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Amphibians and Reptiles of the Madrean Archipelago of Arizona and New Mexico

ROBERT L. BEZY¹ AND CHARLES J. COLE²

ABSTRACT

The Madrean Archipelago in southern Arizona and southwestern New Mexico consists of 22 mountain ranges south of the Mogollon Rim. Herpetofaunal lists for these ranges and a segment of the rim were constructed based on museum specimens from Madrean evergreen woodland, petran montane conifer forest, and interior chaparral. Few or no species have been recorded from these communities in the Sierrita, Little Dragoon, and Big Hatchet mountains, emphasizing the need for additional sampling in the archipelago. A total of 83 species are found in the remaining 20 ranges, with lizards (28) and snakes (35) predominating. No two mountain ranges had the same herpetofauna. Species richness varies from 15 to 44 (mean 28.1). Phenetic analyses of herpetofaunal similarity among the ranges identify three groups: a northern group with eight ranges from the Rincon Mountains to the Pinaleno Mountains to the Sierra Ancha; a southwestern group consisting of the Baboquivari, Santa Rita, Pajarito, and Patagonia mountains; and a southeastern group with seven ranges from the Huachuca and Whetstone mountains to the Animas Mountains; the Mogollon Rim segment is placed as the first "branch" of the phenogram. The analyses place the Patagonia Mountains in the SW group and the Huachuca Mountains in the SE group, although the two are connected by woodland. The Madrean line separating the northern group from the two southern groups approximates the southern limit of interior chaparral. The ranges of the southwestern group are in contact with semitropical Sonoran desert scrub at low elevations, whereas Chihuahuan desert scrub and semidesert grassland surround the southeastern ranges. With few exceptions, published studies of phylogeography within species suggest that divergence among montane populations in the archipelago does not predate the Pleistocene. Phylogeographic

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analyses using nuclear and mitochondrial gene sequences and including all ranges of the Madrean Archipelago inhabited by a species are needed to determine the extent to which shared historic biogeographic events may underlie the groups of mountain ranges identified on the basis of herpetofaunal similarities in this study.

INTRODUCTION

The distribution of biota on islands has long fascinated biogeographers (e.g., Wallace, 1881; Darlington, 1938; MacArthur and Wilson, 1967; Rosen, 1975). Much of this work is focused on islands separated by aquatic environments, yet biogeography remains understudied for the biota of exclusively terrestrial archipelagos such as those composed of mountain ranges isolated by lowlands with biotic communities that are unfavorable to the montane species (sometimes referred to as “sky islands”).

For more than a century, southeastern Arizona has been recognized as having an unusually high number of species (Mearns, 1907; Swarth, 1929; Van Rossem, 1936; Gloyd, 1937; Marshall, 1957), sometimes referred to as a *biodiversity hotspot*. The species richness can be attributed to the topography of the region, with isolated mountain ranges reaching 3000 m and supporting mesic pine-oak woodlands and dense conifer forests. These ranges rise from biotically diverse lowlands where two major North American deserts, the Sonoran and Chihuahuan, meet, and the vast Great Plains reach their western terminus. The area has become known as the Madrean Archipelago owing to its isolated mountain ranges scattered across the 500 km gap between the northern end of Mexico’s Sierra Madre Occidental and the Mogollon Rim (fig. 1).

Surprisingly, few lists of amphibians and reptiles have been published for ranges in the archipelago, but species richness is high in the few U.S. Madrean ranges inventoried to date (e.g., Lowe, 1992; Morrison et al., 1995; Turner et al., 2003; Swann et al., 2005; Flesch et al., 2010).

Here we present, analyze, and discuss data for the distribution of species of amphibians and reptiles among the mountain ranges of the Madrean Archipelago of Arizona and New Mexico based on museum vouchered records. These provide a descriptive biogeography of the ranges of the archipelago and reveal distributional patterns, which we discuss. The study also highlights ranges that remain poorly sampled and for which additional field work is needed. We hope this paper will stimulate thorough sampling of populations within the Madrean region for phylogeographic analyses of DNA sequences that may identify repeated phylogenetic patterns within the archipelago (e.g., Barber, 1999; Leaché and Reeder, 2002; Holycross and Douglas, 2007; Tennesen and Zamudio 2008; Burbrink et al., 2011).

MATERIALS AND METHODS

STUDY AREA

The study area was delineated to include the mountain ranges in Arizona and southwestern New Mexico that support Madrean evergreen woodland (= “woodland”) as determined by



FIGURE 1. Map of the Madrean Archipelago in southeastern Arizona and southwestern New Mexico with the 23 ranges for which herpetofaunal lists were constructed.

examination of the map of biotic communities of the Southwest by Brown and Lowe (1980). The westernmost range is the Baboquivari Mountains at ca. 110.6°W in Pima County, Arizona; the easternmost is the Big Hatchet Mountains at 108.4°W in Hidalgo County, New Mexico. The southern limit was set at the U.S. boundary, as the herpetofauna of most of the Mexican ranges of the Madrean Archipelago (= “archipelago”) remain sparsely sampled (e.g., Van Devender et al., 2013). The northern boundary was set at the Mogollon Rim (= “rim”) in Arizona at ca. 34.4°N near Strawberry in Gila County, as Madrean evergreen woodland reaches its northern limit just below the rim at 32.2°N.

MOUNTAIN RANGES

Mountain ranges were included in the study if they have Madrean evergreen woodland and/or petran montane conifer forest (= “forest”). Mountain blocks were considered to be separate ranges if they were not bridged by either of these two biotic communities or by interior chaparral (= “chaparral”). For Madrean ranges, the one exception is that the Huachuca Mountains in Arizona (east of the Canelo Hills) were considered separate from the Patagonia Moun-

TABLE 1

Pairwise comparisons of geographic distance (km, above diagonal) and the Simpson coefficient for herpetofaunal similarity (S, below the diagonal) among 19 mountain ranges in the Madrean Archipelago and a segment of the Mogollon Rim.

