Southwestern Animal Communities in the Late Pleistocene

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A conspicuous feature of terrestrial communities in southern New Mexico and Arizona is their Mexican flavor. Outstanding among biogeographic problems of the Southwest is the history of this Mexican element. Within the Sonoran and Chihuahuan deserts, the desert grassland, the encinal, and the mountain forests we encounter Mexican species or genera. Few of these species penetrate the Colorado Plateau of northern Arizona or central New Mexico. This observation is embodied in Lowe's term "Sub-Mogollon." It is illustrated by his distributional analysis in this symposium.

Those species with continuous ranges and non-relict distributions are of little help to the biogeographer. The gila monster, Heloderma suspectum, the black-tailed rattlesnake, Crotalus molossus, and the ground squirrel, Citellus variegatus, are found in the Mexican Plateau or its escarpment. They also range throughout lowland or both montane and lowland habitats in the Southwest. Presumably they occupy this region because of an adjustment to a climatic regimen essentially arid, subtropical, and endowed with summer Monsoon precipitation.

Of greater biogeographic interest are species confined to isolated habitats and thus to varying degrees discontinuous in their ranges. If the plants or animals concerned are not readily dispersed by wind, man, or other artificial means, their broken distribution may reflect a history of environmental change. In the case of desert fishes which inhabit small springs or headwater tributaries of exinct pluvial lake basins, the history of isolation is quite clear. It is the outcome of desiccation of pluvial lake drainages which occupied the Great Basin during the Wisconsin and earlier glacial periods (Hubbs and Miller, 1948).

'Contribution No. 10, Program in Geochronology, University of Arizona. This study was supported in part by a grant from the American Philosophical Society.

Isolated in the desert ranges, such as the Chiricahuas of extreme southeastern Arizona, relict populations of terrestrial vertebrates also seem to reflect past environmental change. To connect Chiricahua populations of Sectoporus scularis, S. jarrorii, Peromyscus difficilis, and others (table 1) with related Mexican populations in the Sierra Madre would require a corridor of oakpire woodland across intermontane divides presently supporting desert grassland and scrub.

It is difficult to establish limits on vertical and ecological distributions of the montane species, and we may anticipate some surprises. For example, S. scalaris, the bunch grass lizard, is generally associated with yellow pine-bunch grass habitats above 7000 ft. However, its discovery at about 5000 feet in the Chiricahuas, at 4000 ft. in the Santa Catalinas (both in Gehlbach, 1956), and at 4300 ft. in the Empire Valley, makes its separation from Mexican populations a matter of relatively slight climatic change.

could explain the growth of trees, such as Pinus leiophylla, on certain ridges and slopes decidedly below their expected limits elsewhere (Marshall, 1957: 33). preliminary analysis) influence the lower limit of woodland and the Institute of Atmospheric Physics (see McDonald, 1956, Finally, regional climatic anomalies, presently under study by (Shreve, 1919, 1922; Blumer, 1910, 1911; Marshall, 1957: 31-32). tures of woodland and forest in the various desert mountains appeared crucial in determining the structural and floristic feaelevation, top elevation mass, bedrock composition, and slope all now foremost in vegetation analysis (McIntosh, 1958). Base level tive demonstration of species patterns and the continuum concept In effect this conclusion anticipated the more elegant quantitaor shrubs occupied the same vertical range (Shreve, 1915:111-112). in the Catalina Mountains revealed that no two species of trees ago. Shreve's classic investigation of climate and vegetation zones Ecological study of the desert mountains began fifty years

The high montane faunas of the Southwest are poor in species. In the Chiricahuas, 70 species of terrestrial vertebrates (reptiles, amphibians, and small mammals) occur near the mountain foot at 5000 feet. Twelve occupy the top at 9500 feet (fig. 1, table 2). This decline with altitude can be related to two features: first, the small area of mountain top forest, compared with extensive lowland habitats; second, the well-known effect of biotic depauperization with increase of elevation or latitude. We may infer a rough relationship between primary productivity and the number of species inhabiting communities along altitudinal or latitudinal gradients.

