

PRELIMINARY OBSERVATIONS ON MAMMALIAN FAUNAL RELATIONSHIPS, CANYONLANDS NATIONAL PARK, UTAH¹

INTRODUCTION.--Canyonlands National Park comprises about 425 square miles of canyons and mesas in southeastern Utah. Established in 1964, the Park includes the confluence of the Colorado and Green rivers. The major rivers divide the Park--and the rest of eastern Utah--into three disjunct land masses (Fig. 1). Elevations in the Park range from about 4000 to nearly 7000 feet. This range of relief dictates a wide variety of ecological conditions and a complex distribution of biotic communities. Although the Park was established to preserve its scenic grandeur and its vast exposures of the geologic record, it includes a biotic mosaic of intriguing diversity and subtlety.

Knowledge of the mammals of the Canyonlands is scanty. Too rough for railroad builders and too precipitous and dry to farm, the area was circumvented by the exploratory parties that provided our basic knowledge of mammals elsewhere in the West--the Railroad Surveys of the 1850's and the Biological Survey of the early 1900's. Stockmen have utilized the area for grazing sheep and cattle for a century, but only the uranium rush of the 1950's opened the region to exploration and formal survey. The boom having passed its crest, the land remains a wilderness in many respects, its natural history mostly unstudied.

Studies of ecological distribution and community structure of mammals in the Park were begun in the summer of 1971 with the cooperation of the National Park Service and supported in part by a grant from the Society of the Sigma Xi. Data accumulated in the initial field season are incomplete, but sufficient to allow preliminary observations on faunal relations within the Park and in adjacent parts of the Colorado Plateau.

Forty-one species of mammals are known to occur in Canyonlands National Park, documented by museum specimens, or by observations of animals or their certain sign. An additional 20 species are of suspected occurrence or are known to have occurred within historic time. Of the total probable fauna of 61 species, two species are insectivores, 18 bats, two lagomorphs, 24 rodents, 12 carnivores and three artiodactyls.

Topography.--Canyonlands National Park is a showcase for the effects of erosional processes on a land surface dominated by flat-lying sedimentary strata. The principal erosive forces have been the master streams of the area, augmented by their host of ephemeral tributaries. Colluvial mass-wasting also has had obvious effects. Given a suite of powerful geomorphic agents, the existing topographic pattern has been dictated by differential resistance of sedimentary strata and the distribution of faults, joints and folds. According to Baars (1971), the character of slopes, ledges and benches is controlled primarily by differential resistance, whereas the distribution of buttes, pinnacles, ridges and gorges is controlled largely by joint patterns.

The general sedimentary pattern is an alternation of resistant cliff- or rim-forming sandstones (Wingate, White Rim) with less resistant shales, which form slopes and terraces. Striking complexity is based on the recurrence of simple geomorphic events. Topographic diversity underlies the patent complexity of biotic distributions.

Vegetation.--The vegetation of Canyonlands National Park currently is under study by Mr. Walter L. Loope, of the Department of Range Science, Utah State University,

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Logan. The principle technique is the "comprehensive method" of Kuchler (1967), using aerial photography and ground-level survey; this study will provide a baseline for future detailed ecological studies within the Park. In the meantime, cruder analyses of plant distribution will have to be used. Kuchler (1964) mapped three types of "potential natural vegetation" in the area: galleta (Hilaria jamesii) grassland, a blackbrush (Coleogyne ramossima) community and pinon-juniper woodland. Although dominance changes locally, these types point out associations that are, in fact, reflected in mammalian distributions. On relatively stable interfluvies, thin, silty soils form. Such flats and rock-bound "parks" are clothed with grassland. Oryzopsis, Hilaria, Stipa, Sporobolus and Bouteloua are important genera of grasses; Yucca, Opuntia, Gutierrezia, Artemisia and Ephedra form a prominent shrub synusia, the composition of which varies locally, in part, perhaps, with grazing history. Areas of rimrock and canyon walls are a common topographic type. These areas frequently are precipitous; typical substrate is a coarse, unstable colluvial rubble. The vegetation on such sites includes a variety of shrubs, among them Cowania, Quercus, Shepherdia and Lahonia. Juniper-pinon woodland occurs locally in such situations, and also on rocky mesa-tops. The understory in this community varies, apparently with edaphic conditions. Phreatophytic "bottoms" along the major rivers are dominated by native willows (Salix) or exotic saltcedar (Tamarix). Sandy washes of ephemeral streams (and adjacent floodplains) support stands of halophytic shrubs (Sarcobatus, Atriplex).

