

In Search of the Madrean Line: Biogeography of Herpetofauna in the Sky Island Region

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Abstract—In 1992 Charles H. Lowe proposed a major partition in the distribution of the herpetofauna of southern Arizona and New Mexico between the Madrean Archipelago and the Rocky Mountains along a line that parallels the present-day Interstate 10. We categorized species by elevation and geographic region and used spatial analysis to explore the existence and location of a Madrean Line. We found a difference in area occupied by species north and south of Interstate 10, and located a clear boundary where Lowe's predicted line occurs. In addition, we found a very strong east (Chihuahuan Desert) and west (Sonoran/Mojave Desert) pattern.

Introduction

In a paper presented during a symposium on research at Saguaro National Park in 1992, the eminent herpetologist Charles H. Lowe proposed the existence of a major biogeographic boundary in the Sky Island area of the southwestern United States (Lowe 1992). Lowe called this line the Madrean Line, and declared that it was “as sharp as the world's most famous one, Wallace's Line” (Lowe 1992). Wallace's Line, named for the great British naturalist Alfred Russell Wallace, separates the Asian-dominated fauna of the northwestern islands of Indonesia and the Australian-dominated fauna of the southeastern islands (Wallace 1860).

Lowe's paper, which appears in the symposium proceedings, contains a number of ideas that he developed over more than 50 years of activity as a passionate herpetologist and ecologist of the Southwestern United States and Northern Mexico. For herpetologists, Lowe's biogeographic analysis is of greatest interest. Herpetologists are drawn to southern Arizona both for the region's diversity and the many tropical species that occur at the northern edge of their range. A recurring theme of amphibians and reptiles in the area is that a species may be plentiful in one mountain range, but absent at the same elevation in an adjacent range. The differences between Saguaro National Park (Rincon Mountains) and the Santa Rita Mountains, for example, are striking. Although the 1,800 m contours of each range are separated by <25 km, 5 snakes, 3 frogs, and 3 lizards that occur in the Santa Ritas are absent in the Rincons.

So what are the patterns of distribution, and why do they exist? Using montane rattlesnakes as an example, Lowe (1992) established his Madrean Line along the route where today's Interstate 10 (I-10) runs generally east-west across eastern Arizona and western New Mexico. His paper concludes that the northern distribution of the Madrean species is primarily

limited by climatic factors, particularly lower temperatures and lower summer rainfall.

Several detailed herpetological inventories have occurred in the Arizona Sky Islands since Lowe's paper (e.g., Turner et al. 2003; Swann and Schwalbe 2002), and genetic research is greatly improving our understanding of the biogeography within species (e.g., Zumudio et al. 1997). In addition, geographic information systems (GIS) allow us to quickly map and analyze distributional patterns. The major objective of this paper was to use spatial analysis to explore whether a north-south biogeographic boundary for herpetofauna occurs in the Sky Island region, and where it is located. A second objective was to explore east-west distribution patterns and other aspects of the biogeography of reptiles and amphibians in the area.

Methods

We used published species distribution maps (Stebbins 1985) to categorize and compare distributions for amphibians and reptiles that occur in the Sky Islands. Range maps are problematic because all species distributions are patchy to some degree, but Stebbins (1985) has the advantage of being particularly detailed for southern Arizona, in part because of the author's collaboration with Charles Lowe. For consistency with range maps we also used Stebbins' (1985) species classification with one exception, the Arizona black rattlesnake (*Crotalus oreganus cerberus*) due to recent taxonomic revision (Pook et al. 2000; Douglass et al. 2002) and its importance in Lowe's paper. Range maps for all species present in southern Arizona were digitized using the GIS mapping software ArcView 3.3.

Species were categorized by local elevation range (above 1,524 m only, and all species) and biogeographic province (east/Chihuahuan, south/Madrean, west/Sonoran-Mojave, north/Rocky Mountain, and others). We assigned species to

elevation range categories using published sources (e.g., Lowe et al. 1989) in combination with our experience and knowledge of local experts (C. R. Schwalbe and R. Repp). We recognized that categorizing species by elevation is problematic because individuals are occasionally found well outside of areas where they are most common. We determined biogeographic province based on whether the major area of a species distribution occurred east, west, north, or south of the Arizona Sky Islands. We were conservative in this categorization and excluded species that have ranges that are localized, disjunct, or distributed in more than one direction from our study area.