The desert mountains are not exclusively populated by southern, Mexican elements. There are Rocky Mountain species or subspecies which find their southern limits here. The mammals Microtus longicaudus in the Pinalenos, Peromyscus maniculatus rufinus in the Chiricahuas and Sacramentos, the salamander Aneides hardyi in the Sacramentos, the birds Sitta canadensis and Hylocichla guttata in the Chiricahuas are suitable examples. In general the faunal pattern seems to match the floristic division noted by Shreve (1915: 40), i.e. Rocky Mountain elements are most obvious in the montane forests above 7000 ft. while the Mexican flavor is strongest in oak-pine woodland and grassland at lower elevations.

How can we explain the origin of montane relicts in the Southwest? There are at least three possible biogeographic hypotheses: (1) accidental arrival analogous to the colonization of

cceanic islands; (2) Tertiary arrival with Isolation during late Tertiary aridity; (3) one or several Pleistocene arrivals and post-glacial isolation.

The first of these suggestions carries some weight in terms of those trees and birds which enjoy a high dispersal potential. Marshall (1957: 67) favors it with regard to the Mexican oak-pine woodland birds in the Southwest. Gadow's observation (1930) on the colonization of the top of Volcano Jorullo by pine (Pinus montezumae) is one of remarkably few cases in which the ability of a coniferous tree to cross an ecological barrier in a hurry has been demonstrated. In theory, the accidental arrival of montane reptiles and mammals on Jorullo and other isolated mountains would be much more difficult. In the absence of evidence that small, terrestrial vertebrates filter across major ecological barriers, it seems reasonable to interpret their distributions as the result of climatic change.

Turning to the paleoclimatic record, it is necessary to postulate Tertiary isolation in the face of the following: (1) very close taxonomic relationship betwen relict montane populations in the Southwest and Mexico (Bogert and Oliver, 1945:332-333); (2) Pleistocene pollen evidence of major climatic change in the Southwest, specifically the San Augustine Plains (Clisby and Sears, 1955) and Rampart Cave (Shutler and Martin MS); (3) the extinct pluvial lakes and their Full-glacial correlation in the Great Basin (Broeker and Orr, 1958).

Such evidence does not exclude the probability of extensive and important Tertiary migrations. But it does make Tertiary biogeography irrelevant to the problem at hand, the isolation of the desert mountain biota. We may infer that Pleistocene climatic change was of sufficient amplitude to establish forest corridors between mountains in Mexico, the Southwest, and the Rockies.

The peculiar feature of the Southwestern blota, as I have stressed, is the large number of Madrean Mexican species which find their northern limits on montane forest populations. This is an inverted image of the classic Arctic-Alpine pattern. While it is reasonable to explain the distribution of Sorex vagrans, Microtus longicaudus, and Aneides as Full-glacial relicts (Findley, 1955; Murray, 1957), an inconsistency arises if we interpret the northern isolates of S. scalaris, S. jarrovii, and other Mexican animals and plants in such terms.

In brief, it appears to me that the montane Mexican element did not reach the Southwest at the same time as northern (Rocky Mountain) species. I would suggest that the most recent arrival of Mexican woodland elements is no older than the postglacial period. A rash guess would put the time of montane woodland interconnection at 3000 to 8000 years ago. This coincides with the Thermal Maximum of eastern North America and the Altithermal of the west. To generate a woodland corridor in this period may seem extremely improbable to those who associate climatic warming with drought. However, the special subtropical

monsoon circulation of the Southwest permits us to consider another element in the climate, the summer rains. Perhaps it would be helpful to restate the blotic evidence:

