
- Pough, F.H., 1969. Physiological aspects of the burrowing of sand lizards (*Uma*, Iguanidae) and other lizards. *Comparative Biochemistry and Physiology* 31, 869–884.
- Poulson, S.R., John, B.E., 2003. Stable isotope and trace element geochemistry of the basal Bouse Formation carbonate, southwestern United States: implications for the Pliocene uplift history of the Colorado Plateau. *Geological Society of America Bulletin* 115, 434–444.
- Rabinowitz, D., Cairns, S., Dillon, T., 1986. Seven forms of rarity and their frequency in the flora of the British Isles. In: Soulé, M.E. (Ed.), *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer Associates, Sunderland, pp. 182–204.
- Reynolds, R.E., 1991. The Shoshone Zoo. Rancholabrean assembly from Tecopa. In: Reynolds, J. (Ed.), *Crossing the Borders: Quaternary Studies in Eastern California and Southwest Nevada*. San Bernardino County Museum Association Special Publication, Redlands, CA, pp. 158–162.
- Reynolds, R.E., Reynolds, R.L., 1994. Depositional history of the Bitter Springs Playa paleontologic site, Tiefert Basin, Ft. Irwin National Training Center, CA. In: Reynolds, R. (Ed.), *Off Limits in the Mojave Desert*. San Bernardino County Museum Association Special Publication, pp. 56–60.
- Richmond, J.Q., Reeder, T.W., 2002. Evidence for parallel ecological speciation in scincid lizards of the *Eumeces skiltonianus* species group (Squamata: Scincidae). *Evolution* 56, 1498–1513.
- Ricketts, T.H., Dinerstein, E., Olson, D.M., Loucks, C.J., Eichbaum, W., DellaSala, D., Kavanagh, K., Hedao, P., Hurlley, P.T., Carney, K.M., Abell, R., Walters, S., 1999. *Terrestrial Ecoregions of North America: A Conservation Assessment*. Island Press, Washington, DC.
- Riddle, B.R., Hafner, D.J., Alexander, L.F., Jaeger, J.R., 2000. Cryptic vicariance in the historical assembly of a Baja California peninsular desert biota. *Proceedings of the National Academy of Sciences of the United States of America* 97, 14438–14443.
- Rodríguez-Robles, J.A., de Jesús-Escobar, J.M., 2000. Molecular systematics of New World gopher, bull, and pinesnakes (*Pituophis*: Colubridae), a transcontinental species complex. *Molecular Phylogenetics and Evolution* 14, 35–50.
- Ronquist, F., 2004. Bayesian inference of character evolution. *Trends in Ecology & Evolution* 19, 475–481.
- Saiki, R.K., Gelfand, D.H., Stoffel, S., Scharf, S.J., Higuchi, R., Horn, G.T., Mullis, K.B., Erlich, H.A., 1988. Primer-directed enzymatic amplification of DNA with a thermostable DNA polymerase. *Science* 239, 487–491.
- SEMARNAP. 2000. Norma Oficial Mexicana, NOM-059-ECOL-2000. Protección ambiental. Especies nativas de México de flora y fauna silvestres. Categorías de riesgo y específicamente para su inclusión, exclusión o cambio. Lista de especies en riesgo, México, D.F., México.
- Sharp, R.P., Glazner, A.F., 1997. *Geology Underfoot in Death Valley and Owens Valley*. Mountain Press Publishing Company, Missoula.
- Siddall, M.E., Kluge, A.G., 1997. Probabilism and phylogenetic inference. *Cladistics* 13, 313–336.
- Spaulding, W.G., 1990. Vegetational and climatic development of the Mojave Desert: the last glacial maximum to the present. In: Betencourt, J.L., Van Devender, T.R., Martin, P.S. (Eds.), *Pack Rat Middens: The Last 40,000 Years of Biotic Change*. University of Arizona Press, Tucson, AZ, pp. 166–199.
- Spaulding, W.G., 1991. A middle Holocene vegetation record from the Mojave Desert of North America and its paleoclimatic significance. *Quaternary Research* 35, 427–437.