Range	Baboquivari	Santa Rita	Pajarito	Patagonia	Mule	Whetstone	Dragoon	Huachuca	Chiricahua	Peloncillo	Animas	Galiuro	Santa Catalina	Rincon	Pinalaño	Santa Teresa	Pinal	Mazatzal	Sierra Ancha	Rim
Baboquivari		59	26	83	147	70	143	107	186	236	254	126	70	80	156	153	153	183	191	257
Santa Rita	0.95		21	11	67	21	64	29	107	156	183	70	46	24	104	107	134	201	197	281
Pajarito	0.81	0.80		14	93	61	107	107	140	177	210	123	87	79	104	107	136	199	196	277
Patagonia	0.71	0.93	0.81		57	17	61	0	96	136	191	84	77	47	117	131	166	233	223	321
Mule	0.57	0.83	0.83	0.61		47	11	21	33	94	97	77	107	74	94	133	186	260	246	343
Whetstone	0.57	0.90	0.62	0.52	0.57		31	20	79	147	150	53	53	20	83	100	140	211	200	291
Dragoon	0.60	0.87	0.67	0.53	0.53	0.67		61	26	50	73	26	67	40	49	84	140	214	197	293
Huachuca	0.81	0.76	0.65	0.70	0.83	0.86	0.73		71	104	136	83	86	56	114	134	173	243	234	324
Chiricahua	0.76	0.73	0.64	0.52	0.74	0.71	0.87	0.76		11	33	20	83	63	14	64	126	204	181	286
Peloncillo	0.81	0.81	0.75	0.63	0.65	0.71	0.73	0.69	0.72		13	116	174	139	100	159	217	311	276	374
Animas	0.47	0.80	0.60	0.67	0.73	0.73	0.53	0.80	0.87	0.93		133	190	153	130	181	239	324	301	399
Galiuro	0.60	0.80	0.67	0.53	0.53	0.60	0.67	0.73	0.80	0.73	0.47		24	30	17	14	36	113	97	193
Santa Catalina	0.71	0.69	0.67	0.59	0.78	0.71	0.80	0.61	0.61	0.63	0.67	0.73		7	57	49	54	117	113	210
Rincon	0.62	0.77	0.77	0.55	0.59	0.62	0.73	0.82	0.77	0.77	0.60	0.80	0.95		64	63	94	161	154	246
Pinalaño	0.67	0.68	0.64	0.48	0.70	0.62	0.60	0.75	0.64	0.54	0.67	0.80	0.75	0.77		4	61	141	121	220
Santa Teresa	0.57	0.71	0.57	0.64	0.50	0.64	0.57	0.79	0.64	0.64	0.43	0.64	0.86	0.71	0.86		20	100	73	174
Pinal	0.48	0.57	0.53	0.33	0.61	0.67	0.47	0.53	0.43	0.40	0.53	0.67	0.67	0.68	0.71	0.71		7	10	90
Mazatzal	0.62	0.66	0.57	0.41	0.61	0.71	0.60	0.49	0.48	0.53	0.60	0.80	0.69	0.77	0.71	0.79	0.77		0	0
Sierra Ancha	0.67	0.63	0.53	0.48	0.57	0.71	0.67	0.63	0.53	0.47	0.60	0.80	0.72	0.91	0.79	0.79	0.67	0.69		0
Rim	0.33	0.50	0.50	0.41	0.48	0.48	0.47	0.61	0.43	0.39	0.60	0.47	0.61	0.64	0.54	0.57	0.50	0.54	0.71	

tains (west of the San Rafael Valley) in spite of the two being bridged by woodland. This was done to evaluate potential differences in their herpetofaunas, as indicated by our original familiarity with these areas. Also, the Sierra Ancha and the Mazatzal Mountains were considered as separate ranges, although they are joined by forest via the Mogollon Rim (fig. 1, table 1).

SPECIES

A preliminary list of species found in southeastern Arizona and southwestern New Mexico was compiled based on our field experiences over more than 40 years and the range maps in Degenhardt et al. (1996), Stebbins (2003), Brennan and Holycross (2009) and accounts in the *Catalogue of North American Amphibians and Reptiles*. Names follow Crother (2012) with few exceptions.

Some putative species were included in broader taxa, particularly ones that have been recognized from analyses of DNA sequences but that lack clearly diagnostic morphological features and/or lack a well-defined geographic range owing to sparse sampling for molecular data. These composites include: *Sceloporus magister* (includes *S. bimaculosus* and *S. magister* of Schulte et al., 2006, but suggested by Leaché and Mulcahy, 2007, to represent a single species); *Aspidoscelis sonora* (includes *A. flagellicauda* and *A. sonora* of Lowe and Wright, 1964); *Hypsiglena torquata* (includes *H. chlorophaea*, *H. jani*, and *H. "Cochise"* of Mulcahy, 2008); and *Lampropeltis pyromelana* (includes *L. knoblochi* and *L. pyromelana* of Burbrink et al., 2011). Owing to sparse sampling in the Madrean region for DNA analyses of the *Sceloporus undulatus* complex (Leaché and Reeder, 2002) we assigned all populations in the area to *S. cowlesi* although in some cases they may represent discrete montane and lowland forms that have not yet been teased apart.

DISTRIBUTION

From June to November 2013, data for museum vouchers from Arizona and New Mexico for 111 species found in or near the study area were downloaded from available collections from HerpNET (<http://www.herpnet.org>) and from the Arizona State University collection from MABA (<http://www.madrean.org/symbfauna/collections/index.php>). Data from the AMNH were accessed directly from the herpetology collection data base. When correct identification of specimens was doubtful, we examined the specimens or requested digital photographs for confirmation. Localities with which we were not personally familiar, but which were considered potentially to be within mountain ranges, were located on Terrain Navigator and then viewed with Google Earth containing a layer with a digitized version of Brown and Lowe's 1980 map of Southwestern Biotic Communities downloaded from the Nature Conservancy (http://azconservation.org/downloads/5biotic_communities_of_the_southwest_gis_data). Species with localities that were found to be in Madrean evergreen woodland, petran montane conifer forest, or interior chaparral were scored as present in the range ("montane occurrences"). Localities found to be in plains and great basin grassland, semidesert grassland, Chihuahuan desertscrub, and Sonoran desertscrub were not interpreted as indicating species presence in a range (= "nonmontane occurrences"). When a locality was located very near a biotic community boundary, it was viewed at near-ground level in Google Earth to help make the assignment. A significant portion of the localities were sufficiently vague to preclude definitive biotic community assignment and were ignored when in doubt. Some localities appeared to represent base camps where specimens were pooled from surrounding areas and these were used only when supported by additional localities in the range.

For the Whetstone Mountains, museum specimens were augmented for three species from Madrean evergreen woodland by records listed in Turner et al. (2003). These authors vouchered each species by depositing specimens in the University of Arizona collection, but the specimens were not necessarily from woodland. Four species were added to the herpetofaunal list for the Rincon Mountains that were not vouchered by museum specimens but listed by Flesch et al. (2010) as occurring at high elevation in the range.

For several species we limited distribution to ranges listed in publications: *Anaxyrus microscaphus* (see Sullivan, 1993), *Lithobates chiricahuensis*, *L. pipiens*, and *L. yavapaiensis* (see Platz and Mecham, 1979; Platz and Frost, 1984; Platz, 1993; Goldberg et al., 2004b). We realize that ongoing research indicates the existence of additional populations of these species.

