# THE RIPARIANNESS OF A DESERT HERPETOFAUNA[1]

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*Abstract: Within the Mojave, Sonoran, and Chihuahuan Desert subdivisions of the North American Desert in the U.S., more than half of 143 total amphibian and reptilian species perform as riparian and/or wetland taxa. For the reptiles, but not the amphibians, there is a significant inverse relationship between riparianness (obligate through preferential and facultative to nonriparian) and desertness. In addition to the nondesert species (N=36) present, there are two evolutionary kinds of desert species in the herpetofauna: true desert species (N–20), and desert-included species (N=87); the former are obligate specialists, the latter are facultative generalists. Quantitative aspects of desertness, riparianness, species richness, nondesert taxa and others are examined.*

A large part of the herpetofauna of North America is located extensively and abundantly in riparian habitats. No other terrestrial vertebrate group is a better indicator of the biological health of riparian ecosystems. Within the "warm deserts" of the Southwest United States more than half of the total amphibian and reptilian species perform as riparian and/or wetland taxa.

Riparian taxa are obligate, preferential, or facultative components of riparian ecosystems. Thus including the nonriparian condition, four levels of riparianness (R), or riparian dependency, are recognized (Dick-Peddie and Hubbard 1977, Johnson, and others 1987). Moreover, for deserts, in addition to the distinction between desert species and nondesert species, there is a clear distinction between two evolutionary kinds of desert species: true desert species and desert-included species. True desert species are obligate specialists in the real sense that they have evolved within desert environments, while the desert- included species tend to be facultative generalists that include desert environments in their much wider and often widely extensive ecological and geographical distributions. Thus including the nondesert condition, three levels of desertness (D) are recognized (Lowe 1968; and others, 1986):

| Desertness | | Riparianness | |
|---|---|---|---|
| Nondesert | (ND) | Obligate | (RO) |
| Desert | (D) | Preferential | (RP) |
| Desert-Included | (DI) | Facultative | (RF) |
| Obligate Desert | (DT) | Nonriparian | (NR) |

The North American Desert.–There are four major subdivisions in the North American Desert of Shreve (1942, 1951): Chihuahuan Desert, Sonoran Desert, Mojave Desert, Great Basin Desert. Creosotebush *(Larrea divaricata) is* one of the abundant dominants absent from the Great Basin Desert, sometimes referred to as a "cold desert." 'The three major subdivisions in which creosotebush is among the major dominants are referred to here and elsewhere as "warm deserts." These are the Chihuahuan, Sonora, and Mojave Deserts.

In this preliminary report the data for the areas of these three major desert subdivisions that occur in the U.S. sector are extracted from a database that includes the amphibians and reptiles from the larger area of all four subdivisions of the North American Desert. Thus the present report contains in addition to all of the Mojave Desert, only those parts of the Chihuahuan Desert and the Sonoran Desert that lie north of the U.S.A.–Mexico international boundary; most of the geographic area of the Chihuahuan and Sonoran Deserts lie in Mexico. In the present work–involving less than the entire North American Desert herpetofauna–the database involves a total of 12 potential R on D combinations for a total of 143 taxa requiring direct field observation; that yields a potential number greater than 1700 for determinations. There are certain combinations for R and D that are "invalid" or "error" combinations, a subject treated in a longer (subsequent) report on this subject for the North American Desert herpetofauna inclusive of the United States and Mexico.

The Semidesert Grassland.–In the international borderlands of the study area, the North American desert-grassland, or semidesert grassland, lies adjacent to the warm deserts. It is sometimes not understood that the desert-grassland is grassland, not desert. Present deserts evolved out of grasslands and scrublands during the late Tertiary (Axelrod, 1950, 1958, 1979). Throughout the desert areas of the world, biologists make a correct distinction between the desert proper, i.e., desertscrub and its adjoining grassland, steppe, or scrubland. In our Southwest, the Holocene dry-tropic grasslands, called desert-grassland (Shreve 1917) or semidesert grassland (Little, 1950), obviously represent grassland environments. While the present quantitative analysis has been cognizant of desert environment versus nondesert environment, and of desert species versus nondesert species, the difficult cases of the mosaics and ecotones of desertscrub versus semidesert grassland, especially in the Chihuahuan Desert arena, provide a particularly difficult challenge for ecologic and biogeographic analysis.

[1] Presented at the California Riparian Systems Conference; September 22-24, 1988; Davis, California.