We defined our study area as a rectangle of approximately 60,000 km² centered roughly around the north end of the Driest Mountains east of Wilcox, Arizona (figure 1). This is only a portion of the region considered the “Sky Islands” as defined in this volume but includes nearly all the species north of Mexico (where species distributions are less well-documented) and approximately the same area north and south of Interstate 10. We calculated each species’ range falling within this region and totaled the distribution of all species. We used a 2-tailed t-test (Zar 1996) to determine whether the ranges of species north and south of I-10 were significantly different. We created contour maps of species distributions by biogeographic province by combining species ranges. We considered the location of the Madrean Line to be the zone of overlap of 50% contours of the north/Rocky Mountain and south/Madrean

biogeographic provinces, and conducted a similar analysis for the geographic boundary between west/Sonoran-Mojave and east/Chihuahuan herpetofauna.

Results

Montane Species

North-south distributions for 12 high-elevation species are summarized in table 1. Nine have largely Madrean ranges; of these, seven do not occur north of I-10, while two occur in the Pinalenos and one occurs in the Galiuros. We categorized only one montane species, the Arizona black rattlesnake, as having a predominantly northern distribution. It occurs in all the major ranges in our study area north of I-10, and does not occur south of it. Two species, the Sonoran mountain kingsnake (*Lampropeltis pyromelana*) and the short-horned lizard (*Phrynosoma douglassii*) occur in all of the Sky Islands and range well to the north and south. For montane species, we found a significant difference in range occupied north and south of the current route of I-10 ($t_{11} = -2.366$, $p = 0.037$).

All Species Combined

We categorized 83 species in our study area. We considered four species to be northern or Rocky Mountain in distribution,