LOCALITY DATA

Locality data were downloaded via the MABA website from the herpetology collection of Arizona State University (ASU). The following institutions provided locality data via the Herpnet portal: California Academy of Sciences (CAS); Carnegie Museum of Natural History (CM); Cornell University, Museum of Vertebrates (CU); Field Museum of Natural History (FMNH); University of Kansas Natural History Museum (KUNHM); Natural History Museum of Los Angeles County (LACM); Louisiana Museum of Natural History, Louisiana State University (LSU); Museum of Comparative Zoology, Harvard University (MCZ); Milwaukee Public Museum (MPM); Museum of Southwestern Biology, University of New Mexico (MSB); Museum of Vertebrate Zoology, University of California (MVZ); Sam Noble Oklahoma Museum, University of Oklahoma (OMNH); San Diego Natural History Museum (SDSNH); Texas Cooperative Wildlife Collection, Texas A&M University (TCWC); University of Texas (TNHC); University of Arizona Museum of Natural History (UAZ); University of Colorado Museum (UCM); Florida Museum of Natural History, University of Florida (UF); Smithsonian National Museum of Natural History (USNM); Amphibian and Reptile Diversity Research Center, University of Texas at Arlington (UTA); Centennial Museum, University of Texas at El Paso (UTEP); Peabody Museum, Yale University (YPM). The San Diego Natural History Museum provided digital images.

STATISTICAL ANALYSES

As species numbers for the ranges were small and unequal, and sampling effort for the ranges was unequal, we employed the Simpson small-sample coefficient for paired faunal comparisons: $S = C/N1$ where C is the number of shared species and $N1$ is the number of species in the range with the fewest species (Simpson, 1960; Fallow, 1979). Ranges were clustered using UPGMA (unweighted pair group method with arithmetic mean) with the Simpson coefficient in PAST (<http://folk.uio.no/ohammer/past>). Least squares regressions were calculated with Systat 13.

RESULTS

MOUNTAIN RANGES

A total of 23 ranges in the study area were identified as having Madrean evergreen woodland or petran montane conifer forest (fig. 1). Two ranges, the Sierrita Mountains, Pima County, Arizona, and Little Dragoon Mountains, Cochise County, Arizona, were eliminated owing to lack of records. A few species have been vouchered from Texas Canyon along the SE side of the Little Dragoons, but none could be clearly identified as having been collected in woodland. The Big Hatchet Mountains in Hidalgo County, New Mexico, reach an elevation of 2549 m with woodland; the range is currently being inventoried by others and was not included in the study.

The remaining 20 ranges in the study area are listed in table 1 and appendix 1. Several of these include smaller satellite ranges: Baboquivari (Quinlan, Coyote), Santa Rita (San Cayento), Pajarito (Atascosa), Galiuro (Winchester), and Chiricahua (Dos Cabezas, Swisshelm, Pedregosa).

SPECIES

A total of 111 species were identified as potentially occurring in or near the Madrean study area. Examination of museum records indicated that eight of these fail to reach the area: *Aspidoscelis xanthonota*, *Crotaphytus nebrius*, *Dipsosaurus dorsalis*, *Phrynosoma goodei*, *Urosaurus graciosus*, *Chionactis occipitalis*, *Crotalus cerastes*, and *Phyllorhynchus decurtatus*.

DISTRIBUTION

Of the 103 species found in the study area, 83 (81%; 1 salamander, 16 anurans, 3 turtles, 28 lizards, and 35 snakes) have at least one montane record (i.e., a museum specimen taken in Madrean evergreen woodland, petran montane conifer forest, or interior chaparral; appendix 1). The number of species per range varies from 15 (Galiuro, Santa Teresa) to 44 (Santa Rita) with a mean of 31.2, but no two mountain ranges have the same herpetofauna. The montane herpetofauna is most diverse for snakes (a mean of 12.8 species per range), lizards (11.2) and anurans (4.7).

Across the 83 species of amphibians and reptiles, the mean number of ranges occupied by a species is 6.8. The most widely distributed species are: *Hyla arenicolor* (17 ranges), *Aspidoscelis sonorae* (19), *Elgaria kingii* (17), *Phrynosoma hernandesi* (18), *Sceloporus clarkii* (20), *Urosaurus ornatus* (20), *Coluber bilineatus* (19), *Crotalus molossus* (17), and *Thamnophis cyrtopsis* (18).

Eleven species have a montane record for only one range. Most (6) of these are lowland species with an incidental record in chaparral or woodland. Four species that are more widely distributed on the Colorado Plateau are present in the study area only at the Mogollon Rim (*Lithobates pipiens*, *Aspidoscelis velox*, and *Plestiodon multivirgatus*) or in the nearby Mazatzal Mountains (*Aspidoscelis pai*). The *Thamnophis rufipunctatus* complex is present at the rim and also occurs to the south in the Sierra Madre Occidental. *Sceloporus poinsettii* is widely distributed to the east and is present in Madrean woodland only in the Animas Mountains of southwestern New Mexico.

HERPETOFAUNAL SIMILARITY

Cluster analysis using UPGMA and the Simpson similarity coefficient suggests the existence of three clusters of montane herpetofauna in the study area (figs. 2, 3): a northern cluster (Sierra Ancha, Mazatzal, Pinal, Santa Teresa, Santa Catalina, Rincon, Galiuro, and Pinaleño mountains) and a southern cluster composed of a southwestern cluster (Baboquivari, Santa Rita, Patagonia, and Pajarito mountains) and a southeastern cluster (Whetstone, Huachuca, Dragoon, Mule, Chiricahua, Peloncillo, and Animas mountains). The Mogollon Rim is placed as the first “branch” of the phenogram.

GEOGRAPHIC DISTANCE

Least squares regressions of the Simpson S values on minimum straight-line distances (km) between the mountain ranges were calculated for pairwise comparisons of ranges within phenetic groups ($S = 0.768 - 0.00020 \text{ km}$) and between phenetic groups ($S = 0.707 - 0.00057 \text{ km}$; fig. 4). The slopes of the lines were found not to be significantly different from each other or from 0, suggesting minimal effect of geographic distance on faunal similarity. A significant difference was found between the Y intercepts ($t = 2.924$, $df = 167$, $p = <0.01$), reflecting greater similarity within the phenetic clusters of ranges.

DISCUSSION

Gloyd (1937) delineated herpetofaunal regions in southern Arizona and placed the western limit of the Madrean zone in the Santa Rita Mountains. Marshall's 1957 seminal work on avifauna of the Mexican pine-oak woodland was the first modern treatment of the biogeography of the archipelago. He also contributed importantly to our knowledge of the herpetofauna, including the discovery of *Crotalus willardi* in the San Luis Mountains long before the population was known to herpetologists, described as a distinct subspecies, and placed on the endangered species list (see Greene, 1997, for details).