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There is a recent regional tendency to use the synonym semidesert grassland, recommended by the U.S. Forest Service. The synonym desert- grassland also continues to be used, as it has been for most of this century.

Recent Reports.–During recent years there has been a sharp increase in field research directed to amphibian and reptilian populations in Southwest riparian ecosystems. [In the manuscript editing process, a brief review of these papers was eliminated by the Station editors to "reduce non-relevant reference listings."]

## Methods

The areas in the North American Desert for the present analysis, i.e., the study area, lie outside of the Great Basin Desert. Specifically they are the parts of the Mojave, Sonoran, and Chihuahuan Deserts that lie in the six United States of California, Nevada, Utah, Arizona, New Mexico, and Texas. The scheduled degree of desertness (desert to nondesert) and riparianness (obligate to nonriparian) was determined for each amphibian and reptilian taxon in the study area. These ecological determinations for the taxa are provided from direct field observations, mostly those of the author in the southwestern United States and northern Mexico. Over several years colleagues have been generous in both verifying and extending the database for some of the species in and between both California and Texas, which are the longitudinally limiting U.S. states in the desert coverage reported. These field experts are Robert L. Bezy, George L. Bradley, Charles J. Cole, F. R. Gehlbach, S. F. Hale, Peter A. Holm, Howard E. Lawler, Brent E. Martin, Hugh K. McCrystal, Philip C. Rosen, C. R. Schwalbe, Robert C. Stebbins, Thomas R. Van Devender, John W. Wright, and Richard G. Zweifel.

It is worth noting in this connection that there are two sources of commonly used information that are inadequate for this type of fauna- wide ecological analysis. These are the field guides for, and the museum specimens of, the amphibians and reptiles. These two sources often have been abused as substitutes for lack of worker-knowledge in ecological and biogeographical investigations requiring ecological input for reports in both the primary and nonprimary literature. The obvious reason that field guides in particular cannot provide the detailed ecological information required is the fact that the modern field guides and similar books were never intended for this type of service and obviously are not designed for providing it. Among the several existing field guides for amphibians and reptiles in North America, with regard to treatment of the natural biotic communities in which the species live as well as in its illustration and other excellence, by far the best in the West is by Stebbins (1985).

Because in both theory and practice riparianlands (characterized in important part by imported water) fall within the broader concept of "wetlands," there is some current confusion in their application to plant and animal taxa occurring on natural western landscapes. Part of the problem lies in the often strong and confusing seasonal periodicity of both in-situ water (wetlands) and imported water (riparianlands) in desert environments. Table 1 indicates an expected concordance in the concepts and thus the schedules for wetland species status (developed in the eastern U.S.) and riparian species status. This schedule from obligate riparian to nonriparian (Table 1) was used in the present investigation.

The regression model (Fig. 1) employed for the testing reported here for the herpetofauna involves a streamlining of riparian and wetland terminology. For example, the spadefoot toads (genus *Scaphiopus*) perform as both obligate wetland and obligate riparian corridor species (WO/RO) in arid and semiarid environments. In the present study such are scored with a single value for OBLIGATE, whether the taxon is primarily or wholly RO or WO, or RO/WO or WO/RO. Moreover, for further simplification as in modeling, RO is used to represent the obligate position on the riparian/wetland ordinate. An essential notation is that a taxon whether plant or animal is an obligate riparian one when it is directly dependent on the riparian system during any phase of its life cycle.

