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The Influence of the Balcones Escarpment on the Distribution of Amphibians and Reptiles in Texas

HOBART M. SMITH AND HELMUT K. BUECHNER*

It is a common observation that the geographic ranges of many plants and animals are limited by the Balcones Escarpment in Texas, but little critical study has been made of the rôle of the escarpment as a natural boundary. The area offers much material for studies in speciation. The escarpment is in fact the eastern edge of the Edwards Plateau, an elevated area of features markedly different from those of adjacent territories. The plateau is xeric in nature, having less rainfall, scrubbier and more scant vegetation, a porous soil, little standing water, and an evaporation rate exceeding the precipitation rate. Surrounding lowlands are of mesic character, with more rainfall, lush vegetation, less porous soil, much standing water, and a rainfall rate exceeding the evaporation rate.

Various degrees and sorts of distributional limitation are exhibited by the numerous species occurring there, depending upon interaction of the wide variety of ecological conditions on the one hand, with on the other hand the physiological tolerances, life histories, habits, evolutionary history, etc., of the individual species. As the conditions are limited in occurrence, so are the animals limited; and as there are innumerable combinations of potentially limiting factors, so are there innumerable distributional patterns among the species concerned. The purpose of the present paper is to analyze the extent of limitation exercised by the factors correlated with the escarpment upon the geographical distribution of reptiles and amphibians in Texas.

*Department of Zoölogy, University of Illinois, Urbana, and Department of Fish and Game, Agricultural and Mechanical College of Texas, College Station.

Most of the material for the discussion presented here was plotted in map form for all the amphibians and reptiles reported from Texas. These maps are based solely upon published reports, materials in the Texas Cooperative Wildlife Collection at the Agricultural and Mechanical College of Texas, and specimens in the private collection of Bryce C. Brown.

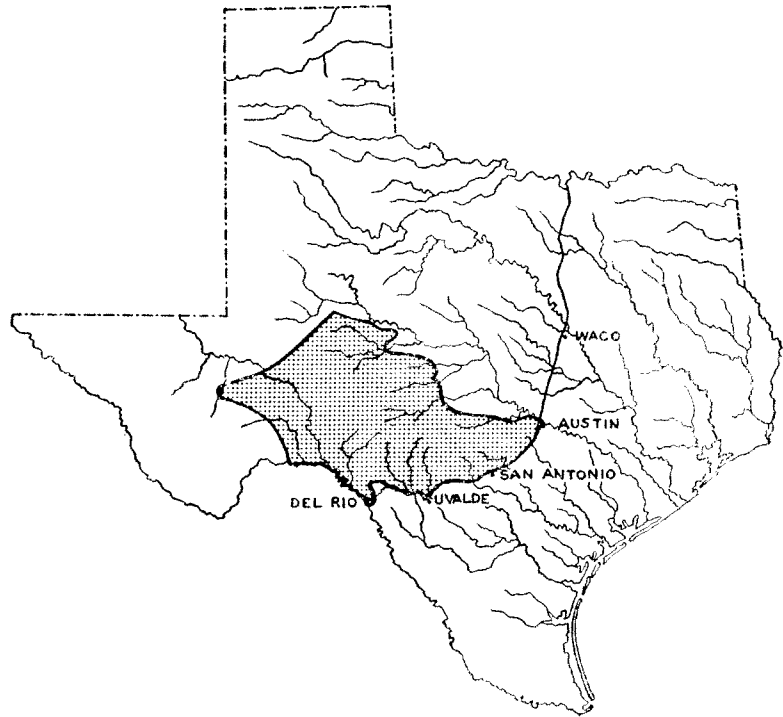


Figure 1. The Edwards Plateau of Texas, indicated by stippled area. The Balcones Escarpment forms its eastern and southern boundaries.

