ECOLOGICAL DISTRIBUTION OF RODENTS IN CANYONLANDS NATIONAL PARK, UTAH

David M. Armstrong[1]

ABSTRACT.— Studies of microhabitat of 14 species of rodents by cluster analysis suggested that the diverse landscapes of Canyonlands National Park, Utah, include six broad "habitat-types": (1) rimrock; (2) desert shrublands; (3) saxicoline woodland and sagebrush; (4) oakbrush; (5) riparian deciduous woodland; and (6) grasslands. *Perognathus parvus* and *Neotoma cinerea* were the species most strongly associated with single "habitat-types," desert shrub and saxicoline woodland, respectively. *Peromyscus maniculatus* and *P. truei* were the species associated with the broadest ranges of habitats. The rodents with the most similar habitats were *Neotoma mexicana* and *Peromyscus boylii*; *Eutamias quadrivittatus, P. truei,* and *P. crinitus*; *Ammospermophilus leucurus* and *P. maniculatus*; and *Dipodomys ordii* and *Onychomys leucogaster*.

An understanding of ecological distribution of organisms is important for both interpretation and management of ecosystems. Typically the vertebrate ecologist describes patterns of ecological distribution in terms of vegetational associations recognized *a priori*. The purpose of this paper is to allow the rodent fauna itself to define salient patterns of environmental features in Canyonlands National Park and meaningful associations of mammalian species. This not only provides a description of environmental patterns, but allows field naturalists to check their sense of the landscape against mammalian habitats, rather than the opposite (i.e., forcing species' distributions into their view of environmental pattern).

Canyonlands National Park preserves some 450 square miles (1170 km^2) of spectacular canyons and mesas in San Juan and Wayne counties, southeastern Utah. The park includes the confluence of the Green and Colorado rivers, which are entrenched in canyons up to 2000 ft. (610 m) deep. These canyons divide the park (and the rest of southeastern Utah) into three distinct land masses. Elevations in the park range from about 3750 to nearly 7000 feet (1150–2135 m). This range of relief dictates a wide variety of physical conditions and a complex distribution of biotic communities.

Knowledge of mammals of the Canyonlands is rather scanty. The area was ignored by the exploratory parties that provided fundamental knowledge of mammalian distribution elsewhere in the West, such as the Railroad Surveys of the 1850s and the Bureau of Biological Survey in the early 1900s. John Wesley Powell's expeditions of the 1870s paid almost no attention to the biota of the region. Although the U.S.-IBP Desert Biome Project worked over much of the desert Southwest, no study area was located on the Colorado Plateau (MacMahon 1976).

The Canyonlands Section of the Colorado Plateau physiographic province is a showcase for the effects of erosion on an arid land dominated by flat-lying sedimentary strata. For details of geology, see Baars (1971) and Lohman (1974). The climate of Canyonlands is arid, with hot summers, cold winters, and pronounced diel fluctuations in temperature. Mean annual precipitation is about 7.5 in., about one-third of which falls during the third quarter of the year, usually as local, torrential thunderstorms (Tanner 1965). Excepting the immediate vicinity of the master streams, perennial surface water is limited to a few widely scattered springs and seeps. Bare rock comprises more than half of the surface. Where soils have formed, they are reddish, gravelly to silty loams, moderately

[1]Department of Integrated Studies and University Museum, University of Colorado, Boulder, 80309.

alkaline in reaction (Wilson et al. 1975). Undeveloped aeolian sands and silts are present locally.