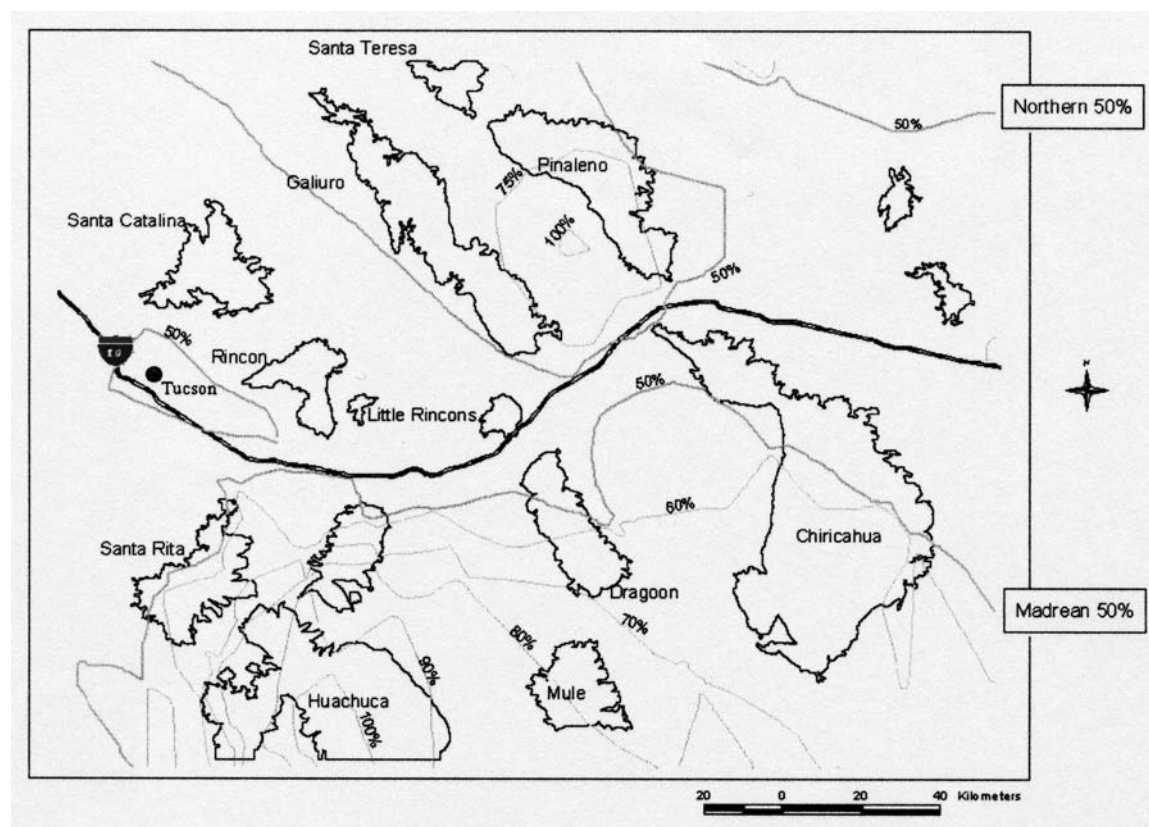


Figure 1—Contour intervals for number of species of reptiles and amphibians of southern/Madrean ($n = 17$) and northern/Rocky Mountain ($n = 4$) distributions that occur in the southeastern Arizona Sky Island region. The 50% contour for southern species runs roughly west-east of I-10 Route 10, proposed as the Madrean Line by Lowe (1992). The 50% contour for northern species is less well-defined and contains a disjunct contour island near Tucson.

Table 1—High elevation reptiles and amphibians of the major southeastern Arizona Sky Islands in relation to the “Madrean Line,” proposed by Charles H. Lowe (1992) to parallel the modern route of I-10. Mountain ranges are arranged from north (top) to south (bottom). Species abbreviations: CROR = *Crotalus oreganus*, CRPR = *C. pricei*, CRWI = *C. willardi*, CRLE = *C. lepidus*, EUCA = *Eumeces callicephalus*, HYEX = *Hyla eximia*, HYAU = *Hylactophryne augusti*, SCSC = *Sceloporus scalaris*, SCVI = *S. virgatus*, SCJA = *S. jarrovi*, PHDO = *Phrynosoma douglassii*, LAPY = *Lampropeltis pyromelena*. Province abbreviations: N = North/Rocky Mountain, S = South/Madrean, W = Widespread.

North Species Province	CROR N	CRPR S	CRWI S	CRLE S	EUCA S	HYEX S	HYAU S	SCSC S	SCVI S	SCJA S	PHDO W	LAPY W
Santa Theresa	X										X	X
Pinaleno	X	X								X	X	X
Galiuro	X									X	X	X
Santa Catalina	X										X	X
Rincon	X										X	X
I-10												
Dragoon				X				X		X	X	X
Whetstone			X	X				X		X	X	X
Chiricahua		X		X				X	X	X	X	X
Santa Rita		X	X	X	X		X	X		X	X	X
Huachuca		X	X	X	X	X	X	X		X	X	X
South												

17 species to be of southern or Madrean in distribution, 23 species to be of eastern or Chihuahuan distribution, and 21 to be of western or Sonoran/Mojave in distribution. For all species combined, we found a significant difference in range occupied north and south of the current route of I-10 ($t_{96} = -3.239$, $p = 0.002$). For southern species only, the 50% contour interval falls along a line that roughly parallels I-10 (figure 1). The 50% contour interval for northern species also falls in this general vicinity; in fact all but one of the four species only occurs north of I-10.

The 50% contour intervals for eastern and western species overlap in the southern half of the study area east of the Huachuca Mountains in the San Pedro River Valley (figure 2). North of I-10, the western species 50% contour runs northwest from Saguaro National Park, and the eastern 50% contour runs northeast.

Discussion

Is There a Madrean Line for Herpetofauna?

