Biogeography of Amphibians and Reptiles in Arizona

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Abstract—*We examined patterns of species richness for amphibians and reptiles in Arizona and evaluated patterns in species distribution between ecoregions based on species range size. In Arizona, the Sonoran Desert has the highest herpetofauna diversity, and the southern ecoregions are more similar than other regions. There appear to be distinct low- and mid-elevational faunas. There was no difference in elevational measures or species range sizes between species groups. However, species widespread in one ecoregion tended to have larger distributions in other ecoregions. Relating similarity indices to phylogenies and paleontological information will help us better understand the patterns of colonization and speciation that make Arizona such a herpetologically diverse place.*

Introduction

Arizona has long fascinated herpetologists. Beginning with the early railroad-related surveys and continuing to the present with the herpetofauna-as-pets upsurgence, Arizona has long been a Mecca for both amateurs and professionals in the field (e.g., Kauffeld 1957; Kauffeld 1969; Bartlett 1987). Only in a few other States can one observe such a diversity of reptiles and amphibians and experience such a wide range of habitats in which they occur. Among these animals, Arizona has species that are greatly modified for sand-swimming (*Chilomeniscus cinctus*) and arboreal foraging (*Oxybelus aeneus*); or that are venomous (*Micruroides euryxanthus*, *Crotalus* spp.), toxic (*Bufo alvarius*), cryptic (*Phrynosoma* spp.), alert and speedy (*Draconoides callisaurus*, *Cnemidophorus* spp., *Masticophis* spp.), slow and deliberate (*Gopherus agassizii*), or visually stunning (*Lampropeltus pyromelana*). One of only 2 venomous lizards occurs here (*Heloderma suspectum*), and there are more rattlesnake species here than anywhere else in the United States.

Given the diversity of species, and the attention received from professional and amateur herpetologists, it is surprising that no Statewide biogeographic analysis of Arizona's herpetofauna exists. Gloyd (1937) defined faunal areas in southern Arizona according to the distribution of its herpetofauna, but paid no attention to northern Arizona. Stewart (1994), Lowe (1994), and Morafka and Reyes (1994) assessed the herpetofaunas of the Mojave, Sonoran, and Chihuahuan Deserts, respectively. More locally, Lowe (1992) made the case for a north-south boundary line demarcating northern and southern species near Tucson, and assessed differences in faunas at Saguaro National Park by elevation. Lastly, Duellman and Sweet (1999) included Arizona in a comprehensive biogeographic analysis of the amphibians of North America: reptiles were not included. However, to our knowledge there is no Statewide analysis that relates the distribution of all Arizona herpetofauna to faunistic provinces or biogeographic regions.

Inspired by recent re-readings of *The Vertebrates of Arizona* (Lowe 1964), we initiated a biogeographic analysis of Arizona's herpetofauna. The objective of our paper is to use quantitative biogeographic techniques and GIS to determine similarities between regional herpetofaunas in Arizona and to characterize the uniqueness of these taxonomic groups in Arizona.

Methods

Using methods similar to those of Duellman and Sweet (1999), we digitized 125 species distribution maps found in Stebbins (1985) with ARC/view for all herpetofauna species whose ranges occur at least partially in Arizona. We digitized only at the species level; species containing more than one subspecies in Arizona were only considered at the species level. Among amphibians, there are 24 anurans and one salamander (excluded from further analyses). Among reptiles, 50 are snakes, 41 are lizards, and 4 are turtles after excluding introduced species.

We analyzed amphibian and reptile distributions according to Omernik's (1987) ecoregions (table 1), which may be considered as faunistic provinces, defined primarily by the species present and the ecological differences between regions (figure 1). We assigned presence/absence status to each species for each ecoregion and used the entire extent of each ecoregion rather than truncating the species' range at the Arizona border. We excluded established introduced species from our analysis (*Hemidactylus turcicus*, *Rana catesbeiana*, *Xenopus laevis*, *Rana berlandieri*, *Apalone spinifera*, and *Trachemys scripta*, as well as *Ambystoma tigrinum*, whose native range in Arizona is confounded by introductions of non-natives). Two species, *Kinosternon arizonense*, *and Chrysemys picta belli*, have been recently described for Arizona and are not included

Table 1—The size and elevational range of the 6 ecoregions that occur in Arizona (Omernik 1987).