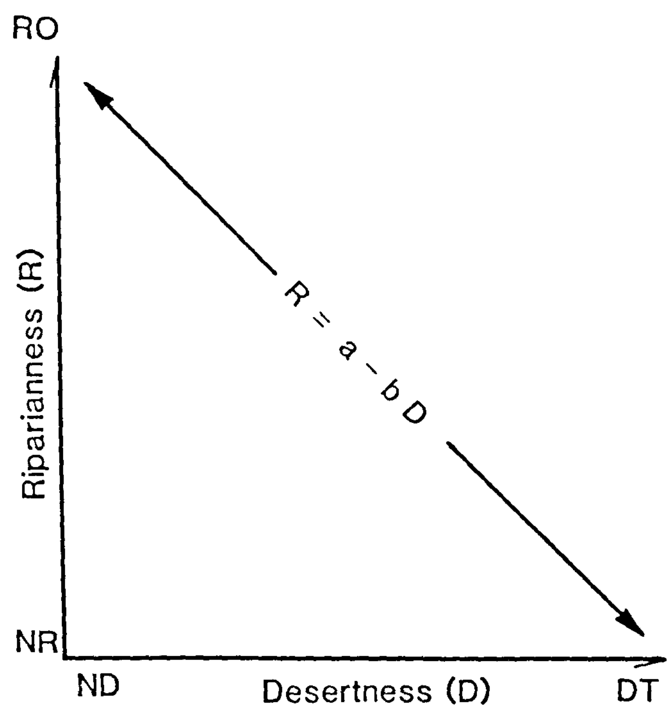


**Figure 1–** Inverse relationship of riparianness on desertness in a desert herpetofauna. Equations in Table 4.

**Table 1 —** Comparative schedules for riparian land and wetland plant species. Wetland schedule after Reed (1986). Riparian schedule modified after Dick-Peddie and Hubbard (1977), and Johnson and others (1987). Frequencies follow wetlands convention (see Reed 1986).

| Riparianlands Species Status | Frequency (%) | Wetlands Species Status |
|---|---|---|
| Obligate Riparian (RO)[1] | >99 | Obligate (OBL) |
| Capable of natural establishment only in the riparian environment | | Always found in wetlands under natural (not planted) conditions; may persist in non-wetlands if planted there by man or in wetlands that have been drained, filled, or otherwise transformed into nonwetlands |
| Preferential Riparian (RP)[2] | 99-67 | Facultative Wetland (FACW) |
| More frequently in the riparian environment than in the adjoining upland | | Usually found in wetlands; occasionally found in nonwetlands |
| Facultative (RF)[2] | 66-33 | Facultative (FAC) |
| Subequally in the riparian environment and the adjoining upland. | | Sometimes found in wetlands; also occurs in nonwetlands |
| Nonriparian (NR)[2] = Upland | <33 | Facultative Upland (FACU) |
| Upland taxon, present or absent in the riparian environment | | Seldom found in wetlands and usually occurs in nonwetlands |

1. Frequency of occurrence--in wetland/riparian versus nonwetland/nonriparian--across the entire distribution of the species.

2. Potentially obligate riparian (RO) locally, as in driest sector of species distribution.

## Results and Discussion

Table 2 indicates the extent and species richness of the herpetofauna. In the total of 143 species in the study area, reptiles outnumber amphibians approximately 4 to 1. Species of lizards and snakes are present in subequal numbers. Separately, the lizards and the snakes each outnumber the turtles by 5 to 1. With lizards and snakes taken collectively (Squamata), the squamate-turtle ratio is approximately 10 to 1.

The North American Desert herpetofauna is, of course, somewhat richer than indicated in Table 2, which represents a smaller total desert area. The final form and content of this table and Tables 3 and 4 await finalization regarding desertness and riparianness for certain taxa, and the actual evolutionary (species) status of others that remain unsettled. For example, to what extent are the genera Gambelia (Leopard Lizards) and Uma (Fringe-toed Lizards) polytypic? Gambelia is treated here as a monotypic genus, and Uma as a polytypic genus with one species in the Mohave-Sonoran desert arena. The introduced error swing between maximum splitting and maximum lumping is about 2%. While none of the few remaining systematic and ecologic decisions referred to above will affect significantly the overall conclusions drawn from the data set, all of them are of much interest for the completeness as well as correctness of the data set.

| | N | % |
|---|---|---|
| Amphibia | | |
| Salamanders | 2 | 7.4 |
| Frogs and Toads | 25 | 92.6 |
| Total Amphibians | 27 | 100.0 |
| Amphibian % of Herpetofauna | | 18.9 |
| Reptilia | | |
| Turtles | 11 | 9.5 |
| Lizards | 54 | 46.5 |
| Snakes | 51 | 44.0 |
| Total Reptiles. | 116 | 100.0 |
| Reptilian % of Herpetofauna | | 81.1 |
| Total Herpetofauna | 143 | 100.0 |

**Table 2** – Number (N) and percent of totals for species in the combined herpetofauna within the Mohave, Sonoran, and Chihuahuan subdivisions in the United States sector of the North American Desert.