FEATURES OF THE ESCARPMENT AND ADJACENT AREAS

Location. The Balcones Escarpment forms an arc through central Texas, starting from Waco, extending southward through Austin to San Antonio, and then swinging west to Del Rio on the Rio Grande (see Fig. 1). It is not a single long vertical cliff, but rather a series of breaks in the earth's crust, forming cliffs, hills and plateaus up to a height of about 1000 feet. The highest parts are in the vicinity of Austin, San Antonio, and Uvalde; northward from Waco and westward from Uvalde the escarpment gradually decreases in height until it is recognizable only through the presence of small fault lines.

Climate. In passing through a distance of 10 to 20 miles across and at right angles to the escarpment in the vicinity of Austin, San Antonio, or Uvalde, one encounters conspicuous changes in the climate, vegetation, and animal life. In many places the change in vegetation is as sharply defined at the fault lines as a fence row between areas under different types of land use.

The Edwards Plateau, which lies northwest of the escarpment, has a much drier climate than the area to the east of the plateau. The average rainfall is about 25 to 30 inches on the plateau, about 10 to 15 inches less than the area east of the escarpment. The plateau temperatures are a few degrees cooler than the lower elevations. During every month of the year the evaporation on the plateau exceeds the amount of precipitation. This accounts for the dryness of the climate. Very little of the water which falls is available for plant growth, and permanent bodies of open water are seldom found. The fault area of the escarpment, however, is characterized by many clear, spring-fed streams. There are also several large caves with permanent water.

Vegetation. The xeric nature of the biota west of the escarpment is well expressed in the plateau vegetation (Buechner, 1944). An extensive carpet of oak and cedar covers most of the area, with eastern mesophytes (cypress, elm, hickory, ash, birch) finding a suitable habitat along the main streams. The oak-cedar woodland is more closely related to the vegetation of the lower slopes of the Rocky Mountains than to the blackland prairie and post oak-hickory forest to the east or the mesquite chaparral to the south (Tharp, 1939). There is a conspicuous difference not only in species of plants, but also in the growth form of the vegetation. As a result of the dry climate, the tree species are stunted, forming a midget woodland, which becomes a low mat at higher elevations on hill tops as well as farther west on the plateau.

Animal Life. The influence of the escarpment on animal life is as marked as the correlation between climate, soils, and vegetation. This is to be expected, since animal life, vegetation, and the physical environment all interact to produce the large entities known as ecosystems. Specific comparisons of the mammalian fauna and avifauna on either side of the escarpment have never been made. Nevertheless, in comparing the birds of Kerr County on the Edwards Plateau with those of Brazos County about 150 miles to the east (Buechner, 1946), it becomes obvious that the Balcones Escarpment has a definite limiting influence on birds. The birds of Kerr County have greater affinities to the more western bird life than to that of the east. The breeding birds there consist of more than twice as many western and southwestern forms as eastern. About 56 per cent of all the breeding birds in Kerr County find their range limits in the county, which is not far from the escarpment.

This figure compares fairly well with the 77 per cent of amphibians and reptiles that find their range limits at the escarpment.

A further study of other animals and of plants involved at the escarpment may lead to a definite percentage criterion useful in designating biotic areas. Indications from the present study are that the amount of permissible overlap at a natural boundary may be much higher than normally expected, even when a large number of plant and animal species are brought into consideration.

INFLUENCE OF THE ESCARPMENT ON AMPHIBIANS AND REPTILES

Since there is considerable variance in the effect of the escarpment on the various groups of amphibians and reptiles, our analysis is made by natural groupings. The species and subspecies were segregated, on the basis of their distribution, into several categories. We tabulated them, for each of the five groups (to wit, salamanders, anurans, lizards, snakes, turtles), as follows: (1) *limited* (that is to say, kinds which occur at the escarpment but do not cross it extensively in any direction) classified in turn as eastern, western, northern, southern or endemic (autochthonous species, defined as species originating in a certain area but now occurring to a limited extent in adjacent areas, were counted as endemic); (2) *overlapping* (kinds which occur extensively on both sides of the escarpment); or (3) *peripheral* (kinds which do not occur at the escarpment). The latter we again grouped as eastern, western, southern or northern.