Lowe (1992) coined the term Madrean Archipelago for the region and defined the Madrean line separating the herpetofauna associated with the Sierra Madre Occidental from that of the Rocky Mountains and Colorado Plateau, using the complementary distributions of species of *Crotalus* as examples. The Madrean line subsequently has been examined and discussed in terms of the herpetofauna by Stitt et al. (2005), Swann et al. (2005), Archie et al. (2006), and Flesch et al. (2010). Those studies were hampered by the absence of species lists of amphibians and reptiles for many of the ranges.

Our approach involves examining the occurrence (presence or absence) of species in montane biotic communities rather than designating “indicator species,” or assigning “ecological affinities.” The species lists (appendix 1) are based on museum vouchers with localities that were found to be within a range's Madrean evergreen woodland, petran montane conifer forest, or interior chaparral as mapped by Brown and Lowe (1980). A total of 83 species were thus

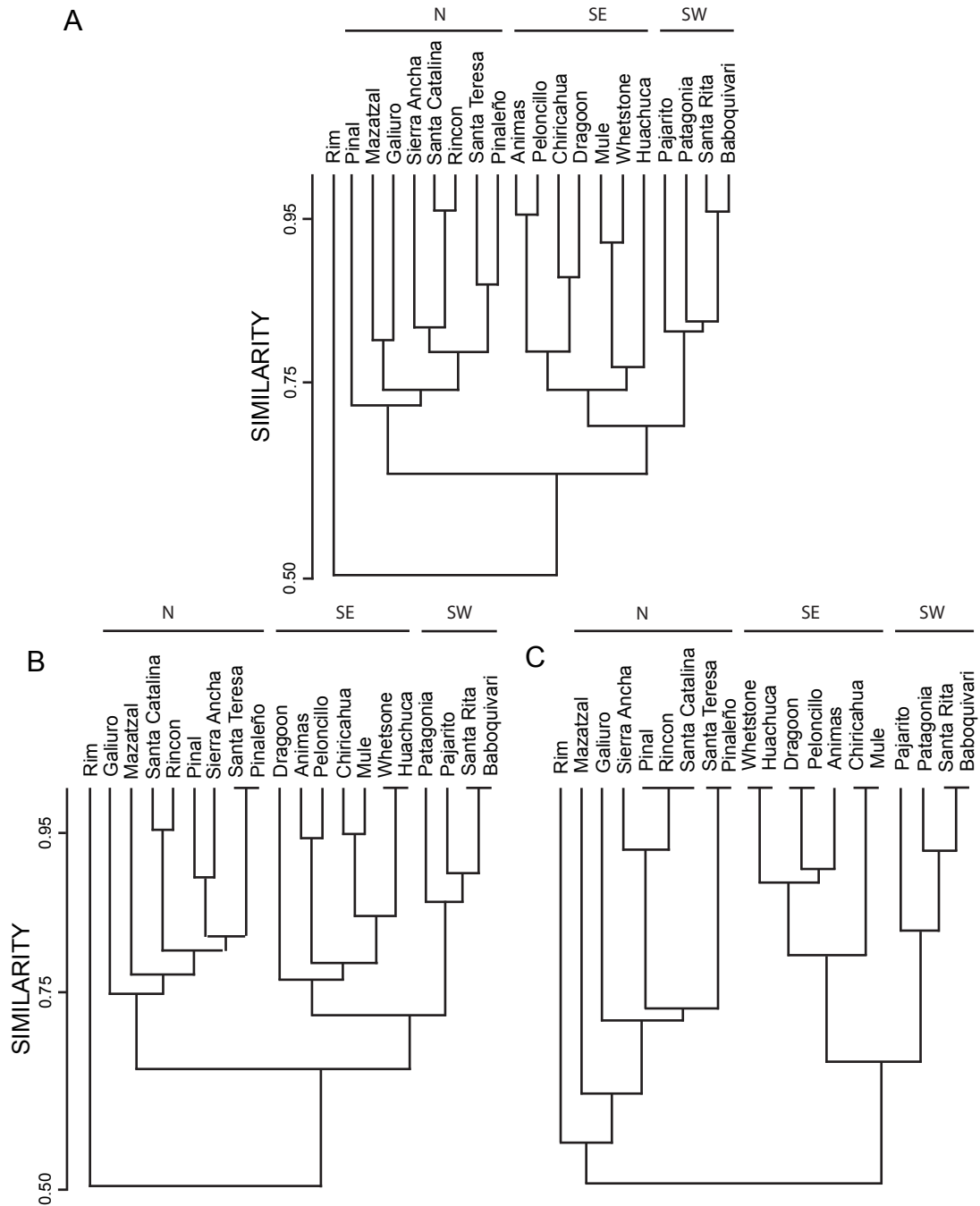


FIGURE 2. Phenograms of the 20 mountain ranges based on UPGMA clustering of the Simpson coefficient of similarity (S) among the herpetofaunas, using **A**. all 83 species recorded from Madrean evergreen woodland, petran montane conifer forest, and interior chaparral (appendix 1); **B**. 57 species, with 26 species eliminated as occurring primarily in desert and grassland; **C**. 28 species that were considered to occur primarily in Madrean evergreen woodland and higher elevations.

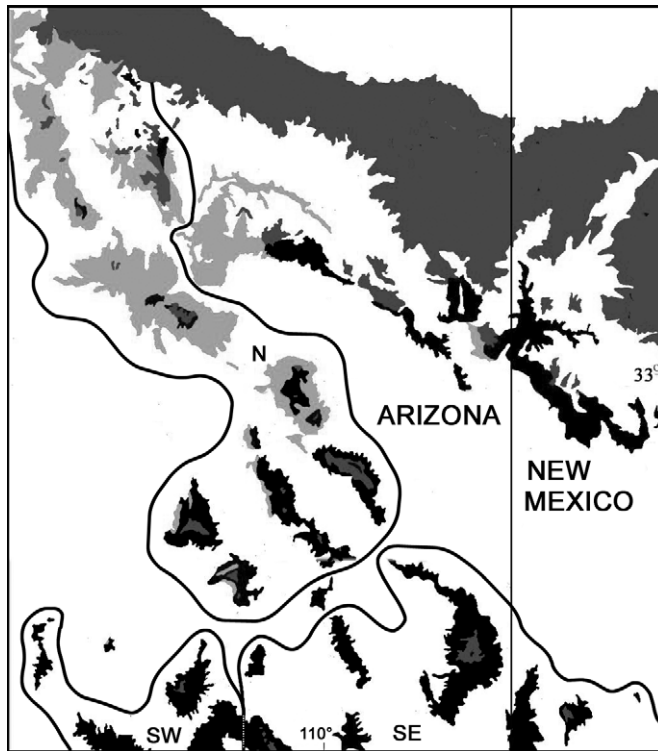


FIGURE 3. Map of mountain ranges of the Madrean Archipelago with lines delineating the three phenetic groups recognized from UPGMA clustering using the Simpson coefficient of similarity (S) among the herpetofaunas.

documented in the ranges; with few exceptions, the 562 range occurrences were substantiated by multiple localities within each of the montane biotic communities.