Tables 3 and 4 indicate the degree of desertness in the herpetofauna and its correlation with riparianness. The data for the reptiles (Table 4) fit the regression model (Fig. 1) that predicts an inverse relationship between desertness (X) and riparianness (Y). Ultimate adaptations underlying the strong negative correlations seen in Ta-

| | DT (N) | DI (N) | ND (N) |
|---|---|---|---|
| Amphibia (N = 27) | | | |
| Salamanders | 0 | 1 | 1 |
| Frogs | 1 | 17 | 7 |
| species sums | 1 | 18 | 8 |
| % of total 27 | 3.7% | 66.7% | 29.6% |
| desert vs. nondesert | | 70% | 30% |
| Reptilia (N = 116) | | | |
| Turtles | 1 | 1 | 9 |
| Lizards | 11 | 34 | 9 |
| Snakes | 7 | 34 | 10 |
| species sums | 19 | 69 | 28 |
| % of total 116 | 16.4% | 59.5% | 24.1% |
| desert vs. nondesert | | 76% | 24% |
| Herpetofauna (N = 143) | | | |
| species sums | 20 | 87 | 36 |
| % of total 143 | 14.0% | 60.8% | 25.2% |
| desert vs. nondesert | | 75% | 25% |

**Table 3 —** Number (N) and percent of totals for true desert (obligated desert) species (DT), desert-included (facultative desert) species (DI), and non-desert species(ND). See Table 1.

| taxa (species) | df | regression equation | *r* | *P* |
|---|---|---|---|---|
| all reptiles | 114 | R = 3.566 - 0.962 D | -0.763 | <.001 |
| turtles | 9 | R = 4.130 - 1.174 D | -0.938 | <.001 |
| lizards | 52 | R = 3.270 - 0.814 D | -0.677 | <.001 |
| snakes | 49 | R = 3.487 - 0.958 D | -0.744 | <.001 |
| lizards and snakes | 103 | R = 3.362 - 0.875 D | -0.707 | <.001 |

**Table 4 —** Regression equations for riparianness (R) on desertness (D) for reptilian groups collectively within the Mohave, Sonoran, and Chihuahuan sub-divisions of the U.S. sector of the North American Desert. See Fig. 1.

ble 4 are the taxa-specific water balance ratios and the reptilian amniotic egg. Within the boundaries set by those constraints, trophic and other energy-behavioral adaptations drive the habitat-selection exhibited.

The data for amphibians do not fit the inverse R on D model for reptiles. Amphibians as a group in a desert environment are (entirely to essentially) obligate, and thus the degree of riparianness (Y) is for the most part statistically independent of degree of desertness (X). As indicated in Fig. 2, the R on D regression coefficients for amphibian taxa in desert environments are predicted to be not significantly different from zero ($b \approx 0$). In natural habitats wherever they are, the primary reproductive wedlock of the anamniotic amphibians to water and water-wetness is overriding.

## Summary and Conclusions

Desertness.–Nondesert species, and desert species of two evolutionary types, characterize the desert herpetofauna. The two kinds of desert species are (1) true desert species which are obligate specialists, and (2) desert-included species which are facultative generalists; the two are non-equivalent desert species.

In a herpetofaunal total of 143 species in the North American Desert study area, a respectable 25% (25.2) are nondesert species (ND). In the 75% (74.8) that are desert species (D), 61% are desert-included species (DI), and 14% are true (obligate) desert species (DT)–a small but not unexpectedly small percentage of true desert species in the North American Desert.

Riparianness.–The descriptor Riparian is used in this report as a generic term inclusive of both the riparian and the more purely wetland situations; riparian (and wetland) species are either obligate, preferential, or facultative, and the nonriparian species are upland species.

Approximately 40% (41.2) of the 143 total species in the herpetofauna are nonriparian (NR). Nearly 60% (58.8) are riparian and/or wetland species and exhibit various degrees of compensation for moisture, with more than half of the 60% (37.1%) restricted to the obligate riparian (RO) and/or obligate wetland (WO) ecological position.

Relative Species Richness.–There are approximately 4 reptilian species to every 1 amphibian species in the North American "warm desert" ecosystems investigated. Similarly , turtles are outdistanced about 5 to 1 by both the lizards and the snakes. The lizards and snakes are virtually equal in species richness.

Reptiles.–A total of 116 reptilian species comprise approximately 80% (81.1) of the total herpetofauna in the 3-desert study area. A combined 105 species of lizards and snakes comprise 90% (90.5) of the reptilian species in the study area, with approximately half of the 90% contributed by each systematic group–46.5% lizards, 44.0% snakes. Turtle species (N = 11) comprise the remaining approximate 10% (9.5) of the reptilian total.