We found good evidence of the existence in the state of 38 kinds of anurans, 18 salamanders, 44 lizards, 93 snakes, and 23 turtles, making a total of 216. Fifty-six per cent (122) of the total Texan herpetofauna (with a range of from 50 to 67 per cent among the 5 groups) reach the escarpment. Of these, 77 per cent (94) are limited there, and 11 per cent (total range 1 to 42 per cent) are endemic.

Not all of the range limits considered here are sharply marked off. Among those designated as limited by the escarpment, there may be a slight overstepping, particularly at the Del Rio and Waco ends where the escarpment levels out. In a number of cases the eastern portion of the escarpment forms a sharply defined boundary of the range of the species or subspecies while the southern face is insignificant and the range extends southward over it or beyond the entire southern portion of the Rio Grande. In all such cases it is obvious that low humidity, which occurs in an area similarly outlined, is more significant than any other factor. Species thus partially limited (i.e., by only the eastern face of the plateau) we have nevertheless tabulated as "limited."

It is obvious that no two independent analyses by different investigators are likely to arrive at exactly the same conclusion, since estimates of poorly known ranges must at the present time be highly arbitrary. Likewise arbitrary is the extent of overlapping of the escarpment accepted as commensurate with the definition of "limited" forms. These and other variables make the present estimates subject to later revision.

Anurans. There are 38 forms of the order Salientia whose reported occurrence in Texas is unquestioned. Of these, 50 per cent reach the escarpment. About half of the remaining 50 per cent are of eastern distribution, and most of these belong to the genera *Hyla* and *Rana*, whose requirements for a humid climate are apparently so restricted that they are unable to range as far west as the escarpment.

Of the frogs and toads that do reach the Balcones region, 74 per cent find their range limits there. Most of these are eastern frogs whose requirements for an aquatic habitat cannot be met extensively enough beyond the escarpment. Western forms which find their eastern limit there are toads and spadefoots adapted to a xeric type of habitat. Two frogs, *Eleutherodactylus latrans* and *Syrhopus marnockii*, are adapted to the limestone ledges, cliffs, and caves that front the Edwards Plateau, and are endemic to this area. The species may be tabulated as follows.

LIMITED BY ESCARPMENT

Western

Bufo cognatus
Bufo debilis
Bufo punctatus
Scaphiopus couchii
Scaphiopus hammondi

Eastern

Bufo valliceps valliceps
Hyla cinerea cinerea
Hyla versicolor chrysoscelis
Pseudacris clarkii
Pseudacris streckeri
Rana catesbeiana
Scaphiopus hurteri

Endemic

Eleutherodactylus latrans
Syrhopus marnockii

OCCURRING ON BOTH SIDES

Acris crepitans
Bufo compactilis
Bufo woodhousii woodhousii (mostly west)
Microhyla olivacea
Rana pipiens

NOT REACHING ESCARPMENT

Western

Bufo insidiosus
Hyla arenicolor
Scaphiopus bombifrons
Syrrophus gaigeae

Southern

Bufo horribilis
Hyla baudinii baudinii
Hypopachus cuneus cuneus
Leptodactylus labialis
Syrrophus campi

Eastern

Bufo woodhousii fowleri
Hyla crucifer crucifer
Hyla femoralis
Hyla squirella
Hyla versicolor versicolor
Pseudacris nigrita triseriata
Microhyla carolinensis
Rana areolata areolata
Rana clamitans
Rana palustris

Salamanders. Of the 18 kinds of salamanders whose reported occurrence has been verified, 67 per cent occur at the escarpment, and all of these are at their range limits. The five kinds endemic (or autochthonous) to the escarpment are correlated in distribution with the caves and cave waters, artesian wells, and spring-fed streams of the area. All but one of the non-endemic salamanders are eastern or southern forms. Since this group of amphibians is more restricted to an aquatic environment than is any other group under consideration, it is the one affected most by the change towards drier conditions at the Balcones region. The species may be tabulated as follows.