PHENETIC CLUSTERS

The phenogram (fig. 2A) derived from our species lists identifies two major clusters in the Madrean Archipelago: a southern group of 11 ranges (the Baboquivari, Santa Rita, Pajarito, Patagonia, Whetstone, Mule, Huachuca, Dragoon, Chiricahua, Peloncillo, and Animas mountains) and a northern group of eight ranges (the Pinaleno, Santa Teresa, Rincon, Santa Catalina, Galiuro, Pinal, Sierra Ancha, and Mazatzal mountains) with the Mogollon Rim sample placed as the first "branch." The group allocations of the Sierrita, Little Dragoon, and Big Hatchet mountains remain to be determined. Of the 83 species found in woodland and/or chaparral in the area, 20 (24%) occur only in the southern group, 15 (18%) only in the northern group of ranges (including the rim), and 48 (58%) in both. The northern and southern groups of mountain ranges are separated by Lowe's (1992) Madrean line.

The Pinaleno Mountains were pointed out by Lowe (1992) to have Madrean as well as Mogollon species of *Crotalus*. Our phenogram (fig. 2A) places the range in the northern group,

nearest to the geographically proximate Santa Teresa Mountains. The Pinaleño herpetofauna includes three exclusively northern group species (*Coluber taeniatus*, *Crotalus cerberus*, and *Thamnophis elegans*). *Crotalus pricei* is the only species in the Pinaleño Mountains that otherwise is known exclusively from southern ranges. This occurrence continues to present a puzzling biogeographic anomaly.

The phenogram (fig. 2A) indicates the existence of two clusters within the southern group: a southwestern group composed of four ranges (the Baboquivari, Santa Rita, Pajarito, and Patagonia mountains) and a southeastern group containing seven ranges (the Whetstone, Mule, Huachuca, Dragoon, Chiricahua, Peloncillo, and Animas mountains). Of the 67 species found in the southern group, 13 (19%; including *Gastrophryne mazatlanensis*, *Lithobates tarahumarae*, *Gyalopion quadrangulare*, and *Oxybelis aeneus*) are found only in the southwestern group, 12 (18%; including *Hyla wrightorum*, *Aspidoscelis exsanguis*, *Sceloporus poinsettii*, and *S. virgatus*) only in the southeastern group, and 42 (63%) in both. The two clusters are not isolated in terms of biotic communities, as Madrean evergreen woodland is continuous between the Patagonia Mountains (southwestern group) and the Huachuca Mountains (southeastern group) via the Canelo Hills.

Pairwise comparisons of faunal similarity (Simpson S) between ranges are consistent with the three clusters identified in the phenetic analyses (table 1). Comparisons within the northern group (mean S = 0.76) are higher than those between the northern group and either the southwestern group (0.59) or the southeastern group (0.60). Mean S values are higher for pairwise comparisons within the southwestern group (0.84) and within the southeastern group (0.73) than between the two groups (0.69). Regression analyses indicate that the effect of geographic distance on herpetofaunal similarity is not statistically significant, but confirm higher similarity (S) for within-group comparisons (table 1, fig. 4).

The present data do not identify species that define the three phenetic clusters (appendix 1). *Crotalus cerberus* is absent in southern group ranges and present in all ranges of the northern group, except that it has yet to be vouchered from the Santa Teresa Mountains. *Crotalus lepidus* is present in all ranges of the southeastern group except the Mule Mountains and is present in the Santa Rita Mountains of the southwestern group. *Craugastor augusti* is present in all four southwestern group ranges (Bezy et al., 1966; Enderson et al., 2004) but also occurs in the Huachuca Mountains of the southeastern group. *Sceloporus jarrovii*, often viewed as a Madrean indicator species, is absent in the Pajarito Mountains, present in the Galiuro, Pinaleño, and Santa Teresa mountains, and appears to have been introduced into the Santa Catalina Mountains (Archie et al., 2006).

SPECIES RICHNESS

We have not attempted a statistical analysis of factors with which species richness is correlated. On casual inspection, it does not appear that richness is correlated with the maximum elevation of the range. The highest species numbers in the archipelago are found in two ranges of the southwestern group: the high-profile Santa Rita Mountains (maximum elevation 3881 m with petran montane conifer forest; 44 species) and the low profile Pajarito Mountains (1957

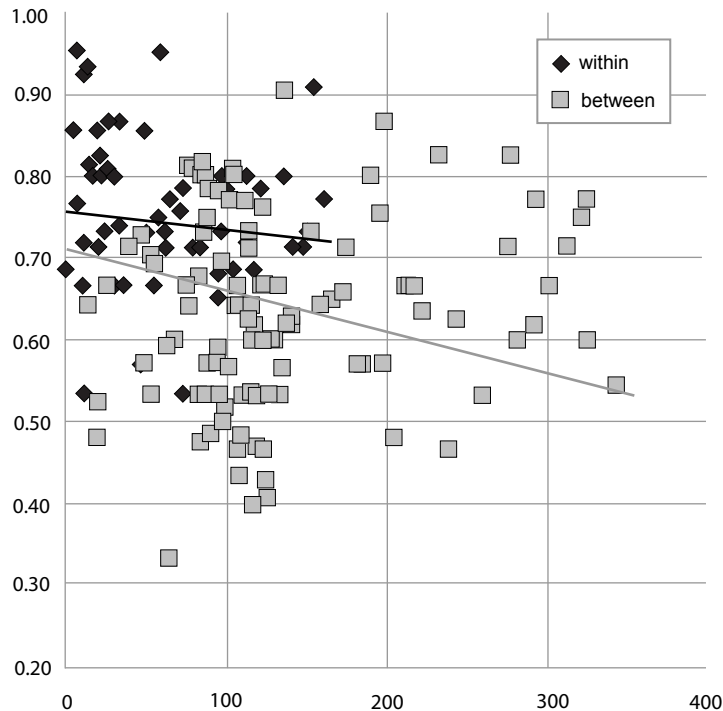


FIGURE 4. Regression analysis of the Simpson coefficient of similarity (S) on geographic distance (km) for pairwise comparisons of mountain ranges and herpetofaunas within the three phenetic groups (black diamonds and line: $S = 0.768 - 0.00020 \text{ km}$) and between the groups (gray squares and line: $S = 0.707 - 0.00057 \text{ km}$).

m with Madrean evergreen woodland; 41 species). Other species rich ranges include the Huachuclas (2885 m, 38 species), Chiricahuas (2986 m, 35 species), and Peloncillos (1829 m, 35 species) in the southeastern group, and the Santa Catalina (2791 m, 36 species) and Mazatzal Mountains (2334 m, 35 species) in the northern group.