Methods.--Field effort during the summer of 1972 consisted of 6611 trapnights, apportioned unevenly among 43 localities. Data were obtained on some 460 individual rodents; in addition, occasional mist-netting yielded a number of bats. Mammals of other orders were documented by observation of animals and/or sign. The following remarks apply only to rodents, however.

ECOLOGICAL DISTRIBUTION.--For each specimen taken, the nearest plant was recorded; if no plant was nearby, a physical descriptor of the trap-site was noted (rock, woodrat den, etc.). After judicious lumping of closely similar terms, 31 descriptors were employed. Species of rodents associated with each descriptor were listed. Similarities between these faunal lists were calculated, using the "faunal resemblance factor" of Duellman (1965:677):

$$FRF = 2C / (N_1 + N_2)$$

(where C is the number of species common to two faunal lists, N_1 is the size of one sample and N_2 is the size of the other). The number of species pertinent to any given descriptor ranged from ten ("boulders") down to only one for several of the categories.

FRF values were subjected to elementary cluster analysis by the "weighted pair-group" method of Sokal and Sneath (1963:309). The resulting similarity phenogram (Fig. 2) is of some interest, although absolute values are distorted by the sample sizes involved. Roughly speaking, descriptors cluster together according to physiographic situation: A, open sites with thin soils or stabilized dunes; B, rocky outcrops and rims; D, rubble slopes and terraces. Group C is a miscellaneous cluster including descriptors of disturbance (house, brushpile, Opuntia) as well as of floodplains with alkaline soils (Atriplex, Sarcobatus). Group E includes five descriptors that show no particular resemblance inter se or to other clusters. This seems to be an artifact of sample size. Where vegetation is concerned, all clusters have more physiognomic than floristic integrity.

primary association is with cluster A (loosely, "grasslands"). For the remaining eight species, the primary association is with cluster B (roughly, juniper-pinon woodland and/or broken terrain). Two other clusters have strong (albeit secondary) mammalian associates. Four species (A. leucurus, D. ordii, P. maniculatus, P. boylii) show associations with cluster C (miscellaneous and/or halophytic shrubs) of 15 per cent or more. A single species (Neotoma mexicana) is associated at all strongly (above 10 per cent, in this case, 25 per cent) with cluster D (saxicoline shrubs).

ECOLOGICAL AMPLITUDE.--Another concept--and one closely related to fidelity--is the ecological amplitude of a species. How wide a range of conditions does it occupy? An impression of this can be gained by contrasting numbers of descriptors associated with each species. This number ranged from two (Neotoma albigula, N. cinerea) to 16 (Peromyscus maniculatus). As might be expected, there is significant correlation ($r = 0.8$, $p = 0.01$) between number of descriptors and sample size. This does not mean, however, that the more individuals taken, the more descriptors will be involved (although that certainly is part of the explanation). It also is true that the more euryecious a species, the more common--widespread and abundant--it can be, and perhaps the more trappable it is. When more data are available, ecological amplitude should be amenable to factor analysis.

A rough index of specific ecological amplitude might be derived by dividing the number of individuals by the number of descriptors. This ratio varies from 2.0 for several species (Ammospermophilus leucurus, Dipodomys ordii, Peromyscus maniculatus--all grassland species) to 6.0 for Neotoma albigula and N. cinerea. Two seemingly stenecious kinds of Peromyscus have relatively high indices (P. truei, 4.95, P. crinitus, 5.25); that is, they are relatively frequently associated with a given descriptor. These also are the species with the greatest numbers of individuals. The rather narrow range of conditions under which they occur is amply represented in Canyonlands National Park. Another species of Peromyscus (P. maniculatus) shows a low ratio (2.19), suggesting a euryecious species. This also is the species most closely associated with group C in the cluster analysis above. Here as elsewhere over its broad range, the deer mouse is associated with "miscellaneous communities" as a sort of mammalian "weed," an opportunistic invader of ephemeral habitats. Where the native habitat is undisturbed (by man or otherwise), P. maniculatus is a surprisingly "rare" species.