LIMITED BY ESCARPMENT

Western

Ambystoma tigrinum mavortium

Southern

Diemictylus meridionalis

Endemic

Eurycea latitans
Eurycea nana
Eurycea neotenes
Plethodon glutinosus albagula
Typhlomolge rathbuni

Eastern

Ambystoma texanum
Ambystoma tigrinum tigrinum
Manculus quadridigitatus
Plethodon glutinosus glutinosus
Siren intermedia nettingi

NOT REACHING ESCARPMENT

Eastern

Ambystoma maculatum
Ambystoma opacum
Ambystoma talpoideum
Amphiuma means tridactylum
Desmognathus fuscus brimleyorum
Diemictylus viridescens louisianensis

Lizards. Forty-four lizards are recorded in Texas, and 52 per cent of them reach the escarpment. Of these, all but two (95 per cent) are limited at the fault area. In contrast to amphibians, which require water for at least a stage of their life history, the reptiles are much more tolerant of the dry conditions on the Edwards Plateau: there are more western species limited by the escarpment than there are of eastern and southern species. The reverse is true of amphibians. The species of lizards are as follows.

LIMITED BY ESCARPMENT

Western

Cnemidophorus gularis gularis
Coleonyx brevis
Crotaphytus collaris collaris
Eumeces brevilineatus
Eumeces obsoletus
Gerrhonotus liocephalus infernalis
Holbrookia texana
Sceloporus poinsettii
Sceloporus undulatus consobrinus
Urosaurus ornatus ornatus

Eastern

Anolis carolinensis
Cnemidophorus sexlineatus
Eumeces fasciatus
Eumeces laticeps
Holbrookia propinqua
Leiolopisma laterale
Ophisaurus ventralis
Sceloporus undulatus hyacinthinus

Southern

Eumeces tetragrammus
Sceloporus variabilis marmoratus

Endemic

Holbrookia maculata lacerata

OCCURRING ON BOTH SIDES

Phrynosoma cornutum
Sceloporus olivaceus

NOT REACHING ESCARPMENT

Western

Cnemidophorus grahamii
Cnemidophorus gularis octolineatus
Cnemidophorus perplexus
Cnemidophorus tessellatus tessellatus
Crotaphytus collaris baileyi
Phrynosoma douglassii hernandesi
Phrynosoma modestum
Sceloporus magister magister
Sceloporus merriami merriami

Eumeces gaigei

Eumeces multivirgatus

Eumeces taylori

Gambelia wislizenii wislizenii

Holbrookia maculata approximans

Sceloporus merriami annulatus

Urosaurus ornatus schmidti

Uta stansburiana stejnegeri

Eastern

Eumeces anthracinus

Southern

Crotaphytus reticulatus

Sceloporus grammicus disparilis

Sceloporus cyanogenys

Snakes. Of the 93 species or subspecies of snakes for which we find authentic records from Texas, 53 range up to or across the escarpment; 57 per cent of the ophidian fauna is thus involved in the escarpment area. Of those involved, 70 per cent are limited by the escarpment. Most of the forms not reaching the cliffs are western species. Only ten are eastern species, including three forms of *Natrix* and one of *Farancia*. The species of snakes which are limited are divided almost equally among mesic eastern forms and xeric western or southern forms, indicating a wide range in physiological adaptivity—wider by all odds than in any other reptilian or amphibian order or suborder. The species may be tabulated as follows.