The herpetofaunas of several ranges remain poorly documented, particularly for nocturnal species. The most extreme example of this is the Sierrita Mountains, Pima County, Arizona, which attain an elevation of 1886 m and have a small stand of Madrean evergreen woodland. We found no museum records from the woodland, which is surprising considering that it is located only 48 km SE of the large herpetological collection at the University of Arizona Museum of Natural History (UAZ). The Little Dragoon Mountains, Cochise County, Arizona, reach an elevation of 2050 m with woodland. A few species have been vouchered from Texas Canyon along the SE side of the range, but none was clearly identifiable as having been collected in woodland.

Relatively few species have been vouchered from woodland or chaparral in the Santa Teresa (15 species), Galiuro (inclusive of Winchester, 15 species) and Dragoon (16 species) mountains. It remains to be determined to what degree this indicates reduced species richness in these low-profile ranges, or, as we suspect, a need for additional field investigation.

INCIDENTALS

Our method for determining the presence of a species in a given range of the Madrean Archipelago avoids designating species as montane or lowland. For example, for the Chiricahua Mountains our list includes *Crotalus pricei*, restricted to high-elevation talus slopes; *Urosaurus ornatus* found from desert and grassland to the summit of the range; and *Terrapene ornata* found in the surrounding grassland, but recorded from Madrean evergreen woodland at one locality in the range.

The question arises as to whether these occasional records of desert and grassland species in Madrean evergreen woodland may have influenced our finding of three phenetic clusters of ranges in the archipelago. For example, in the southeastern cluster, species with records primarily in Chihuahuan Desert and grassland occasionally have been recorded in woodland, whereas in the southwestern and northern clusters there are a few woodland records for species that occur primarily in the Sonoran Desert. Thus, did differences in the occurrence of lowland fauna impact our delineation of range clusters?

Although we favor our first method for constructing the herpetofaunal lists, for the sake of comparison, the complete list was reduced (1) by eliminating the 26 species we considered to occur primarily in desert and/or grassland with occasional incidental records in Madrean evergreen woodland (fig. 2B); and (2) by eliminating all species except the 28 that we considered to occur primarily in Madrean evergreen woodland and higher elevations in the archipelago (fig. 2C). We recognize these designations are subjective and no two herpetologists would necessarily be in agreement on all species.

The resulting alternative phenograms (figs. 2B, 2C) have the same three clusters (northern, southwestern, and southeastern) composed of the same ranges as the phenogram based on the complete species list, except that the rim is placed in the northern group for montane species (fig. 2C). We conclude that incidental occurrences in Madrean evergreen woodland of desert and grassland species do not obscure the range clusters, and may contribute to the resolution of herpetofaunal similarities.

ECOLOGICAL BIOGEOGRAPHY

In the most general terms, the herpetofauna of the Madrean Archipelago can be considered to represent a segment of the transition between the Neotropics and the North Temperate zone. If there were an absence of topographic diversity one might anticipate a simple south to north gradient of decreasing percentage of species adapted to high summer precipitation and mild winter temperatures.

Rosen (2007) detailed a somewhat parallel herpetofaunal shift that occurs west of the archipelago, the transition from Arizona upland thornscrub–desert to the arid Lower Colorado Valley–Mojave Desert. Based on museum vouchers and his field experience he plotted the limits of distribution for eight species pairs of ecologically analogous lizards and snakes. The turnover in the fauna is remarkably abrupt and consistent among species, although slight differences exist between the valley floor and rocky *bajadas* (“slopes”).

Topography plays a major role in the Madrean Archipelago transition. Species ranging north from thornscrub, tropical deciduous forest, and the Pacific slopes of the Sierra Madre Occidental become increasingly restricted to the mountain ranges of the archipelago, as Sonoran and Chihuahuan desertscrub come to dominate the valleys and bajadas (Lowe, 1992; Van Devender et al., 1994). To the north, the increased precipitation and cooler summer temperatures at higher elevations become negatively impacted by winter freezes. The present northern limit of the summer-rainfall adapted Madrean evergreen woodland is just below the Mogollon Rim at ca. 34.07°N, 111.07°W, whereas the winter-precipitation adapted interior chaparral extends southward to the Sierrita Mountains at ca. 31.91°N, 111.22°W (Brown and Lowe, 1980; Brown, 1994). Thus, the two biotic communities overlap by ca. 263 km in Arizona. Across this distance the herpetofauna of the mountain ranges transitions from that associated with the Sierra Madre Occidental to that of the Colorado Plateau.

Our phenetic analyses of herpetofaunal similarities among the ranges indicate that species turnover is greatest across a line separating the Santa Ritas from the Rincons consistent with previous discussions (Lowe, 1992; Turner et al., 2003; Stitt et al., 2005; Swann et al., 2005; Archie et al., 2006; Flesch et al., 2010). This line extends eastward between the Dragoons and the Galiuro-Winchester mountains. Unfortunately, the herpetofaunal similarities of the Sierritas and Little Dragoons remain unknown. Our analyses place the Pinalenos north of the line and the Chiricahua and Animas mountains south of it.

The range limits of individual species of amphibians and reptiles within the archipelago are determined by several ecological factors, but most conspicuous is the gradient from higher summer monsoonal rainfall and higher winter minimal temperatures in the south to higher winter precipitation and lower winter minimal temperatures in the north (data and climographs in Brown, 1994). This gradient is reflected in the biotic communities of the region as the Madrean line marking the southern limit of the northern herpetofaunal group corresponds approximately with the southern limit of interior chaparral and the northwestern limit of the Chihuahuan Desert on the bajadas of the ranges.

The division between the southeastern and southwestern groups of ranges is of particular interest as it separates the Patagonias from the Huachucas, which are connected today by continuous Madrean evergreen woodland. West of the "line" the ranges are largely surrounded by the semitropical Arizona upland thornscrub-desert, whereas to the east the valleys and bajadas are dominated by Chihuahuan desertscrub and semidesert grassland where freezes may occur more than 100 nights a year (Brown, 1994). Climate in the Madrean evergreen woodland may reflect this difference in bajada communities and this may partially explain the restriction of species such as *Oxybelis aeneus* and *Gyalopion quadrangulare* to western ranges in contact with subtropical Arizona upland thornscrub-desert (Van Devender et al., 1994).