Although we humans may see clear distinctions between plant and animal communities in different areas of the earth, such boundaries are difficult to quantify. Both the existence and the position of Wallace's Line have been challenged almost since Wallace first advanced it (Mayr 1944; Whitmore 1981). Lowe (1992) focused only on four species of high elevation rattlesnakes; when all montane reptiles and amphibians are considered (table 1), the location of a major biogeographic boundary in the vicinity of I-10 appears to be largely justified, especially for species with southern distributions. Lowe considered the Pinalenos to be enigmatic, with elements of both northern and southern faunas in a presumably “mountain island outlier of the Rocky Mountain

(northern) massif” (Lowe 1992). With the two Pinaleno exceptions, only one montane southern species, the mountain spiny lizard (*Sceloporus jarrovi*) in the Galiuro Mountains, occurs north I-10. On the other hand, it is clear from table 1 that distribution of montane species is variable and that none of the Sky Islands in our area contain the full complement of southern species. In addition, few reptiles and amphibians in the Sky Islands can really be considered northern in distribution. The example used by Lowe, the Arizona black rattlesnake, is the only montane species with a largely northern distribution in our study area.

Interestingly, the pattern for all species is very similar to that of montane species (figure 1), with the zone of overlap of 50% indicating a broken Madrean Line just south of I-10. The weakness of this line is the result of the low number of northern species.

Factors Limiting Distributions of Sky Island Herpetofauna

It is interesting to speculate on what factors may influence the fairly abrupt northern limit for so many reptiles and amphibians that occur in the Madrean Archipelago. Potential explanations include current or past climatic factors, such as winter low temperature and summer rainfall, geographic barriers, dispersal rates ecological factors such as competition or predation, or a combination of these. In discussing the “Pinaleno enigma” Lowe (1992) suggested that the Pinalenos were never earlier united by highlands to either the northern or southern mountains, but “witnessed the comings and goings—during the last dozen-odd glacial and interglacial faunal and floral dispersions—of Madrean taxa and Rocky Mountain taxa during the cyclical waxing and waning of their northern and southern distributional limits.” While suggesting that the presence of both northern and southern rattlesnakes in the Pinalenos reflect