LIMITED BY ESCARPMENT

Western

Agkistrodon mokeson laticinctus
Arizona elegans elegans
Crotalus molossus molossus
Crotalus viridis viridis
Diadophis punctatus docilis
Gyalopion canum
Hypsiglena ochrorhyncha texana
Lampropeltis getulus splendida
Lampropeltis triangulum gentilis
Leptotyphlops dulcis
Masticophis taeniatus ornatus
Rhinocheilus lecontei tessellatus
Sonora episcopa
Thamnophis eques cyrtopsis

Eastern

Agkistrodon mokeson mokeson
Agkistrodon piscivorus leucostomus
Crotalus horridus atricaudatus
Diadophis punctatus stictogenys
Haldea striatula
Haldea valeriae elegans
Heterodon contortrix contortrix
Lampropeltis getulus holbrooki
Lampropeltis triangulum amaura
Micrurus fulvius tenere
Natrix grahamii
Natrix sipedon confluens
Sistrurus miliarius streckeri
Tropidoclonion lineatum
Tantilla gracilis
Storeria occipitomaculata occipitomaculata
Thamnophis sirtalis sirtalis

Southern

Coluber constrictor stejnegerianus
Masticophis taeniatus schotti
Sonora taylori
Tantilla nigriceps fumiceps

Endemic

Natrix harteri
Thamnophis rufipunctatus (in this area)

OCCURRING ON BOTH SIDES

Coluber constrictor flaviventris
Crotalus atrox
Elaphe laeta laeta
Elaphe obsoleta confinis
Heterodon nasicus nasicus
Lampropeltis calligaster calligaster
Masticophis flagellum testaceus
Natrix erythrogaster transversa

Natrix rhombifera rhombifera
Ophedrys aestivus
Pituophis catenifer sayi
Salvadora lineata
Sistrurus catenatus tergeminus
Storeria dekayi texana
Thamnophis marciana
Thamnophis sauritus proximus

NOT REACHING ESCARPMENT

Western

Agkistrodon mokeson pictigaster
Crotalus lepidus lepidus
Crotalus lepidus klauberi
Crotalus scutulatus scutulatus
Diadophis regalis regalis
Elaphe bairdi
Elaphe subocularis
Hypsiglena ochrorhyncha ochrorhyncha
Lampropeltis alterna
Leptotyphlops humilis segregus
Leptotyphlops myopica dissecta
Masticophis taeniatus taeniatus
Salvadora grahamiae
Salvadora hexalepis deserticola
Sonora semiannulata blanchardi
Tantilla atriceps
Tantilla nigriceps nigriceps
Thamnophis macrostemma megalops
Thamnophis sirtalis parietalis
Trimorphodon wilkinsonii

Northern

Diadophis punctatus arnyi
Ophedrys vernalis blanchardi

Eastern

Agkistrodon mokeson austrinus
Carphophis amoena vermis
Coluber constrictor constrictor
Crotalus horridus horridus
Farancia abacura reinwardtii
Masticophis flagellum flagellum
Natrix cyclopion cyclopion
Natrix erythrogaster erythrogaster
Natrix sipedon clarkii
Rhadinaea flavilata

Southern

Coniophanes imperialis imperialis
Drymarchon corais erebennus
Drymobius margaritiferus margaritiferus
Ficimia streckeri
Heterodon nasicus kennerlyi
Lampropeltis triangulum annulata
Leptodeira annulata septentrionalis
Masticophis taeniatus ruthveni

Turtles. The turtles are considerably less tolerant of environmental conditions than other reptiles. There are 23 species of freshwater turtles authentically reported in Texas, 15 of which reach the faulted area. Ten of the latter, or 67 per cent, are restricted. All but one of these are eastern or southern species. Perhaps one reason for the relatively high percentage of range limitations among the turtles is that proper egg-laying conditions are not found on the Edwards Plateau. The soil is so thin and rocky on the plateau that only a small percentage of the area provides soil of sufficient depth and proper texture for burying eggs. The species may be listed as follows.