HISTORICAL BIOGEOGRAPHY

It is difficult to estimate how long the herpetofaunal transitions between the three range groups may have been located in their present position. During the past 10,000 years and throughout much of the late Pleistocene the distribution and composition of woodland, chap-

arral, grassland, and desert biotic communities in the Southwest have been in dynamic flux (Van Devender, 1977, 1990; Van Devender and Spaulding, 1979; Betancourt et al., 1990). Woodlands composed of single-needle piñon (*Pinus monophylla*), junipers (*Juniperus*) and scrub oak (*Quercus turbinella*) occurred 11,000 B.P. in what is now the Sonoran Desert, suggesting a climate dominated by winter rainfall and cool summer temperatures. This may have favored the occurrence of species of amphibians and reptiles associated with the Colorado Plateau south of the present Madrean line. The present range limits, particularly for species such as *Oxybelis aeneus* and *Gyalopion quadrangulare*, may date from 4,000 B.P. when the climate became more subtropical (Van Devender et al., 1994). During each major climatic shift relictual populations of some species may have survived in various ranges of the archipelago resulting in a distributional mosaic such as seen in montane species of *Crotalus* and *Tantilla*. Such mosaic patterns of distribution may be responsible for the lack of correlation between herpetofaunal similarity and geographic distance between ranges (fig. 4), but they appear not to have completely obscured the existence of the three groups of mountain ranges recovered in our analyses (figs. 2, 3). Again, it should be emphasized that these groups represent the results of phenetic clustering of overall herpetofaunal similarity values among the ranges. None of these groups is definable by species that are both (1) present in all ranges within the group, and (2) absent from all other ranges within the study area.

Do the groups of Madrean ranges identified in our phenetic analysis of the herpetofauna exclusively reflect Recent geographic patterns of ecoclimatic factors, or do they also contain the signature of deeper historical biogeographic events? The near absence of species of amphibians and reptiles endemic to ranges within the Madrean Archipelago obfuscates reconstruction of the historical biogeography in the region based on the phylogenetic relationships of species. However, phylogeographic analyses of gene sequences among populations in the ranges offer a potential venue for detecting signatures of deeper historical vicariant events.

A number of species found in the archipelago have been included in studies of DNA phylogeography, e.g., the *Ambystoma tigrinum* complex (see Shaffer and McKnight, 1996), *Anaxyrus punctatus* (see Bryson et al., 2012a), *Craugastor augusti* (see Goldberg et al., 2004a), *Gastrophryne mazatlanensis* (see Streicher et al., 2012), *Hyla arenicolor* (see Bryson et al., 2010; Klymus and Gerhardt, 2012), *Hyla wrightorum* (see Gergus et al., 2004), *Lithobates chiricahuensis* (see Goldberg et al., 2004b), *Phrynosoma hernandesi* (see Zamudio et al., 1997), *Sceloporus slevini* (see Bryson et al., 2012b), the *Sceloporus undulatus* complex (see Leaché and Reeder, 2002), *Sceloporus virgatus* (see Tennessen and Zamudio, 2008), *Xantusia bezyi* (see Sinclair et al., 2004), *Crotalus cerberus* (see Douglas et al., 2006); *Crotalus willardi* (see Holycross and Douglas, 2007); *Lampropeltis pyromelana* (see Burbrink et al., 2011), and *Thamnophis rufipunctatus* (see Wood et al., 2011).

In the majority of these studies, the mountain ranges in the archipelago were too sparsely sampled to evaluate the potential of the gene segments and populations to shed light on the historical biogeography of the region. For others, molecular divergence seems to be minimal. For example, Gergus et al. (2004) found no fixed differences in allozymes between the *Hyla wrightorum* from the Huachuca Mountains, Mogollon Rim, and the northern Sierra Madre Occidental, although a unique mitochondrial haplotype was fixed in the populations of the Huachuca Mountains.

Barber (1999) included many of the ranges in his initial study of phylogeography of *Hyla arenicolor*. He recovered a southern clade (2B) extending from the Huachuca and Pajarito mountains to the Rincon Mountains, a northern clade (2A) from the Rincon and Santa Catalina mountains to the Pinaleno Mountains, and a southeast-central clade (1A) extending from the Peloncillo and Chiricahua mountains to near the Mogollon Rim. The distributions of these clades are only vaguely congruent with the range groups identified in this paper. In subsequent work, RFLP data have been used to increase phylogenetic resolution (Klymus and Gerhardt, 2012) and nuclear gene sequences have been examined to clarify the role of hybridization in the phylogeny of the complex (Bryson et al., 2010), but these studies have not significantly altered the composition of the clades found in the archipelago.

Burbrink et al. (2011) examined phylogeography in *Lampropeltis pyromelana* using sequences from both nuclear and mitochondrial genes, and concluded that populations associated with the Mogollon Rim and Colorado Plateau (*L. pyromelana*) diverged from those of the Madrean Archipelago (*L. knoblochi*) prior to the Pleistocene. Sequences from several southern ranges (Santa Rita, Pajarito, Patagonia, Huachuca, Chiricahua, Peloncillo, and Animas mountains) were examined, but unfortunately the study did not include samples from any of the Arizona ranges that extend north to the rim (Rincon, Santa Catalina, Pinal, Mazatzal, and Sierra Ancha mountains).

Using sequences from nuclear and mitochondrial genes for populations of the *Thamnophis rufipunctatus* complex, Wood et al. (2011) estimated divergence times between three core populations of 0.53 and 0.16 mya. They concluded that Pleistocene climatic fluctuations led to shifts along elevational gradients but not to wholesale latitudinal shifts. Further, they hypothesized that during warm, dry cycles, the low-elevation populations of this aquatic species likely were extirpated, thus reducing gene flow between the high-elevation core populations.

One of the most interesting studies of phylogeography of the herpetofauna in the archipelago is that of *Sceloporus virgatus* by Tennesen and Zamudio (2008). They examined mitochondrial gene sequences from multiple localities in the four ranges at the northern limit of the species distribution, finding that the within-range samples exhibited reciprocal monophyly and that the between-range divergence time estimates were greater than 1 mya. This is an intriguing finding considering that two of the ranges (Animas and San Luis mountains) are presently connected by a woodland corridor that is within the elevational scope of the species (Cole, 1963; Tennesen and Zamudio, 2008). Thus, past conditions favoring woodland and chaparral across the bajadas of the archipelago do not necessarily indicate that gene exchange occurred between all populations.

From research to date, a pattern of congruent topologies of phylogeographic relationships among populations of species in the Madrean Archipelago has not emerged, at least for amphibians and reptiles. Additional studies employing samples of multiple populations of all ranges inhabited by a species and utilizing both nuclear and mitochondrial markers are needed to determine whether gene tree topologies are sufficiently congruent among montane populations to signal shared vicariant events that may underlie the phenetic groups of ranges identified in this study.

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APPENDIX 1

The occurrence of 83 species of amphibians and reptiles in 19 mountain ranges of the Madrean Archipelago and a section of the Mogollon Rim.

