Herpetology of the American Madrean Archipelago and Adjacent Valleys

Lawrence L. C. Jones
Wildlife Program, USDA Forest Service, Coronado National Forest, Tucson, AZ

Abstract—*Approximately 110 species of amphibians (18 frogs and toads, and 1 salamander) and reptiles (47 snakes, 39 lizards, and 5 turtles) are known from the American Madrean Archipelago and adjacent valleys. The high diversity of the herpetofauna comes from a variety of factors, including a convergence of biotic communities representing deserts, grasslands, and mountains. Other environmental and ecological factors weigh heavily into the equation, making this one of the nation's richest herpetofaunas. Certain taxa are particularly speciose, including whiptails, rattlesnakes, and spiny lizards. Seventeen species are Mexican forms that barely enter the United States.*

Introduction

The American Madrean Archipelago (Sky Islands) and associated lowlands and foothills of southeastern Arizona and southwestern New Mexico (herein referred to as the Northern Sky Islands Realm, NSIR) is comprised of a series of mountains and valleys spanning over 7,000 vertical feet, from desertscrub to subalpine forests. This elevational range accounts for large differences in local climatic conditions, as well as supporting numerous biotic communities and a biologically diverse flora and fauna. This paper is a brief synthesis of the current knowledge of the NSIR's herpetofauna, with some discussion of the primary ecological and evolutionary factors accounting for such a high biodiversity. This paper also helps form a foundation for herpetological management on the Coronado National Forest (Jones and Painter, this volume).

Biological Diversity

The NSIR has long been known to harbor a diverse flora and fauna, and several papers addressed the topic in the first Madrean Archipelago symposium (DeBano and others 1995). The number of taxa from the NSIR includes about 2,100 species of plants (McLaughlin 1995), 466 species of birds (Davis and Russell 1991), 110 species of mammals (Bowers and others 2004), over 240 species of butterflies (southeastern Arizona, Bailowitz and Brock 1991), and most of the >176 species of mollusks reported by Bequaert and Miller (1973), plus many new species described after these accounts were published.

Amphibians and reptiles are also well-represented. Using the taxonomy of Crother and others (2000, 2003) and range maps of Stebbins (2003), primarily, we estimate the NSIR to have about 110 native species of reptiles and amphibians, as follows: 18 frogs and toads, 1 salamander, 47 snakes, 39 lizards, and 5 turtles and tortoises. Thus, the area has amongst the highest herpetofaunal diversity in the United States.

Biogeographic Origins of the Species

Lowe (1964) discussed the dizzying array of names and categories of various biogeographic units in Arizona, and due to space constraints, we will not delve into those discussions. Rather, we feel the most appropriate term for a functional biogeographical unit for our purposes is Herpetofaunal Assemblage (HA), which is analogous to *Faunal Area* of Gloyd (1937). HA designations are based on geography, herpetofaunal distribution patterns, and vegetative communities. We did not use the NSIR area itself for HA species designations. We feel there are three basic biotic (vegetative) communities, each with two HAs; these are described in table 1. Biotic communities generally relate to elevational differences, with deserts being the lowest, grass- and shrublands intermediate, and montane communities the highest.

To demonstrate the NSIR's herpetofaunal contributions, we assigned each species to one or more of the HAs, based on their "typical pattern of distribution and/or presumed origin." While this was done subjectively, in most cases their patterns were clearly allied to one or more of the HAs. Relative contributions of each HA to the NSIR herpetofauna were computed by tallying occurrences on a spreadsheet. For each species (row), a 1 was scored in each HA (column), where the animal typically occurs. These were tallied and columns divided by the grand total. The relative contributions (rounded) are: Chihuahuan Desert (22%), Sonoran Desert (21%), Great Plains (14%), Semidesert Grass- and Shrublands (22%), Madrean (17%), and Petran (5%). Clearly, all HAs contribute to the biodiversity, but the greatest contributions come from the southern and low- to mid-elevation HAs, while there is less contribution from montane and northern communities.

Table 1—Herpetofaunal assemblages recognized in this paper.

Biotic community	Herpetofaunal assemblage	Description
Desertscrub	Sonoran Desert	Primarily the Arizona Upland subdivision, to the west of our area.
	Chihuahuan Desert	Desertscrub lying southeast of our area
Grass- and Shrublands	Semidesert Grasslands	This includes the semi-desert grasslands, mesquite bosques, and other shrublands, and elements of subtropical thornscrub. This accounts for the mid-elevation grass- and shrublands of foothills and valleys at the desert and montane interface, primarily south of our area.
	Great Plains	A vast area of grasslands lying northeast of our area.
Montane	Petran	Oak/juniper woodlands to coniferous forests lying to the north of our area, allied to the Rocky Mountains.
	Madrean	Oak/juniper woodlands to coniferous forests to the south of our area allied to the Sierra Madre Occidental.

Other Mechanisms of Biodiversity

In addition to the biogeographic considerations discussed above, there are other environmental, ecological, and evolutionary factors contributing to biodiversity. There is a long growing season and many lowland species are surface-active much of the year. There is also a dual rainy season, with a spring peak of activity following the green-up produced by winter rains, then a larger peak during the summer monsoon season. In addition, special habitat features within biotic communities augment biodiversity by increasing habitat diversification. Riparian areas, meadows, talus slopes, and lentic and lotic habitats are examples of special features that can be found among different biotic communities.