A strong inverse relationship between desertness (D) and riparianness (R) emerges for the three major reptilian groups in the North American Desert-turtles, (Fig. 2) lizards, and snakes. While this relationship was predicted from the model, the correlation is stronger than expected, especially when all groups are combined ($r=-0.763, P < .001$). In the ecological data on desertness (D) and riparianness (R) for lizards and snakes, a strong pattern similarity is seen for them in the desert area treated; the sums for the lizards and snakes are nearly identical, and neither the slopes nor the intercepts are significantly different.

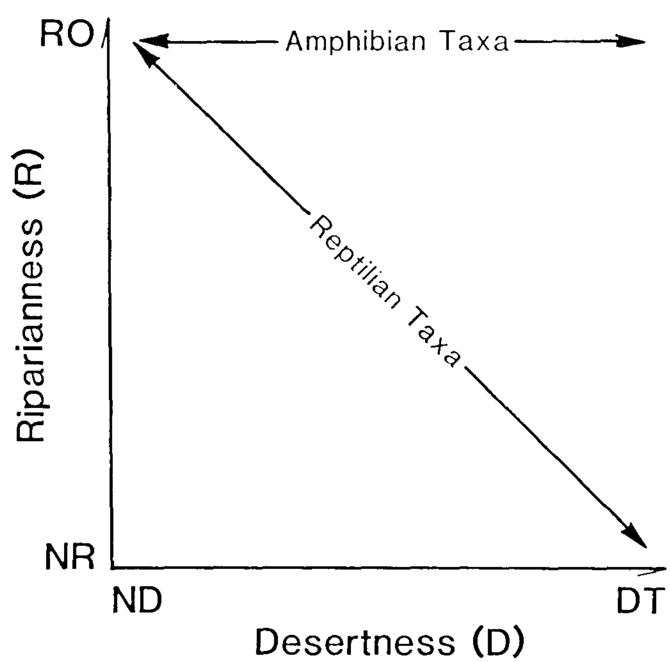


Figure 2. The relationship of riparianness and desertness in amphibian and reptilian taxa in the North American Desert herpetofauna.

Amphibians.–A total of 27 amphibian species comprise approximately 20% (18.9) of the herpetofauna of the desert study area. All but two of the 27 are frogs and toads. The other two are salamanders, the Tiger Salamander (*Ambystoma tigrinum*) which is a desert-included species, and the Desert Slender Salamander (*Batrachoseps aridus*) which is a nondesert species in the desert-edge.

Unlike the reptiles, amphibians as a group in the North American Desert do not exhibit an inverse relationship between desertness (D) and riparianness (R). The flat-curve model for amphibians predicts a regression coefficient not significantly different from zero for riparianness (NR-RO) independent of degree of desertness (ND-DT). In the theory underlying the model there is an anamniotic versus amniotic hypothesis for the amphibian R on D pattern distinction from that of reptiles. It is at least clear from the test thus far that (with the exception of Batrachoseps and Hylactophryne) the desert-arena amphibians in the North American Desert require reproductive surface water at sufficient depth .(> 1 cm) for a period > 10 days; they are the most clearly obligate riparian/wetland taxa in the desert herpetofauna and include both DI and DT desert species.

Nondesert (ND) Species.-Eight amphibians and 28 reptiles, for a total 36 species, make the 25.2% nondesert taxa. A few are man's introductions, some are post-climax relicts. Some nondesert native species in the North American Desert established originally on riparian river and stream corridors of transported water well into the desert arena-inter-biome water from sources and sheds often from outside the desert region as well as transported water from within its overall geographic limits. Today that water may be permanent, seasonally intermittent, or torrentially ephemeral. In some cases the nondesert native species within now-arid environments were present where they are, as resident populations, under more mesic environmental conditions that preceded the more recent establishment of current desertscrub environments. Moreover, earlier less-arid climate in general is beyond reasonable doubt associated in various degrees with both mechanisms- riparian corridors and in-situ residency.

## Acknowledgements

Under methods are listed the names of many herptologists who have assisted me in the present work. I thank also R. Roy Johnson of the U.S. National Park Service who has been of able assistance in matters riparian and who is currently reporting on desert riparian systems for the U.S. Fish and Wildlife Service. The work has been supported by grants and contracts from the National Park Service, National Science Foundation, The Arizona Foundation, and University of Arizona Research Fund 302787.

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