Vegetation of the Canyonlands varies widely with physiographic setting, edaphic conditions, available moisture, and grazing history. Hayward et al. (1958) described four principal vegetation types in the vicinity of Arches National Park: (1) cottonwood-willow-tamarisk floodplain, (2) northern desert shrub, (3) pinyon-juniper woodland, and (4) hanging gardens. Although dominance changes locally, these types point out associations that are recognizable in the landscape (and are reflected in mammalian distributions to some extent). On relatively stable interfluves, thin, silty soils form. Such flats and rockbound parks are clothed with grassland. *Oryzopsis, Hilaria, Stipa, Sporobolus,* and *Bouteloua* are important genera of grasses; *Yucca, Opuntia, Gutierrezia,* and a variety of annual forbs are present also. Areas of rimrock, slickrock, and canyon walls are a frequent topographic type. These areas often are precipitous; typical substrate is a coarse, unstable colluvial rubble. Vegetation on such sites includes a variety of shrubs, among them *Cowania* and *Shepherdia* on slopes, and *Mahonia* and *Quercus* at bases of cliffs. Woodland of juniper or juniper and pinyon occurs locally on such sites and also on well-drained mesa tops. The understory in this community varies, apparently with edaphic conditions. Phreatophytic cottonwoods (*Populus*) and willows (*Salix*) or exotic saltcedar (*Tamarix*) occur along the major washes. Floodplains support stands of halophytic shrubs (*Sarcobatus, Atriplex*). Sagebrush (*Artemisia*) often occurs in association with junipers or as an overstory on grassy flats. "Hanging gardens" develop locally as mesic associations watered by seepage at contacts between some rock units. These associations are comprised of a striking variety of plants, including *Mimulus, Aquilegia, Habenaria,* and *Rhus*.

Despite generally forbidding physical conditions, Canyonlands National Park supports a diverse vertebrate fauna, including some 60 species of mammals. For general information on the region as a whole, see Hayward et al. (1958). Tanner (1965) provided notes on a few species of rodents. Durrant and Dean (1959) commented briefly on ecological distribution of rodents in Glen Canyon (now inundated by Lake Powell), immediately south of Canyonlands. Johnson (1976) and Clevenger (1977) have presented data on some aspects of ecology of rodents in Canyonlands National Park. For further information on mammals of southeastern Utah, see Benson (1935), Durrant (1952), Durrant and Dean (1959), Kelson (1951), Lee (1960), and Armstrong (1977b, in press).

This report concerns 14 species of rodents, most of them abundant and widespread (vernacular name, sample size in parentheses): *Eutamias quadrivittatus* (Colorado chipmunk, 64), *Ammospermophilus leucurus* (white-tailed antelope squirrel, 23), *Perognathus apache* (Apache pocket mouse, 29), *P. parvus* (Great Basin pocket mouse, 35), *Dipodomys ordii* (Ord's kangaroo rat, 88), *Reithrodontomys megalotis* (western harvest mouse, 24), *Peromyscus crinitus* (canyon mouse, 124), *P. maniculatus* (deer mouse, 128), *P. boylii* (brush mouse, 82), *P. truei* (pinyon mouse, 202), *Onychomys leucogaster* (northern grasshopper mouse, 49), *Neotoma mexicana* (Mexican woodrat, 45), *N. lepida* (desert woodrat, 34), and *N. cinerea* (bushy-tailed woodrat, 20). Rodents represented by too few specimens for analysis are *Spermophilus variegatus, Thomomys bottae, Castor canadensis, Neotoma albigula,* and *Erethizon dorsatum.*

METHODS

Field work on mammals of Canyonlands National Park began in 1972 and continued intermittently to 1978, the principal aim being to provide a range of data on natural history basic to a popular account of the fauna for the National Park Service. Given the broad aims of the research program of which this report is a part, data were gathered by various means. Whatever the source of a specimen, its habitat was described as the most prominent feature of plant cover within 1 m of the trap. When no plant was within this radius, a physical descriptor of the trapsite was noted. Analysis of data follows the method utilized by Armstrong (1977a). The similarity index used is $P_C/P_A + P_B$, where P_C is the sum of percentage occurrences in common, and P_A and P_B are percentage occurrences of the two descriptors under comparison. Use of relative (rather than absolute) frequency obviates some problems of differences in sample size. Cluster analysis was by the unweighted pair-group method of Sokal and Sneath (1963:309). Specimens collected in the course of this work are housed in the University of Colorado Museum.