FAUNAL RELATIONSHIPS.--Relative to the mammalian fauna of Utah as a whole, the local fauna is small (see Fig. 5). Only among bats does it approach the richness of that statewide. A number of biotic associations important in adjacent areas are not represented in Canyonlands National Park. That fact is relevant in attempting to evaluate the efficacy of barriers to mammalian distribution.

As emphasized previously, the Park and the rest of eastern Utah are divided into three disjunct segments by the Colorado and Green rivers. These areas are mostly comparable in climate, physiography, vegetation and other ecologic factors. Nonetheless, mammalian faunas of the three districts differ, as discussed by Kelson (1951) and Durrant (1952). Durrant divided southeastern Utah into three distributional "subcenters" (San Juan, San Rafael, Grand Valley) of the Canyonlands "Province" of the Colorado Plateau "Faunal Area" (Fig. 6). The units, based on areal relationships, are closely analogous to "biotic provinces" of Dice (1943). By implication, Durrant's subcenters include, respectively, the Needles, Haze and Island-in-the-Sky districts of Canyonlands National Park. The Abajo Mountain Subcenter of the Coloradoan Province of the

Southern Rocky Mountains Faunal area is a distributional relic within the San Juan Subcenter.

There is a tendency among zoogeographers to look at a map and to interpret the features shown as barriers--of variable effectiveness--to the distribution of species. However, available maps--even topographic maps indicating gorges thousands of feet deep--show too little ecological detail, easily leading to simplistic conclusions. In southeastern Utah, major streams separate notably dissimilar faunas. Our immediate impulse might be to feature the rivers as barriers to distribution. In fact, however, the barrier is ecological conditions. To be sure, the ultimate barrier--on a scale of thousands of years, perhaps--is the master streams of a region, for they mold the terrain and establish the physical conditions against which biotic distributions have evolved. However, data and subjective field observations suggest that major segments of the fauna do not approach the rivers closely enough to feel their effects as barriers.

In order to analyze faunal resemblances among the disjunct areas in question, faunal lists of rodents were drawn up for each of the three main subcenters based on range maps in Durrant (1952). Faunal resemblances among these lists were calculated at specific and subspecific levels, using the Faunal Resemblance Factor of Duellman (1965:677) described previously. Results are shown in figs. 7 and 8. For comparison, faunal lists were compiled for the three districts of Canyonlands National Park. These lists were drawn as liberally as possible, including taxa of suspected occurrence--however remote the suspicion--as well as those documented. In other words, the two sets of faunal lists were made as nearly similar as possible. Faunal resemblances were calculated as above, and the results are shown in figs. 9 and 10.

Comparison of the results of these analyses is of some interest. In the first place, more taxa are present in southeastern Utah in general than are present in Canyonlands National Park. Indeed, any given district includes at most 80 per cent (Island, 80 per cent, Maze, 68 per cent, Needles, 60 per cent) of the fauna of the larger subcenter in which it lies.

Secondly, broad relationships of the faunas are the same regardless of the scale at which one looks. The Island and the Maze (Grand Valley and San Rafael) are more closely related inter se than either is to the Needles (San Juan). These affinities have been taken to indicate--and rightly so in a certain sense--that the Colorado River below its confluence is a more formidable barrier to mammalian distribution than are either of the principal tributaries, and, furthermore, that the Colorado (Grand Fork) above the confluence is a stronger barrier than is the Green (Durrant, 1952).

Faunal resemblances differ in absolute values in the analyses at different taxonomic levels. Consider first the subspecific level. Faunal resemblance between the Needles and the Maze (San Juan and San Rafael) is low in any case (0.213 vs. 0.250); however, faunal resemblance between districts of the Park is lower (0.424 vs. 0.489) than between the respective faunal subcenters. On the other hand, resemblance between the Island and the Maze (Grand Valley and San Rafael) is stronger (0.581 vs. 0.524) between districts than between faunal subcenters.

