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SOME SALIENTIAN ADAPTATIONS[1]

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According to one common viewpoint, many and perhaps most characteristics of organisms have evolved through protoplasmic response to changing environments so that the present fauna and flora of a given region are generally adapted to the characteristic environment which they now occupy. In extreme cases, the geographic distribution of a species may be partially or wholly controlled by such ecological adjustments; but in less specifically adapted groups, the potential range of a species may not yet have been realized, so that introduction of some of its members into a new region results (or may result) in permanent occupancy of it. Between these two extremes, so many intermediate conditions occur that a whole volume would hardly suffice merely to record them.

Generalizations such as those just stated are practically truisms of biology. They are introduced here only as background for the interpretations of some observations made in recent years among the Salientia of Oklahoma. Twenty-seven species or subspecies of frogs and toads representing five families, and seven genera are now known to occupy this state. But they are not universally distributed; and, more important, they are not distributed consistently in accordance with their taxonomic groupings. For example, in the Hylidae, one species and a number of subspecies of another are limited to the southeastern corner of the state; one occurs only along its eastern edge; another occupies approximately the eastern half, but is ecologically limited to areas of woodland and savannah; one species is limited to regions of grassland, which means, geographically, to approximately the western two-thirds of the state; still another occupies tall-grass prairie and woodland in abundance and mixed prairie rarely. It has not been found in the high plains (short-grass prairie) in western Oklahoma but does occur in New Mexico and in the Texas Panhandle in similar ecological communities. They are distributed over most of Oklahoma but one of these never occurs in deep woods and the other is rarer to the west (short-grass prairies) than to the east (mixed-grass, savannah, and woodland).

1 Based upon a paper presented recently at the Boston Meeting of the A. A. A. S., Dec. 28, 1946.

One might expect the frogs (genus Rana) to be limited to pond and stream sides: but this does not wholly explain their distribution in Oklahoma. Six forms are recognized. One of these is limited to the Northeast, three to the Southeast, and the other two are found abundantly in all parts of the state in proper microhabitats.

In the more terrestrial genus Bufo, seven forms are known. One is found abundantly in the eastern half of Oklahoma wherever woodland or savannah occur, except that it is rare in mountain valleys in the east. Another largely replaces it in such valleys, is very abundant in the eastern woodland areas (except on mountains) but does not enter savannah to the westward. Three species are limited to prairie, one to short-grass in western and southern Oklahoma, one to mixed prairie and the ecotone between this and the tall-grass prairie in the Northeast, the third to the short-grass plains in the West and their ecotone with the mixed prairies in south-west-central Oklahoma. One subspecies is very abundant in all parts of the state except in the southeastern woodlands where its distribution stops quite abruptly as another intergrading subspecies replaces it. The seventh form is very rare and known only from very rough, rocky areas mostly in the west and south.

In Microhyla, two subspecies occur. One is limited to the eastern woodland areas;; the other replaces it to the westward and occupies all of the remainder of the state geographically except the panhandle where it may occur but is as yet unknown. But this second form seems ecologically restricted from low areas since, with ample opportunity to observe it, I have never found it on the flood plains of the larger rivers, whether they adjoined woodland, prairie or savannah in the region under observation.

In the spadefoots (genus Scaphiopus) four species occur, three limited to prairie, the fourth, to savannah and woodland. Two of the prairie-limited species occur only in short-grass plains (western); the second is in all prairie areas. It is, however, rare in the tall-grass prairie to the northeast.

The distributions given are based upon extensive observations in various parts of Oklahoma during eleven years, 1935 to 1946 inclusive, and hence are likely to be basically correct. Assuming their essential soundness, how much are they due to adaptation and how much to mere geographic factors exclusive of ecology? This problem has received my attention during the past four or five years during which I have studied and collected at least once in every part of the state—in many portions of it at several times.

Since the reproductive period of any organism, and the early period of the growth of its young, are critical ones for survival, these phases of life histories have been studied in greatest detail. All observations except measurements have been in the field, often at night during breeding activities of the adults; but tadpoles, resulting from breeding at known times, have also been under observation at many times and places, both day and night.

The greatest difference in adult behavior appears to be associated with a differential reaction to rainfall among the prairie-limited species, on the one hand, and among the woodland-savannah limited species on the other. In Bufo, for example, none of the prairie-limited forms have ever been found breeding except in temporary water during or immediately after rains of a half inch or more, regardless of season. But the species not so limited in distribution often breed in the springtime when no recent rain has occurred. In Pseudacris, one species *(Ps. clarkii)* is limited to prairie and behaves like the prairie limited toads; another *(Ps. streckeri)* is not prairie-limited, and does not thus behave.