- 'Marshall's sequence of montane vegetation types (1957: 32) shows that, as one proceeds southward into Mexico, pine-oak woodland and forest zones occur at lower levels.
- 1. Isolated mountains of the Southwest harbor a woodland biota derived mainly from the Mexican Plateau.
- 2. Parts of this blota are entirely confined to montane habitats, i.e. they include species unknown in the intermontane grassland or desert scrub.
- 3. Parts of this blota have relatively low accidental dispersal potential, i.e. terrestrial vertebrates.
- 4. Among the isolated montane populations studied closely, no important taxonomic differences have been reported in either reptiles and amphibians (Bogert and Oliver, 1945) or mammals (Hoffmeister and Goodpaster, 1954).
- 5. The present lower limit of the montane Mexican element is about 5000 feet, or roughly 1000 feet above the intermontane divides through northern Sonora, southern New Mexico, and southern Arizona. To obtain a continuous distribution of the Mexican montane element would require a climatic change sufficient to replace desert grassland and scrub, the present vegetation of the divides (Marshall 1957: Fig. 2.), with oak-pine savanna. This would not require a major climatic shift.
- 6. There appears to be a relationship between distribution of both lowland and montane Mexican biotas and the summer (Monsoon) rain circulation system of the Southwest.

If the northern limit of the Mexican element were determined by temperature alone we might expect individual species to occupy narrow vertical ranges at their northern outposts. However, both S. scalaris and S. jarrovii occur from 5000 to 10,000 feet in the Chiricahuas and Pinalenos respectively, the northern limits of these species. They occupy a wide altitudinal range here and scarcely exceed it on the Mexican Plateau.

The sudden depletion of Mexican elements, whether oaks (Quercus arizonica, Q. emoryi, and others), pines (Pinus arizonica, P. leiophylla), lizards, snakes (Crotalus pricei, C. Williardi), or mammals (Peromyscus difficilis, P. truei), and their extensive ranges in the summer-rain woodlands to the south suggests an obligate relationship, present and past, on a monsoon climate. Could these species have moved north into Arizona during the last Full-glacial interval of the late Pleistocene?

Pleistocene circulation is a matter of considerable meteorological speculation. I am indebted to J. E. McDonald for pointing out that, in subtropical latitudes, the most obvious effect of a continental ice sheet would be the elimination of the present midcontinent summer high-pressure center. This center is crucial in generating Monsoon summer rains in the Southwest. We may restulate that Southwestern pluvial lakes of Wisconsin age were

nourished almost exclusively by winter precipitation. While the glacio-pluvial climate would lower the ecological limits of montane species, permitting the entry of sprace and other Cordilleran species into the Sierra Madre, it should eliminate the summer rain biota from this area.

Study of recent weather records indicates that rainfall along the equatorial fringes is quite sensitive to changes in high-latitude circulation (Kraus, 1958). The warming of winter in high latitudes has allowed a gradual northward shift of subtropical cells with a rise in summer precipitation in central Mexico (Wallen, 1955: 61). On this basis it is possible to postulate increased summer rainfall near the boundary of the Monsoon system during past periods of high-latitude warming. Specifically, any climatic model for the thermal maximum in the postglacial period of the Southwest should allow for an increase in summer rainfall.

I am aware that such a bioclimatic theory conflicts with the more common view—that the altithermal, drought, and arroyo cutting are essentially synonomous. The fact that it is possible to construct a divergent model may encourage prehistorians and biogeographers to review the evidence.

The present ranges of montane animals and plants, viewed in terms of Pleistocene climatology, suggests that southeastern Ariona and southern New Mexico experienced invasion of Mexican woodland elements in postglacial time. Although they did not restrict such an invasion to the Altithermal, I find that Bogert and Oliver (1945: 332-333) reached essentially the same conclusion: "... the existence of populations belonging to the same species or subspecies that now are represented on mountaintops along the periphery of the deserts (but not in intervening territory) is interpreted as evidence for the belief that a moist period followed the last period of glacial cold." Perhaps pollen study of Late Pleistocene sediments in the Southwest will help to date the entry of montane Mexican animals and plants.