One would predict that each pair of areas would be closer at the specific level than

at the level of ^{sub}species, and this is, in fact, the case. However, differences in faunal ~~semblance~~ still exist among the districts and subcenters, and the pattern of relationships differs slightly from that seen at the subspecific level. The Needles and the Island are more closely related than their respective subcenters (0.875 vs. 0.825); so, too, are the Needles and the Maze (0.733 vs. 0.703). However, the Grand Valley and San Rafael subcenters are more closely related than the districts that they include (0.952 vs. 0.903). Why should these differences exist?

Differences in sample size account for absolute values of the index, but they do not account for the pattern observed among the indices. It seems to me that observed differences relate to ecological factors. Specific mammalian distributions relate closely to ecologic conditions--especially vegetational physiognomy. Vegetation, in turn, is related closely to local and regional physiography. Especially at the specific level, the index is not simply describing the strength of a physical barrier, but also the similarity of community types. For example, the Needles District includes habitat types that are not represented on the Island; the fauna of the Island is more depauperate relative to its broader distributional subcenter than is that of the Needles. On the other hand, the mosaic of habitats in the Maze and on the Island is rather similar. Species that tend to differentiate the broader subcenters simply find suitable conditions neither in the Maze nor on the Island.

If the relationship of subcenters is stronger than that of the included districts, then .. there are species for which conditions are unsuitable in both districts. Some species are stopped short of the ultimate barrier. On the other hand, if relationships of local districts are stronger than those of the subcenters of which they are parts, then both of the local faunas are more-or-less depauperate parts of larger areal faunas. In either case, considerable parts of the regional fauna reach distributional limits short of the ultimate barrier.

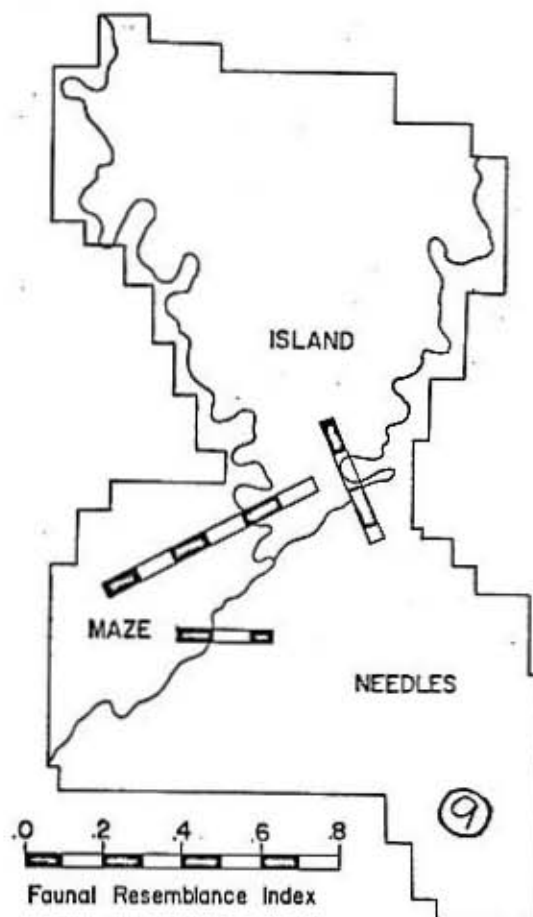
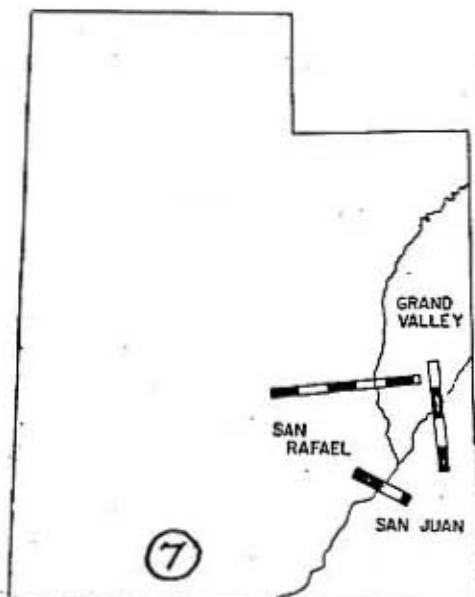
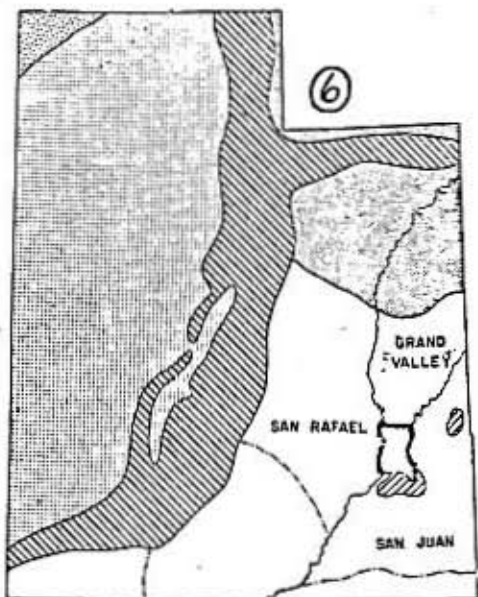
At the subspecific level, we obviously come closer to measuring the efficacy of a local barrier, but still--because mammals are tied to ecologic community-types and community-types are tied to physical attributes of the environment--we have no index of the strength of the ultimate distributional barrier.