Taxon	Baboquivari	Santa Rita	Pajarito	Patagonia	Mule	Whetstone	Dragoon	Huachuca	Chiricahua	Peloncillo	Animas	Galiuro	Santa Catalina	Rincon	Pinaleno	Santa Teresa	Pinal	Mazatzal	Sierra Ancha	Rim	
Caudata																					
<i>Ambystoma mavortium</i>				1				1											1	1	
Anura																					
<i>Anaxyrus cognatus</i>	1						1	1					1								
<i>Anaxyrus microscaphus</i>																			1	1	
<i>Anaxyrus punctatus</i>	1	1	1		1	1	1	1	1	1			1	1	1		1	1	1	1	
<i>Anaxyrus woodhousii</i>			1		1			1							1		1				
<i>Craugastor augusti</i>	1	1	1	1				1													
<i>Gastrophryne mazatlanensis</i>			1																		
<i>Hyla arenicolor</i>	1	1	1	1		1		1	1	1	1		1	1	1	1	1	1	1	1	
<i>Hyla wrightorum</i>								1											1	1	
<i>Lithobates blairi</i>									1												
<i>Lithobates chiricahuensis</i>		1	1				1	1	1	1		1									
<i>Lithobates pipiens</i>																				1	
<i>Lithobates tarahumarae</i>		1	1																		
<i>Lithobates yavapaiensis</i>		1	1																1	1	
<i>Ollotis alvaria</i>		1	1							1			1						1		
<i>Pseudacris maculata</i>																				1	
<i>Spea multiplicata</i>		1	1					1	1	1			1						1		
Testudines																					
<i>Gopherus morafskai</i>			1										1								
<i>Kinosternon sonoriense</i>			1					1	1	1	1		1	1					1	1	
<i>Terrapene ornata</i>									1												
Squamata – Lizards																					
<i>Aspidoscelis burti</i>		1	1	1			1			1			1	1							
<i>Aspidoscelis exsanguis</i>									1	1	1										
<i>Aspidoscelis pai</i>																				1	
<i>Aspidoscelis sonora</i>	1	1	1	1	1	1	1	1	1	1			1	1	1	1	1	1	1	1	
<i>Aspidoscelis tigris</i>		1											1		1				1	1	
<i>Aspidoscelis velox</i>																				1	
<i>Coleonyx variegatus</i>	1	1				1													1	1	
<i>Cophosaurus texanus</i>							1		1	1		1	1	1	1	1	1	1	1	1	

Taxon	Baboquivari	Santa Rita	Pajarito	Patagonia	Mule	Whetstone	Dragoon	Huachuca	Chiricahua	Peloncillo	Animas	Galiuro	Santa Catalina	Rincon	Pinalaño	Santa Teresa	Pinal	Mazatzal	Sierra Ancha	Rim
<i>Crotaphytus collaris</i>					1	1		1	1	1	1		1	1	1		1	1	1	1
<i>Elgaria kingii</i>		1	1		1	1	1	1	1	1	1	1	1	1	1		1	1	1	1
<i>Heloderma suspectum</i>													1				1	1		
<i>Holbrookia elegans</i>	1	1	1	1	1			1	1	1			1	1						
<i>Phrynosoma hernandesi</i>		1	1	1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Phrynosoma solare</i>		1											1						1	
<i>Plestiodon callicephalus</i>	1	1	1	1				1		1										
<i>Plestiodon multivirgatus</i>																				1
<i>Plestiodon obsoletus</i>	1	1	1			1		1	1	1		1		1	1		1	1	1	
<i>Sauromalus ater</i>																				1
<i>Sceloporus clarkii</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Sceloporus cowlesi</i>								1					1	1	1	1	1	1	1	1
<i>Sceloporus jarrovii</i>	1	1		1	1	1	1	1	1	1	1	1			1	1				
<i>Sceloporus magister</i>		1																	1	1
<i>Sceloporus poinsettii</i>											1									
<i>Sceloporus slevini</i>		1				1		1	1											
<i>Sceloporus virgatus</i>									1	1	1									
<i>Urosaurus ornatus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Uta stansburiana</i>															1		1	1		
<i>Xantusia bezyi</i>												1					1	1		
Squamata – Snakes																				
<i>Coluber bilineatus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Coluber flagellum</i>			1																1	
<i>Coluber taeniatus</i>															1	1	1	1	1	
<i>Crotalus atrox</i>		1		1									1							1
<i>Crotalus cerberus</i>												1	1	1	1		1	1	1	1
<i>Crotalus lepidus</i>		1				1	1	1	1	1	1									
<i>Crotalus molossus</i>	1	1	1	1	1	1	1	1	1	1	1		1	1	1				1	1
<i>Crotalus pricei</i>		1						1	1						1					
<i>Crotalus scutulatus</i>																			1	1
<i>Crotalus tigris</i>			1							1										
<i>Crotalus willardi</i>		1		1		1		1		1	1									
<i>Diadophis punctatus</i>	1	1	1	1	1	1		1	1	1	1		1		1				1	1
<i>Gyalopion canum</i>		1	1	1																
<i>Gyalopion quadrangulare</i>		1	1	1																
<i>Hypsiglena chlorophaea</i>		1	1	1	1			1					1		1	1				1

Taxon	Baboquivari	Santa Rita	Pajarito	Patagonia	Mule	Whetstone	Dragoon	Huachuca	Chiricahua	Peloncillo	Animas	Galiuro	Santa Catalina	Rincon	Pinalero	Santa Teresa	Pinal	Mazatzal	Sierra Ancha	Rim
<i>Lampropeltis getula</i>			1										1		1				1	
<i>Lampropeltis pyromelana</i>	1	1	1	1	1			1	1	1	1		1	1	1				1	1
<i>Micruroides euryxanthus</i>		1	1	1	1													1	1	
<i>Oxybelis aeneus</i>			1	1																
<i>Pituophis catenifer</i>		1	1		1	1	1	1	1				1	1					1	1
<i>Rena dissectus</i>					1			1	1											
<i>Rena humilis</i>			1										1							
<i>Salvadora grahamiae</i>	1	1	1	1	1			1	1	1		1	1	1	1	1	1			1
<i>Salvadora hexalepis</i>		1	1	1	1	1		1	1	1	1		1					1	1	1
<i>Senticolis triaspis</i>	1	1	1	1					1	1										
<i>Sonora semiannulata</i>						1		1					1			1	1			
<i>Tantilla hobartsmithi</i>	1	1				1	1			1		1	1	1		1			1	1
<i>Tantilla wilcoxi</i>		1		1				1												
<i>Tantilla yaquia</i>		1	1		1				1	1										
<i>Thamnophis cyrtopsis</i>	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1			1	1
<i>Thamnophis elegans</i>															1					1
<i>Thamnophis eques</i>								1												1
<i>Thamnophis marcianus</i>										1										
<i>Thamnophis rufipunctatus</i>																				1
<i>Trimorphodon lambda</i>	1	1	1		1			1	1	1			1		1			1	1	

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