- Spaulding, W.G., 1999. Middle to late Quaternary environmental changes in Death Valley and vicinity. In: Slate, J.L. (Ed.), Proceedings of the Conference on State of Geologic Research and Mapping in Death Valley National Park. USGS Open-file Report 99-153, Las Vegas, NV, pp. 121–123.
- Spaulding, W.G., Kowler, P.A., Anderson, R.S., 1994. A late Quaternary paleoenvironmental record from the central Mojave Desert. In: Reynolds, R. (Ed.), Off Limits in the Mojave Desert. San Bernardino County Museum Association Special Publication, pp. 56–60.
- Swofford, D.L., 2002. Phylogenetic Analysis using Parsimony. Sinauer Associates Inc., Sunderland, MA.
- Templeton, A.R., 1998. Nested clade analysis of phylogeographic data: testing hypotheses about gene flow and population history. *Molecular Ecology* 7, 381–397.
- Templeton, A.R., 2004. Statistical phylogeographic: methods of evaluating and minimizing inference errors. *Molecular Ecology* 13, 789–810.
- Trépanier, T.L., 2002. Conserving genetic diversity in fringe-toed lizards: a phylogenetic approach. Ph.D. Dissertation, Department of Zoology, University of Toronto.
- Trépanier, T.L., Murphy, R.W., 2001. The Coachella Valley Fringe-toed lizard *Uma inornata*: genetic diversity and phylogenetic relationships of an endangered species. *Molecular Phylogenetics and Evolution* 18, 327–334.
- Turner, F.B., Weaver, D.C., Rorabaugh, J.C., 1984. Effects of windblown sand on the abundance of the fringe-toed lizard (*Uma inornata*) in the Coachella Valley, California. *Copeia* 1984, 370–378.
- US Senate, 1979. Report 151, 96th Congress, 1st session.
- Upton, D.E., Murphy, R.W., 1997. Phylogeny of the side-blotched lizards (Phrynosomatidae: *Uta*) based on mtDNA sequences: support for a midpeninsular seaway in Baja California. *Molecular Phylogenetics and Evolution* 8, 104–113.
- US Department of the Interior, 1980. Endangered and threatened wildlife and plants; listing as threatened with critical habitat for the Coachella Valley fringe-toed lizard. *Federal Register* 45, 63812–63820.
- US Department of the Interior and US Department of Commerce, 1996. Policy regarding the recognition of distinct vertebrate population segments under the Endangered Species Act. *Federal Register* 61, 4722–4725.
- US Fish and Wildlife Service, 1994. Desert Tortoise (Mojave Population) Recovery Plan, Portland, OR.
- Van Devender, T.R., 1977. Holocene woodlands in the southwestern deserts. *Science* 198, 189–192.
- Van Devender, T.R., 1990. Vegetational and climatic development of the Mojave Desert: the last Glacial Maximum to the Present. In: Betancourt, J.L., Van Devender, T.R., Martin, P.S. (Eds.), *Packrat Middens: The Last 40,000 Years of Biotic Change*. University of Arizona Press, Tucson, AZ, pp. 166–199.
- Van Devender, T.R., Burgess, T.L., 1985. Late Pleistocene woodlands in the Bolson de Mapimi: a refugium for the Chihuahuan Desert biota? *Quaternary Research* 24, 346–353.
- Wells, S.G., Brown, W.J., Enzel, Y., Anderson, R.Y., McFadden, L.D., 2003. Late Quaternary geology and paleohydrology of pluvial Lake Mojave, southern California. In: Enzel, Y., Wells, S.G., Lancaster, N. (Eds.), *Paleoenvironments and Paleohydrology of the Mojave and Southern Great Basin Deserts*. Geological Society of America Special Paper 368, pp. 79–114.
- Welsh Jr., H.H., 1994. Bioregion: An ecological evolutionary perspective and a proposal for California. *California Fish and Game* 80, 97–124.
- Wilgenbusch, J.A., de Queiroz, K., 2000. Phylogenetic relationships among the phrynosomatid sand lizards inferred from mitochondrial DNA sequences generated by heterogeneous evolutionary processes. *Systematic Biology* 49, 592–612.
- Woodcock, D., 1986. The late Pleistocene of Death Valley: a climatic reconstruction based on macrofossil data. *Palaeogeography Palaeoclimatology Palaeoecology* 57, 273–283.