LIMITED BY ESCARPMENT

Eastern

Amyda mutica
Chelydra serpentina serpentina
Graptemys pseudographica kobnii
Kinosternon subrubrum hippocrepis
Macrochelys temminckii
Sternotherus carinatus
Sternotherus odoratus
Terrapene carolina triunguis

Southern

Gopherus berlandieri

Endemic

Graptemys pseudogeographica versa

OCCURRING ON BOTH SIDES

Amyda emoryi
Kinostemon flavescens
Pseudemys floridana texana
Pseudemys scripta elegans
Terrapene ornata

NOT REACHING ESCARPMENT

Western

Chrysemys picta bellii
Kinostemon sonoriensis
Pseudemys scripta gaigeae

Eastern

Deirochelys reticularia
Malaclemmys pileata littoralis
Terrapene carolina major
Pseudemys floridana hoyi
Pseudemys floridana mobilensis

DISCUSSION

Importance of Escarpment Area. In Table 1 are summarized the effects of the Balcones Escarpment on the distribution of various groups of amphibians and reptiles. The alligator (*Alligator mississippiensis* Daudin) occurs in Texas, but is not included in the table. About 56 per cent of the 216 amphibians and reptiles recorded for Texas reach or cross the escarpment. The Balcones region forms a natural range limit for 77 per cent of the 122 forms involved in the area. The variation among the different groups is from 67 to 100 per cent. Least influenced are turtles, and next in order of increasing influence are snakes, anurans, lizards, and finally salamanders. The variation is correlated with habitat preferences, physiological tolerances, and life history requirements.

It is of interest to note that the percentage of forms reaching the escarpment area varies relatively little (50 to 67) among the five groups studied. In other words (1) these groups are nearly equally well distributed over the central part of the state, and (2) the proportion of the fauna of the state occurring in the escarpment area is sufficiently large to be of significance as a basis for zoogeographic considerations of general import.

Somewhat similarly indicative is the comparison of the combined counts for all groups of (1) eastern plus northern species and (2) western species, which include most (all but 22) forms in the state with the deletion of the endemic forms. A ratio of virtually 1-1 is obtained (76 western, 79 eastern plus northern).

Limiting Effect of Escarpment. Of those reaching the escarpment, 77 per cent are limited in range at that point, or, as a corollary, 23 per cent occur on both sides. If this were accepted as a general indication, it may be stated that a 75 per cent degree of differentiation in the herpetofauna at any boundary would be required to match the category into which the escarpment bound-

TABLE 1

SUMMARY OF EFFECTS OF ESCARPMENT

Group	Anurans	Salamanders	Lizards	Snakes	Turtles	Total
I. Number in state	38	18	44	93	23	216
II. Number not reaching escarpment	19	6	21	40	8	94
III. Number reaching escarpment	19	12	23	53	15	122
IV. Number limited	14	12	21	37	10	94
V. Endemics	2 (10%)	5 (42%)	1 (4%)	2 (4%)	1 (7%)	11 (9%)
VI. Number on both sides	5	0	2	16	5	28
VII. Per cent reaching escarpment	50	67	52	57	65	56
VIII. Per cent limited	74	100	95	70	67	77
IX. Per cent, VI of III	26 (11)	0	5	30	33 (7)	23
X. Ratio, W to E + N in II + IV	0.5 (9-17)	0.1 (1-11)	3.1 (28-9)	1.2 (34-29)	0.3 (4-13)	1.0 (76-79)
XI. Ratio, W to E, in IV	0.7 (5-7)	0.2 (1-5)	1.4 (11-8)	0.8 (14-17)	0.1 (1-8)	0.7 (32-45)
XII. Ratio, W to E + N, in II	0.4 (4-10)	0.0 (0-6)	17.0 (17-1)	1.7 (20-12)	0.6 (3-5)	1.3 (44-34)

ary may be placed. However, a different figure has been arrived at for the birds (56 per cent), a deficiency which may be attributed to the aerial habits of most birds.

Such wide differences in range limitation of the several groups belonging to only two classes of vertebrates at such a conspicuous natural boundary as that formed by the Balcones Escarpment indicate that consideration of all groups—plant and animal—is extremely important in designating the biotic areas of this region of Texas.