SPECIES DIVERSITY.--In the field, I was impressed by the seeming diversity of communities on broken terrain in contrast to those on level parks or flats. It appeared that grasslands, for example, supported fewer kinds of mammals and lower numbers of individuals than did shrublands on canyon rims. Species diversity is an important attribute of biotic communities and one under active study by a number of ecologists. At this stage in the evolution of the concept, selection among the indices of species diversity is somewhat arbitrary; as Lloyd *et al.* (1960:257) point out, "which one is 'best' depends on which one proves in practice to give the most reliable, surprising ecological predictions and the greatest insight."

Species diversity was calculated according to the index of E. H. Simpson (1949): $\frac{1}{N} = \sum \frac{n(n-1)}{N(N-1)}$, where n is the number of individuals of any given species, and N is the total number of individuals taken in the sample. The index $\frac{1}{N}$ is an estimate of the probability that two individuals drawn from the community at random will be of the same species. Possible values of $\frac{1}{N}$ range between 0 and 1, the higher the

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FAUNAL RESEMBLANCE OF RODENTS, SOUTHEASTERN UTAH.¹

	Subcenter		
	San Juan	Grand Valley	San Rafael
	$\frac{N_{\text{species}}}{N_{\text{subspecies}}}$		
San Juan	$\frac{26}{26}$	$\frac{0.825}{0.489}$	$\frac{0.708}{0.213}$
Grand Valley	$\frac{18}{11}$	$\frac{20}{20}$	$\frac{0.952}{0.524}$
San Rafael	$\frac{17}{5}$	$\frac{20}{11}$	$\frac{22}{22}$

¹Data after Durrant, 1952; index is FRF of Duellman, 1965.

FAUNAL RESEMBLANCE OF RODENTS, CANYONLANDS NATIONAL PARK, UTAH.¹

	District		
	Needles	Island	Maze
	$\frac{N_{\text{species}}}{N_{\text{subspecies}}}$		
Needles	$\frac{18}{18}$	$\frac{0.875}{0.424}$	$\frac{0.788}{0.250}$
Island	$\frac{14}{7}$	$\frac{16}{16}$	$\frac{0.903}{0.581}$
Maze	$\frac{13}{4}$	$\frac{14}{9}$	$\frac{15}{15}$

¹Data from Armstrong, 1972; index is FRF of Duellman, 1965.

SPECIES DIVERSITY OF RODENTS IN CLUSTERS A, B AND D.

Cluster	Diversity Index	
	Simpson ¹	Shannon ²
A	0.147	2.9640
B	0.177	2.7930
D	0.196	2.0379

¹E. H. Simpson, Nature, 163:688, 1949.

²After Lloyd, Zar and Kurr, Amer. Midl. Nat., 72:257-272, 1968.