Ecoregion	Total area (km²)	Area in AZ (km²)	Area in AZ (%)	Elev. range (m)
Arizona Mountains Forests	109,135	61,760	56.6	1,370 – 3,000
Chihuahuan Desert	513,427	32,160	6.23	600 – 1,500
Colorado Plateau Shrublands	326,765	89,929	27.5	1,500 – 4,000
Mojave Desert	131,271	15,039	11.5	0 – 2,000
Sierra Madre Occidental Pine-oak Forests	223,435	6,902	3.09	1,500 – 3,000
Sonoran Desert	222,982	88,729	39.8	0 – 1,500

in this analysis. A consequence of using Stebbins (1985) for this analysis was that we had to use an older taxonomy than is currently recognized, which may underestimate the currently accepted number of species in Arizona by approximately 9% (Averill-Murray, personal communication).

Because the scale of maps in Stebbins (1985) is large and generalized, we proofed species presence/absence according to elevation range (according to Stebbins 2003) and commonly accepted distribution (e.g., *Crotalus lepidus* not known to occur north of the Santa Rita Mountains, *Dipsosaurus dorsalis* not known from Chihuahuan Desert). In ambiguous cases we took a conservative approach and considered a species as present. To determine the degree of similarity between ecoregions, we calculated the Coefficient of Biogeographic Resemblance (Duellman 1990) between each pair, where

Faunal Similarity = $[2C/(N_1 + N_2)][100]$.

Here, C is the number of species common to the two regions, N_1 is the number of species in the first ecoregion, and N_2 is the number of species in the second ecoregion. By multiplying that term by 100 we express similarity as a percentage. Lastly, we estimated each species' distribution in hectares within the 6 ecoregions and compared species range size between ecoregions.

Results

The Sonoran Desert has the most species-rich herpetofauna in Arizona (99 species), followed by the Chihuahuan Desert (94 species) (table 2). The Mojave Desert has the lowest diversity (56 species). The Chihuahuan Desert and Sierra Madre Occidental Pine-oak Forests share the highest percentage of species (94.1%), followed by the relationship between Arizona Montane Forests and Colorado Plateau Shrublands, at 91.0% (table 2). The least relationship between faunas is between the Mojave Desert and Sierra Madre Occidental Pine-oak Forests, which share 49.7% of their faunas.

In Arizona, amphibians and reptiles occur from approximately sea level to the highest elevations; however, the mean elevation occupied is 1,380 m. We found no difference between amphibians and reptiles in mean elevation occupied (t-test, $t_{113} = 0.89$, $p = 0.38$; amphibians-mean = 1,512 m, 95% CI = 1,182 – 1,841 m; reptiles-mean = 1,346 m, 95% CI = 1,177 – 1,515 m), and we found no difference in mean elevation occupied between anurans, lizards, and snakes (ANOVA, $F_{2, 112} = 0.390$, $p = 0.678$; anurans-mean = 1,512 m, 95% CI = 1,181 – 1,843 m; lizards-mean = 1,349 m, 95% CI = 1,096 – 1,602 m; snakes-mean = 1,343 m, 95% CI = 1,114 – 1,573 m).

The distribution of the lowest elevational limit for species' ranges is distinctly bimodal, showing peaks at 0 m and 900 m, with a long right tail (figure 2). We found no difference in lowest elevation occupied by amphibians and reptiles (ANOVA, $F_{1, 113} = 0.213$, $p = 0.656$; amphibians-mean = 634 m, 95% CI = 431 – 838 m; reptiles-mean = 687 m, 95% CI = 583 – 792 m). Also, we found no difference between anurans, lizards, and snakes (ANOVA, $F_{2, 112} = 0.114$, $p = 0.892$; anurans-mean = 634 m, 95% CI = 430 – 839 m; lizards-mean = 696 m, 95% CI = 539 – 852 m; snakes-mean = 681 m, 95% CI = 540 – 823 m).

Thirty-three species may be considered ubiquitous, occurring in all 6 ecoregions, and 4 species can be considered endemic to a given ecoregion. *Chionactis palorostris* and *Uma notata* occur only in the Sonoran Desert, *Hyla regilla* is endemic only to the Mojave Desert, and *Rana blairi* occurs only in the Chihuahuan Desert.