On the evolutionary front, there are species or subspecies coming into contact in the NSIR, which has contributed to biodiversity. The whiptails are the premier example and have undergone an incredibly rapid speciation (Cole and Dessauer 1995). On the sub-species level, there are numerous examples of intergradation. Isolationism is another well-known factor, especially for montane forms. However, genetic diversity has not yet manifested itself on the species level. Animals living at high elevations in the Sky Islands are often genetically distinct from their nearby relatives, since gene flow has not occurred for thousands of years.

Representative and Noteworthy Taxa

Certain taxa are particularly well represented in our area, with several closely related species belonging to one or two genera. These include: whiptails (12 species), rattlesnakes (11 species), spiny lizards (8 species), true frogs (5 species), true toads (5 species), horned lizards (4 species), black-headed snakes (4 species), and gartersnakes (4 species). Often these species are known to co-occur in such small areas by partitioning resources, especially along elevational gradients, or because the NSIR is a mergence zone between HAs.

Whiptail lizards, genus *Aspidoscelis* (formerly *Cnemidophorus*), are particularly speciose in our area (Cole and Dessauer 1995). In addition, there are likely additional cryptic species that have yet to be described. *Aspidoscelis* is an interesting genus because many of the species are unisexual (all female), reproducing by parthenogenesis, resulting from the hybridization of two or more parental stocks (Cole and Dessauer 1995). *Aspidoscelis* are primarily denizens of grass- and shrub-land communities.

Rattlesnakes are represented by 11 species (2 genera) in our area, including about one-third of all known species and 79% of the species known from the United States. Five of the species are mountain dwellers, including 3 Madrean, 1 Petran, and 1 generalist species. The others are valley and/or foothill species. The Twin-spotted rattlesnake, a Madrean species, has been found as high as 10,500 ft. in the Pinaleño Mountains, a seemingly harsh environment for an ectotherm.

There are 8 species of spiny lizards (genus *Sceloporus*) in the NSIR, a genus that is also well represented south of our area (where there are about 77 total species). Along an elevational gradient from desert to subalpine forests, the large spiny lizards are partitioned as such: *S. magister* < *S. clarkii* or *S. poinsettia* < *S. jarrovii*. The smaller species are also habitat-partitioned.

Native ranid frogs include *Rana tarahumarae*, a Madrean endemic, and 4 species of leopard frogs. *Rana chiricahuensis* is a southern grassland to Cordilleran form, while the similar *R. yavapaiensis* is found at lower elevations. *Rana blairi* is a Great Plains species, while *R. subaquavocalis* is a Sky Island endemic.

Biologists have long recognized that our area was biologically important because numerous taxa are primarily Mexican species that barely enter the United States in the vicinity of the Sky Islands. There are currently 17 species of reptiles and amphibians that fall into this category (Stebbins 2003), including the Tarahumara frog, the only species that has been extirpated from our area. Two subtropical thornscrub species (*Oxybelis aeneus* and *Gyalopion quadrangulare*) have extremely limited ranges in southern Arizona, the only place they are found in the United States.

The fact that 19 species of amphibians can eek a living out of such a xeric environment is intriguing. While the mountains may receive fair amounts of rain and snowmelt, most of the species are valley-dwellers, and have developed mechanisms of adapting to xeric conditions, by using behavioral and physiological thermo-and hydro-regulation. Examples include explosive breeding (and rapid development) strategies, diel activity shifts, and seasonal activity shifts.

Discussion

Using terms such as "Appalachian" and "Madrean" to describe the herpetofaunal elements of the NSIR may be misleading, since only some species are allied to those mountains, and geographically, most species are lowland forms. Additionally, many species found in the cores of each of the HAs are often lacking in the NSIR. For example, there are numerous montane species found in the Sierra Madre Occidental of Mexico that are not known from the NSIR (McCranie and Wilson 1987). The same is true for all HAs. Herpetofaunal endemism on the species level is very low in the NSIR, and there is not a distinctive herpetofaunal assemblage of the NSIR and adjacent Mexican Sky Islands.

Thus, from a herpetological perspective, the NSIR is a mergence zone of HAs rather than a biogeographical province itself, or part of the Sierra Madre Occidental proper. This concept is similar to that of Morafka (1977) who termed the NSIR the "Cochise Filter." His designation was primarily directed to the relationship of the Chihuahuan and Sonoran herpetofaunas, whereas ours is extended to include middle and upper elevations. The concept of a filter is helpful, as some species occur up to the NSIR boundaries, while others pass through the boundary. However, we can further refine biogeographic tendencies across the various biotic communities by recognizing the following observed patterns (with examples in brackets): (1) some species do not occur beyond the boundary of an HA adjacent to NSIR (Trans-Pecos Rat Snake, of Chihuahuan Desert); (2) some species occur into the NSIR from an adjacent HA (but not beyond) by interdigitating into appropriate habitat (Sonoran Coral Snake); (3) some species "spill over" from an adjacent HA, occupying at least some atypical habitat in NSIR, but are not found in the opposite HA of the same biotic community (Gila monster, a Sonoran [and Mojave] Desert species); (4) some species are biotic community generalists, being found in both desert communities (glossy snake), both grass- and shrubland communities (Great Plains toad), or both montane communities (i.e., Cordilleran) (Sonoran mountain kingsnake); and (5) some species are habitat generalists, occurring among biotic communities and HAs (gopher snake).

Acknowledgments

We thank D. Sebesta, A. Holycross, C. Painter, T. Skinner, R. Smith, T. Deecken, G. Helbing, T. Newman, and J. Taiz. D. Sebesta and R. Averill-Murray reviewed an earlier draft of the manuscript.

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