It is not improbable that, when adequately known in detail, some "index" group, as for instance the amphibians and reptiles, could be used at least tentatively to establish boundaries of biotic areas. A fairly precise table of correlation should be worked out in advance between the per cent of limitation (or differentiation) and rank of the biotic area.

The degree of endemism (autochthony is not distinguished) is not high. Not all cases counted are clear-cut, and those that are admitted average only 9 per cent for all groups, with a variation of from 42 per cent in salamanders to 4 per cent in snakes and lizards. Endemism apparently varies with extent of isolation from competition, not with degree of adaptability. Salamanders find conditions conducive to isolation more than any other group, inhabiting there, as they do, numerous well-separated artesian drainage systems. Frogs and turtles with their dependence upon humid conditions, find a lesser degree of opportunity for isolation. Least opportunity for isolation is offered to snakes and lizards, and in these the least endemism is found.

Differentiation Contours. The percentage of limitation at the escarpment exhibited by reptiles and amphibians is relatively high. It is obvious that the percentage decreases to the north and south, as the sharpness of the boundary lessens. This phenomenon—distinctness of a barrier in one area, and a gradual lessening of importance away from that area—suggests the value of plotting degree of differentiation of a given fauna by lines spaced at a given interval as for instance 10 per cent. The lines resulting would resemble physiographic contour lines, with a close approach of the lines in areas of great differentiation, a spreading in areas of little differentiation as in the Great Plains. Such contours, if constructed, would aid greatly in the evaluation of biotic provinces.

Differentiation contours in theory would have the advantage of combining the features of the "biotic province" and the "life zone" concepts, each of which by itself is deficient as a measure of natural areas. And again, differentiation contours lend themselves not only to W-E differentiation but also N-S or any other directional line of differentiation.

The difficulties of constructing such contours on a large scale as for the entire United States are such that the idea may be impractical for a number of years; however, it is at least a possible means of natural mapping that deserves consideration.

Degree of Tolerance. Data furnished by the distribution of the herpetofauna in the Balcones Escarpment area offer a means of establishing at least roughly the degree of tolerance by the various groups concerned of the varying conditions occurring in the area (see Table 2). To be considered separately are the average tolerance of the species and the tolerance of the group as a whole. These might well be considered jointly, save for the fact that while numerous species of a given group may overlap a given boundary like the escarpment, the group as a whole is concentrated on one side or the other of the same boundary.

TABLE 2
SUMMARY OF POSSIBLE INTERPRETATIONS

Criteria	Indications		Group Allocation
	Tolerance	Status of Group	
Unbalanced X-Y ratio	group—low	minor,	—————
High percentage of boundary overlap	species—high	ascendent	
Balanced X-Y ratio	group—high	dominant,	Serpentes
High percentage of boundary overlap	species—high	ascendent	
Unbalanced X-Y ratio	group—low	minor,	Anura
Low percentage of boundary overlap	species—low	descendent	Caudata Lacertilia Chelonia
Balanced X-Y ratio	group—high	dominant,	—————
Low percentage of boundary overlap	species—low	descendent	

Degree of tolerance is expressed by two sets of data: by the degree of overlap at the escarpment, and by the ratio of western forms to eastern forms. For these analyses it is preferable to consider only forms reaching the plateau, disregarding the entire state fauna, in order to eliminate a possible source of error introduced by artificial location of political boundaries. The extent of overlap appears to be an index to degree of tolerance of individual species, while the West-East ratio (hereafter called x-y ratio for the sake of brevity and to permit application to situations in which different cardinal directions may be involved from the simple West-East ratio that is important in this particular case) appears to be an index to degree of tolerance in the group as a whole.