The mean species distribution size between all ecoregions was 7,003,718 ha (95% CI = 6,207,660 – 7,799,777 ha). Range size did not differ between class (t-test, $t_{712} = -1.209$, $p = 0.227$; amphibians-mean = 6,028,612 ha, 95% CI = 4,256,603 – 7,800,622 ha; reptiles-mean = 7,250,061, 95% CI = 6,359,404 – 8,140,716 ha), or between anurans, lizards, and snakes (ANOVA, $F_{2, 687} = 1.132$, $p = 0.323$; anurans-mean = 6,028,612 ha, 95% CI = 4,244,086 – 7,813,138 ha; lizards-mean = 6,965,385, 95% CI = 5,600,058 – 8,330,711 ha; snakes-mean = 7,677,135, 95% CI = 6,440,778 – 8,913,490 ha). Those species that had larger ranges in one ecoregion generally had large ranges in adjacent ecoregions (table 3). In pairwise comparisons of distribution size between ecoregions, those pairs that did not have significant positive relationships were usually between lower elevation deserts and adjacent higher elevation ecoregions (table 3). In the lower-elevation deserts, species occupied a larger proportion of the entire ecoregion than in the higher-elevation mountain ranges and shrublands (linear contrast, $t_{684} = -2.94$, $p = 0.003$).

Discussion

Arizona is indeed herpetologically diverse; however, the pattern of diversity is perhaps more complex than generally recognized. Surprisingly, Arizona is only in the top 25th percentile of all the United States for overall herpetofauna diversity,

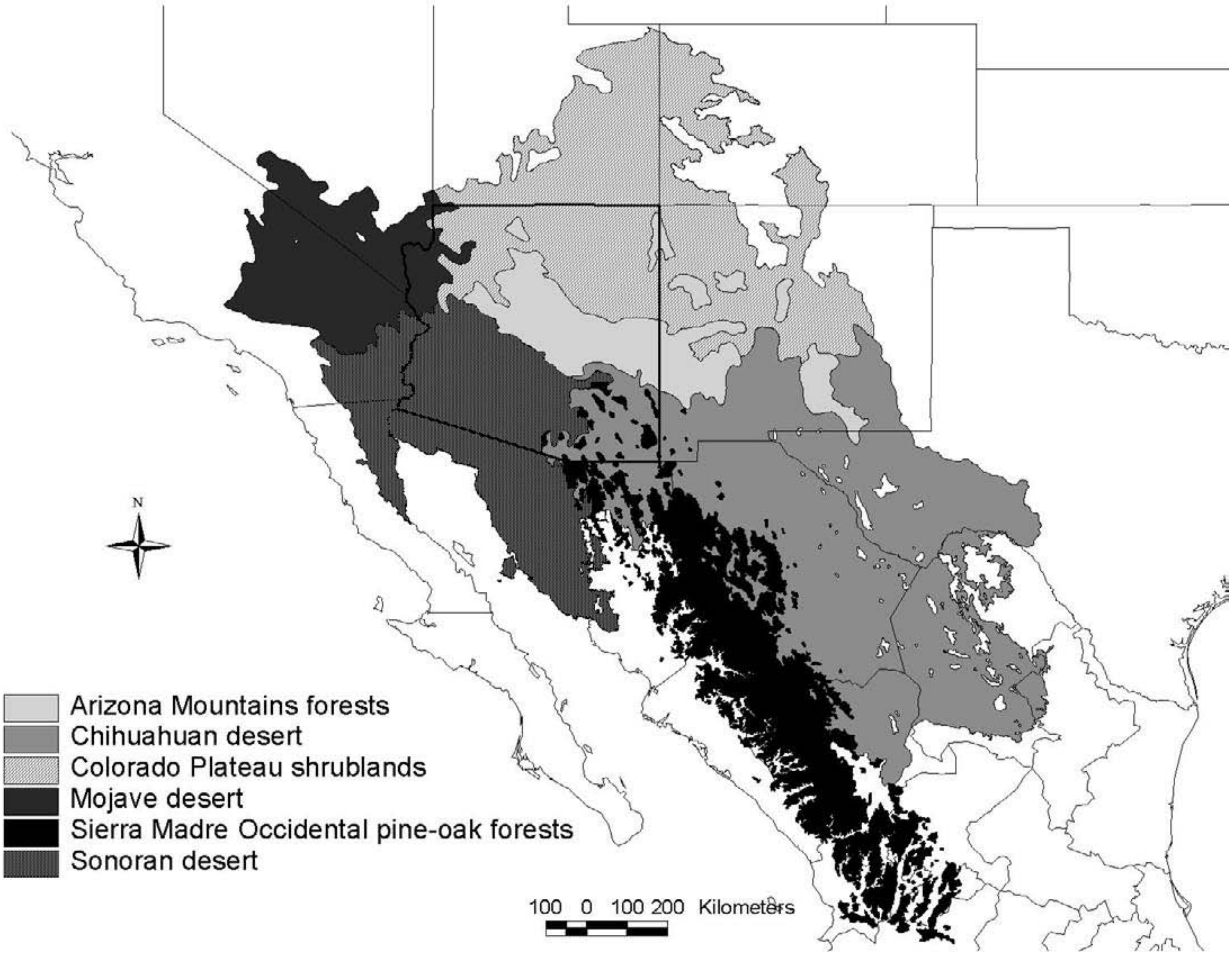

Figure 1—The 6 ecoregions as they occur in Arizona.

but second in the nation for reptile diversity (Stein 2002). Amphibian fauna is relatively depauperate, with Arizona in the lower 50th percentile of all the United States (Stein 2002). Clearly, the generally hot, dry conditions that characterize Arizona's ecoregions are not ideal for animals that have biphasic lifestyles and permeable skins, true toads (Bufonidae) and spadefoots (Pelobatidae) notwithstanding.