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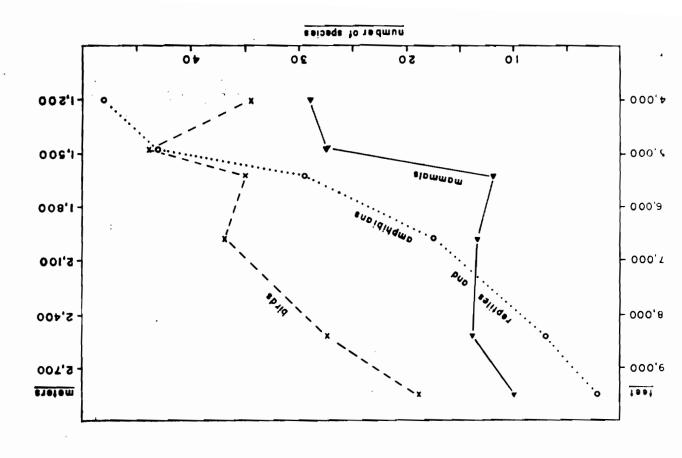


FIGURE 1.

Chiricahua Mountains: (1) passerine birds; (2) small mammals, Orders Insectivom, Rodentia, and Lagomorpha; and (3) reptiles and amphibians. Based on records listed in Table 2. Species-elevation curves for various small vertebrates in the

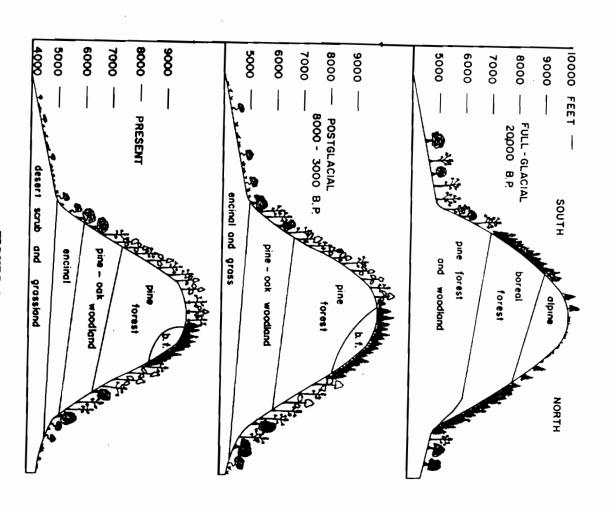


FIGURE 2.

found presently at Nacori, 30° north latitude in northwestern Mexico (cf. Marshall, 1957:). at 32° north latitude. The last woodland-ercinal interconnection vegetation zones at this time may have been subequal to that between ranges is considered of postglacial age. The position of Late Pleistocene changes in vegetation of a desert mountain

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TABLE I.

FOREST AND WOODLAND VERTEBRATES OF THE CHIRICARUA MOUNT AINS

Neotoma mexicana Sorex vagrans Sylvilagus floridanus	tp. maniculatus rufims *P. masutus *P. difficilis	*Sciurus apache Peromyscus boylii	Lampropeltis pyromelana *Crotalus pricei *C. lepidus	*Sceloporus scalaris *S. jarroyi *Eumeces callicephalus	
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a high dispersal potential (bats, birds) are excluded. Those with distribution centers in the Mexican Plateau are indicated by an asterisk (*); those with distribution centers in the Rocky Mountains by a dagger (t). Species occupying lowland as well as montane habitats and those with

Table II. Altitudinal records for vertebrates of the Chirichne Mountains, Arizons. Definite interabire or specimes records are marked "X", doubtful records or those expected on the haris of distribution in adjacent mountains are marked "5". The litter were commed as one shall in the total for each cliration.

A. REPTILES AND AMPRIMANS

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