Species of salamanders, with the least crossing and with next to the most unbalanced x-y ratio, are obviously the least tolerant of all, individually and as a group, of the varied conditions exhibited in the escarpment area. Species of lizards are next, with very little overlap and a distinctly unbalanced x-y ratio (in favor of the western group); obviously lizards are relatively intolerant of mesic conditions. In anurans a rather high per cent of crossing occurs, and the x-y ratio is less unbalanced; as a group they have been able to adjust more successfully to all the peculiar variations in the area of the escarpment than either salamanders or lizards. The data on crossing are undoubtedly distorted, however, due to the fact that anurans, like turtles, can live under essentially mesic conditions near or in streams that penetrate far into areas of xeric conditions. Although five forms are listed as crossing over, three demand mesic conditions, and therefore the actual per cent of crossing might better be regarded as nearer 10 than 26. There is still a higher percentage of crossing in snakes, and a more closely balanced x-y ratio; snakes are indicated as the most tolerant of all groups considered. Turtles, with an apparently high degree of crossing, are incorrectly allocated by these data, since all but one of those crossing the area are aquatic and thus are not subject to the same limiting factors that affect the distribution of the other groups. The tolerance of turtles is better indicated by the extremely unbalanced x-y ratio, which would mark them as even less tolerant than salamanders.

Status of Groups. Among the five groups comprising the herpetofauna of the escarpment area only two combinations of crossing percentages and x-y ratios are represented: (1) a high percentage of crossing combined with a balanced x-y ratio (Serpentes only), and (2) a low percentage of crossing combined with an unbalanced x-y ratio (Anura, Caudata, Lacertilia, Chelonia). There are, however, theoretically two other combinations possible: (3) a high percentage of crossing with an unbalanced x-y ratio, and (4) a low percentage of crossing with a balanced x-y ratio.

It is not unreasonable to suppose that groups with a low tolerance as a whole (an unbalanced x-y ratio) are *minor* groups, as compared with *dominant* groups which possess a high tolerance as a whole. In like fashion, groups whose species possess high tolerance may be considered as *ascendent*, inasmuch as their species are capable, at the present time, of investigating and inhabiting a wide variety of niches; these are distinct from *descendent* groups whose species have become adapted morphologically for life under certain set conditions and do not enter territories with widely different conditions.

Accordingly, snakes may be regarded as now a dominant and ascendent group, vigorous in an evolutionary sense; all other groups here considered

(anurans, salamanders, lizards, turtles) are minor and decadent groups probably receding in importance on the evolutionary scale.

CONCLUSIONS

1. The herpetofauna in the area of the Balcones Escarpment is 77 per cent limited, with a variation from 67 to 100 per cent in the five groups considered.

2. This per cent of limitation is greater than for birds (56 per cent).

3. "Biotic area" boundaries, indicated therefore by such widely varying degrees of limitation, should be considered on the basis of all groups—plant and animal—concerned.

4. "Index" groups to biotic areas should, however, have some significance when correlations are established between degree of limitation and rank of area.

5. An autochthony of 9 per cent is present and may be correlated approximately with a limitation of an entire fauna of about 77 per cent.

6. Differentiation (or Limitation) Contours may be more useful than either Life Zones or Biotic Provinces in mapping the biota of large areas.

7A. Degree of tolerance in gross terms can be interpreted for individual species and for groups as a whole, from data on percentage of crossing and on x-y ratio, respectively.

7B. Likewise the evolutionary status (i.e., whether dominant or minor, ascendent or descendent) of groups can be determined also from crossing percentages and from x-y ratio.

a. Much crossing of an unbalanced fauna indicates a high specific and low group tolerance, and occurs in minor ascendent groups.

b. Much crossing of a balanced fauna indicates a high specific and high group tolerance, and occurs in dominant, ascendent groups.

c. Little crossing of an unbalanced fauna indicates a low specific and low group tolerance, and occurs in minor, descendent groups.

d. Little crossing of a balanced fauna indicates a low specific and high group tolerance, and occurs in dominant, descendent groups.

8. Snakes are regarded as a dominant and ascendent group.

9. Anurans, salamanders, lizards, and turtles are all regarded as minor, descendent groups.

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