Herpetofauna diversity is greatest in the southeastern corner of Arizona (Sonoran Desert, Chihuahuan Desert, Sierra Madre Occidental Pine-oak Forests, in that order), the reasons for which are two-fold. First, in the continental United States, species richness is higher to the south than to the north. Secondly, 4 ecoregions meet here, each with their own assemblage. Sierra Madre Occidental Pine-oak Forests enter Arizona from the south, bringing middle- and high-elevation species from Mexico. Near Tucson, these isolated mountain ranges meet the Arizona Mountains Forests to the north (considered the southern extent of the Colorado Plateau), the Sonoran Desert to the west, and the Chihuahuan Desert to the east. This "hot-spot" of herpetofauna diversity has long been recognized (Gloyd 1937; Lowe 1964; Lowe 1992).

Patterns of greatest herpetofauna similarity involved either the Sierra Madre Occidental Pine-oak Forests (relationship with the Chihuahuan Desert, or with the Sonoran Desert), or the Arizona Mountains Forests (relationship with Colorado Plateau Shrublands). As discussed above, the Sierra Madre Occidental Pine-oak Forests reach their northern terminus where it meets 3 other distinct ecoregions. Here, the definition of elevational range for an ecoregion is undoubtedly somewhat arbitrary, and many species, whether considered "low elevation" or "high elevation," apparently have broad enough physiological tolerances to span across ecoregions where they grade from one to another. A similar effect may be shared between the Colorado Plateau Shrublands and Arizona Mountains Forests, which overlap in elevational range.

The patterns of similarity we found between the Sierra Madre Occidental Pine-oak Forests, the Chihuahuan Desert, and the Sonoran Desert are similar to the patterns recognized for amphibians only by Duellman and Sweet (1999). However, in their analysis, amphibian faunal similarity was greatest between Sierra Madre Occidental Pine-oak Forests and the Sonoran Desert (Coefficient of Biogeographic Resemblance = 64.3%)

Table 2—Relationship of herpetofauna by ecoregion. Number of species shared between ecoregions is in upper right, coefficient of biogeographic resemblance is in italics, lower left, and number of species in each region is in shaded common cell. Highest value is marked with an asterisk (*) and lowest value is underlined. AMF = Arizona Mountains Forests, CD = Chihuahuan Desert, CPS = Colorado Plateau Shrublands, MD = Mojave Desert, MSI = Sierra Madre Occidental Pine-oak Forests, and SD = Sonoran Desert.

	AMF	CD	CPS	MD	MSI	SD
AMF	82	71	71	46	67	68
CD	0.807	94	61	38	88	79
CPS	0.910	0.726	74	47	57	59
MD	0.667	0.507	0.723	56	37	50
MSI	0.766	0.941*	0.682	<u>0.497</u>	93	82
SD	0.751	0.819	0.761	0.645	0.854	99

Table 3—Pairwise correlations between ecoregions for species range size. For pairs that had positive correlations between them, widespread species in one ecoregion were also widespread in the other. Upper right cells represent probability, -- = no relationship, + = p<0.05, ++ = p<0.001. Cells in lower left represent correlation coefficient, N = 115 AMF = Arizona Mountains Forests, CD = Chihuahuan Desert, CPS = Colorado Plateau Shrublands, MD = Mojave Desert, MSI = Sierra Madre Occidental Pine-oak Forests, and SD = Sonoran Desert.

	AMF	CD	CPS	MD	MSI	SD
AMF		++	++	--	+	--
CD	0.4801		++	+	++	++
CPS	0.7897	0.3587		+	--	+
MD	0.1292	0.2162	0.2675		--	++
MSI	0.2741	0.3206	0.0597	-0.0788		--
SD	0.1581	0.3190	0.2023	0.7836	-0.0018	

and second greatest between Coefficient of Biogeographic Resemblance and the Chihuahuan Desert (56.3%). It appears that Duellman and Sweet (1999) took a more liberal approach to assigning species absence to their natural regions (comparable in scale to our ecoregions) than did we. Our ecoregions typically had 2-4 more species than did theirs.