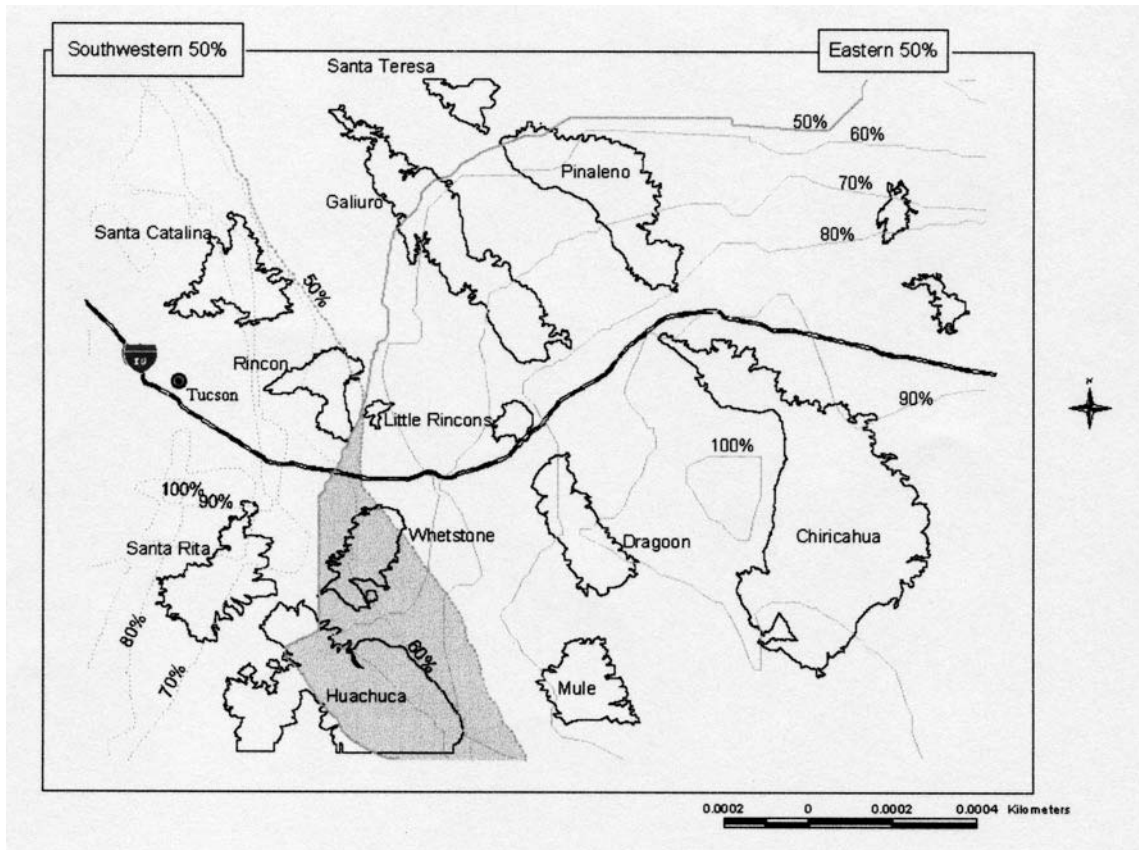


Figure 2—Contour intervals for number of reptile and amphibian species of southwestern/Sonoran-Mojave ($n = 21$) and eastern/Chihuahuan ($n = 23$) distributions that occur in the southeastern Arizona Sky Island region. The 50% contours for southwestern and eastern species overlap in the shaded area south of I-10, just east of the Huachuca Mountains in the San Pedro Valley.

the area's history, he clearly believed that the northern limits of Madrean rattlesnakes, like plants and other taxa, are primarily controlled by colder conditions and diminished summer rainfall from south to north.

General patterns of rainfall and temperature do not appear to differ significantly directly north and south of I-10, but this may be due to the lack of climatological data on the appropriate scale. Low winter temperatures could impact reptiles in a variety of ways, ranging from direct mortality to reducing prey availability. Stomach contents of mountain spiny lizards collected simultaneously by Lowe and C. R. Schwalbe in both the Sierra de los Tigres in northern Sonora and the Pinalenos indicated that only the southern population was actively feeding in winter, although individuals in the Pinalenos would take food if offered (C. R. Schwalbe, personal communication). Despite major climatic shifts since the Miocene, including periods that may have been warmer than the present, evidence is lacking that Madrean species previously ranged further north (Holman 1995).

Evidence from a variety of sources, including studies of other Sky Island taxa, suggests that current distributions of herpetofauna and other taxonomic groups in the Southwestern United States are based largely on past distributions (Van Devender 1994). Mitochondrial DNA data suggest that Sky Island populations of jumping spiders (Salticidae; Masta 2000), and mountain spiny lizards (*Sceloporus jarrovi*; Matt Kaplan,

personal communication) have been genetically isolated for longer than 10,000 years. It seems possible that the northern limits for Madrean species may be the result of a combination of geography and both past and present climate, with northern distributions of southern species limited by winter temperatures during glacial periods and by geographic barriers (e.g., wide grassland and desert valleys) during interglacial periods.

The east-west pattern in our study area is even more striking than the north-south pattern, and it closely follows well-established boundaries (e.g., Brown et al. 1979) for the Sonoran and Chihuahuan Desert biogeographic provinces. Still, the transition between the two areas is quite abrupt and is interesting because the two deserts also share a large number (17 in our study area) of reptiles and amphibians. This and fossil evidence that some species once ranged further west or east than at present (Van Devender 1994; Holman 1995) suggest different explanations for the east-west pattern than for the north-south one.

Although the past may be the major contributing factor to current distributions of reptiles and amphibians in the Sky Island region, the modern world is having a growing influence. In recent years many native species have declined, and introduced species such as bullfrogs (*Rana catesbeiana*) are spreading rapidly on both sides of the Madrean Line. In 1991, Charles Lowe mourned the impending loss of the Avra Valley and regretted that it had not been included in the Tucson

Mountain District of Saguaro National Park (Lowe 1992). Our best hope is that other valleys and mountains will have their protectors, so that the rich herpetological story of this part of the world is one that future generations can experience, and not just hear about in passing.

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