Other species vary in the same way. Again, since the observations are quite extensive, there is little doubt as to their essential correctness. For example, I have a total of 120 records of breeding activities of *Bufo cognatus*, 112 of *Ps. clarkii*, 117 of *Ps. streckeri*, 83 of *Bufo terrestris americanus*, 129 of *Bufo v. woodhousii*, 64 of *Hyla v. versicolor*, 44 of *Ps. triseriata*, 80 of *Microhyla c. olivacea* and comparable numbers in several other species. Never have I found an exception. The prairie-limited forms breed after rain in temporary waters at any time from early spring to early fall; and they do not have a clear-cut breeding season. In contrast, those limited to woodland *do* breed within a definite breeding season. They are influenced to some extent by rainfall but are not controlled by it.

In earlier papers on the spadefoot toads (Bragg, 1944, 1945) I defined two types of breeding pattern (called there the mesic pattern and the xeric pattern) and it was pointed out that the spadefoots have the xeric one. I now wish to emphasize that the xeric pattern is shared by all prairie-limited species in Oklahoma, regardless of their taxonomic groups. And there is no reason to suppose that the phenomena involved are limited to this one state. Similarly the mesic pattern is typical of species limited to the woodland and savannah. Some species which occur in both prairie and savannah (e. g., *M. c. olivacea*) also have the xeric pattern and one species of the savannah and woodland areas shows it also. This is the spadefoot, *Scaphiopus hurterii*, the

only species known certainly in Oklahoma to follow its taxonomic relatives rather than the environment in breeding pattern, although there is some evidence that *Microhyla c. carolinensis* may do so.

From the viewpoint of adaptation, it seems to me significant that amphibians which are limited in distribution to a relatively dry environment should breed only after rains and in temporary water. For to do so consistently obviously serves the biological function of individual, and therefore species, survival. The evidence is in favor of a Darwinian factor in this, for only those which take advantage of the period immediately after rains have much chance for the survival of their tadpoles, season after season. Thus, selection has favored those which varied in the direction of discarding a breeding season in favor of breeding after rain regardless of season.

To emphasize such facts as indicating an adaptation to dry environment one need only to consider evaporation rate in pools and growth rates of tadpoles in them. Spadefoot tadpoles may metamorphose and leave pools in three weeks from egg-laying. Even so, many thousands are lost to the species each year because pools evaporate too quickly. The same is true of the prairie toads. I have seen metamorphosed tadpoles of *Bufo cognatus* leave the pools in 28 days after egg-laying; but, nevertheless, there has not been a generally successful breeding of this species about the city of Norman since 1941; yet each year some eggs have been laid. This lack of success in reproduction has been entirely due to loss of all tadpoles by the total evaporation of the water before the larvae could complete the aquatic phase of existence.

Spadefoot tadpoles seem to have carried these adaptations farther than any of the other forms so far known. Not only do they have an intrinsically faster development than any other North American forms but they seem especially adapted to resist heat. While this has not been studied in detail, as it needs to be, I have seen them developing normally in water at above 35° C., a temperature some mesically adapted tadpoles cannot withstand. Furthermore, the tadpoles of some species become cannibalistic while socially aggregated, thus assuring food to at least some individuals even though most must perish as the pool evaporates. Such activities were described in *S. h. holbrookii* by Ball (1936) working in Connecticut and have been confirmed recently by me for another species in Oklahoma (Bragg, 1946). The Oklahoma observations suggest that such activity is facultative, since individuals of the species involved (*Scaphiopus bombifrons* Cope) had never before been observed in such activities even though I had

watched the development and metamorphosis of its tadpoles on many occasions in Oklahoma and also in New Mexico (Bragg, 1941).

In summary, therefore, we may conclude:

(1) that prairie-limited Salientia in general in Oklahoma (and presumably elsewhere) are able to survive the rigors of a relatively dry environment through having evolved a special breeding behavior, called here the xeric pattern.

(2) that this pattern involves the same factors as those already described for the spadefoot toads, particularly in the lack of a definite breeding season, rainfall being substituted for an internal stimulus in the initiation of breeding activities.

(3) that these prairie forms generally differ from those limited to woodland in their breeding pattern, the one known exception being the savannah spadefoot, *Scaphiopus hurterii*.

(4) that not only adults but also tadpoles are adapted, the latter primarily through the evolution of a fast rate of development (aided of course by increasing heat as the water of the pool warms and evaporation rate increases), and (5) that these adaptations were probably evolved through selection in the Darwinian sense.

Further study of details is planned as time permits.

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