A confounding factor might be the scale at which we performed this analysis. Shaded distribution maps are often not intended for analyses such as ours (Lowe 1994): the broad-scale and conservative approach we took may have obscured some differences between faunas. However, for determining general patterns, we believe our approach is sound and supported by previous biogeographic work (Duellman and Sweet 1999).

Although there were no differences in elevational range between reptiles and amphibians, or between anurans, lizards, and snakes, the emergence of 2 distinct lower-elevational limits (figure 2) is interesting and suggests that species can be clearly categorized by elevation. Lower-elevation species tended to be Mojavean animals with adaptations for fine sand (e.g., *Uma* spp., *Chilomeniscus cinctus*, *Crotalus cerastes*) or saxicoly (e.g., *Sauromalus obesus*, *Lichanura trivergata*), whereas middle-elevation species tended to be those associated with the Chihuahuan Desert or Madrean Sky Islands. A long right tail in figure 2 also indicates the presence of true montane species, those that occur only above 1,300 m.

Our estimate of the number of ubiquitous species seems reasonable. Many species are widely distributed but found only in patches, where habitat is available. Thus, Arizona has species like *Diadophis punctatus*, a wide-spread North American species generally occurring in more mesic areas, showing up in all ecoregions. However, we have probably underestimated local endemism. Some species known to be very limited in distribution, such as *Rana onca*, did not show as endemics in our analysis. In this specific case, *Rana onca* had a geographic range that spanned across the Mojave Desert and Colorado Plateau Shrublands border. It may be that the species actually occurs on the ecotone between the two regions; however, at the large scale of our distribution maps, the range of this and other animals with very small ranges was surely over estimated.

Related to ubiquity and local endemism, animals that occupied a large proportion of one ecoregion were also widespread across ecoregions. This pattern held especially true for lower elevation "desert" species, which occupied higher proportions of those lower ecoregions.

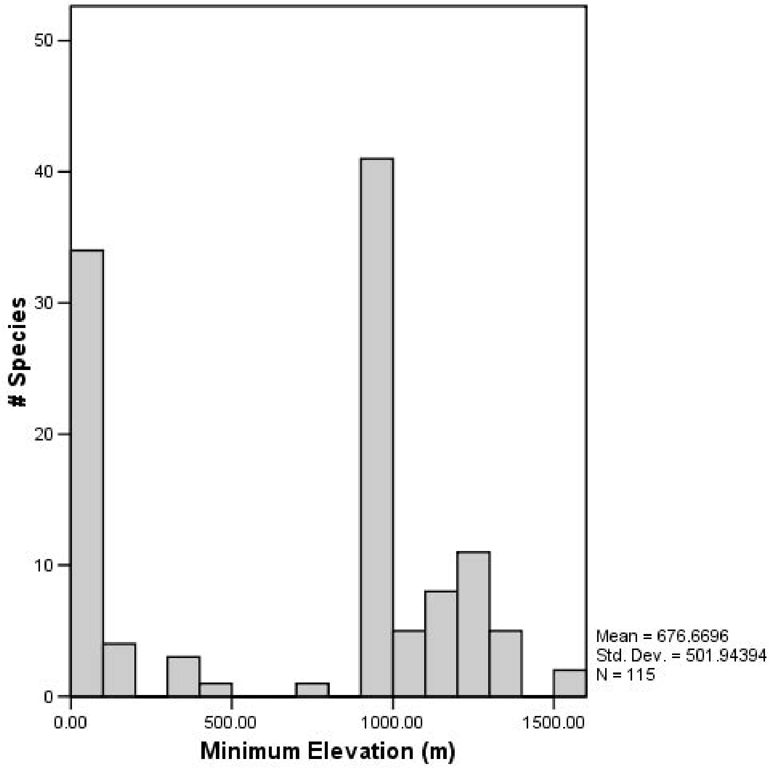

Figure 2—The lower elevational limit for herpetofauna in Arizona

The distribution of herpetofauna in Arizona continues to be a fascinating subject with many questions left to answer. The driving force for studies such as ours is to understand the patterns of colonization and speciation that have led to currently observed diversity. Analyses of faunal similarity between regions is a first step in such an endeavor. Future work should use molecular-based phylogenies and paleontological findings to help reconcile relationships between faunas and ecoregions. These, combined with more detailed analyses of present day faunal distributions including environmental correlates such as annual precipitation and temperature patterns, should provide a deeper understanding of the historical and current distribution of herpetofauna that makes Arizona so unique.

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