Results and Discussion

Analysis of data was designed to answer three kinds of questions: (1) What associations of habitat descriptors have reality to the rodent fauna? (2) How broadly distributed are species across those "habitat types"? (3) What associations of rodents are found in given habitats? An answer to the first question should approximate a "mouse's-eye view" of the mosaic of habitats. The second question approaches the phenomenon of fidelity; how faithful are rodents to their habitat? Reasonable answers here could be quite helpful in making predictive statements about habitat management. Answers to the third question suggest groups of species that may be worthy of further study from the standpoint of niche structure or competitive interactions.

Figure 1 is a cluster diagram of 66 descriptors of habitat, based on indices of similarity of rodents associated with each descriptor. Overall mean similarity in the matrix upon which this diagram was based was 0.1783. Taking a mean similarity of 0.450 as an arbitrary cut-off point, there are nine major subclusters of descriptors in the diagram. Group I includes descriptors of slickrock and rimrock areas, including woodrat dens, most of which are beneath rocky rims. Group II includes many descriptors of open shrublands with poorly developed soils and silty blowouts or dune sand. Group III is quite complex; it includes descriptors of juniper woodland and broken rocky habitats as well as sagebrush stands. Saltbush and tamarisk also appear in this subcluster. Group IV centers around Gambel's oak and represents the relatively mesic brushlands common at bases of cliffs in the Cave Springs area of the Needles District. Group V describes phreatophytic cottonwood-willow woodland of major washes and canyon bottoms.

Group VI includes grasses and forbs typical of open flats. Groups VII, VIII, and IX are closely related neither to each other nor to other subclusters. All represent descriptors with small samples of rodents associated. The closest resemblance of subcluster VII is with group VI; both groups describe grasslands. Groups VIII and IX truly are miscellaneous, although group VIII does include several descriptors of relatively mesic cliffside habitats: *Cowania*, *Cercocarpus*, *Amelanchier*, hanging gardens.

These subclusters form a complex pattern, not as nearly comformable as one might hope with the sorts of habitat-types that have been described by previous workers (e.g., Hayward et al. 1958), or the units that the field naturalist extrapolates from the landscape. One reason for this is the great ecological amplitude of the most abundant species in the sample, *Peromyscus truei*, which is about equally abundant in sagebrush and in juniper stands.

Figure 2 indicates the cumulative percentage distribution of each rodent species with respect to the nine major subclusters identified in Figure 1. This allows a look at the degree of fidelity of species to certain environmental attributes. First, note that all species have an association with a single subcluster of descriptors of greater than 40 percent; indeed, all species except *R. megalotis*, *P. maniculatus*, and *P. crinitus* show primary associations of greater than 50 percent.

Five species, *A. leucurus*, *P. parvus*, *D. ordii*, *R. megalotis*, and *O. leucogaster*, show a primary association with subcluster II, representative of open shrublands on silty to sandy soils. Of these, *A. leucurus* also shows relatively strong secondary associations with groups I and III. Most often, antelope ground squirrels occur in the narrow ecotone between rocky situations and desert flats. *D. ordii* shows strong secondary association with group III. This is due to its frequent occurrence in stands of sagebrush. *Reithrodontomys megalotis* also has a strong secondary association with group III; harvest mice usually are found on floodplains which may have cover of greasewood (Group II), saltbush or tamarisk (group III) or phreatophytic woodland (Group V). *Onychomys leucogaster* is similar in local distribution to *D. ordii* (also see Fig. 3, beyond). The species most strongly associated with group II is *P. parvus*, a species found only in the Maze District. This species is known from a wide variety of habitats in Utah (Hayward and Killpack 1958), but does not seem to be particularly euryecious in the park, occurring mostly under sparse cover of blackbrush (but on a variety

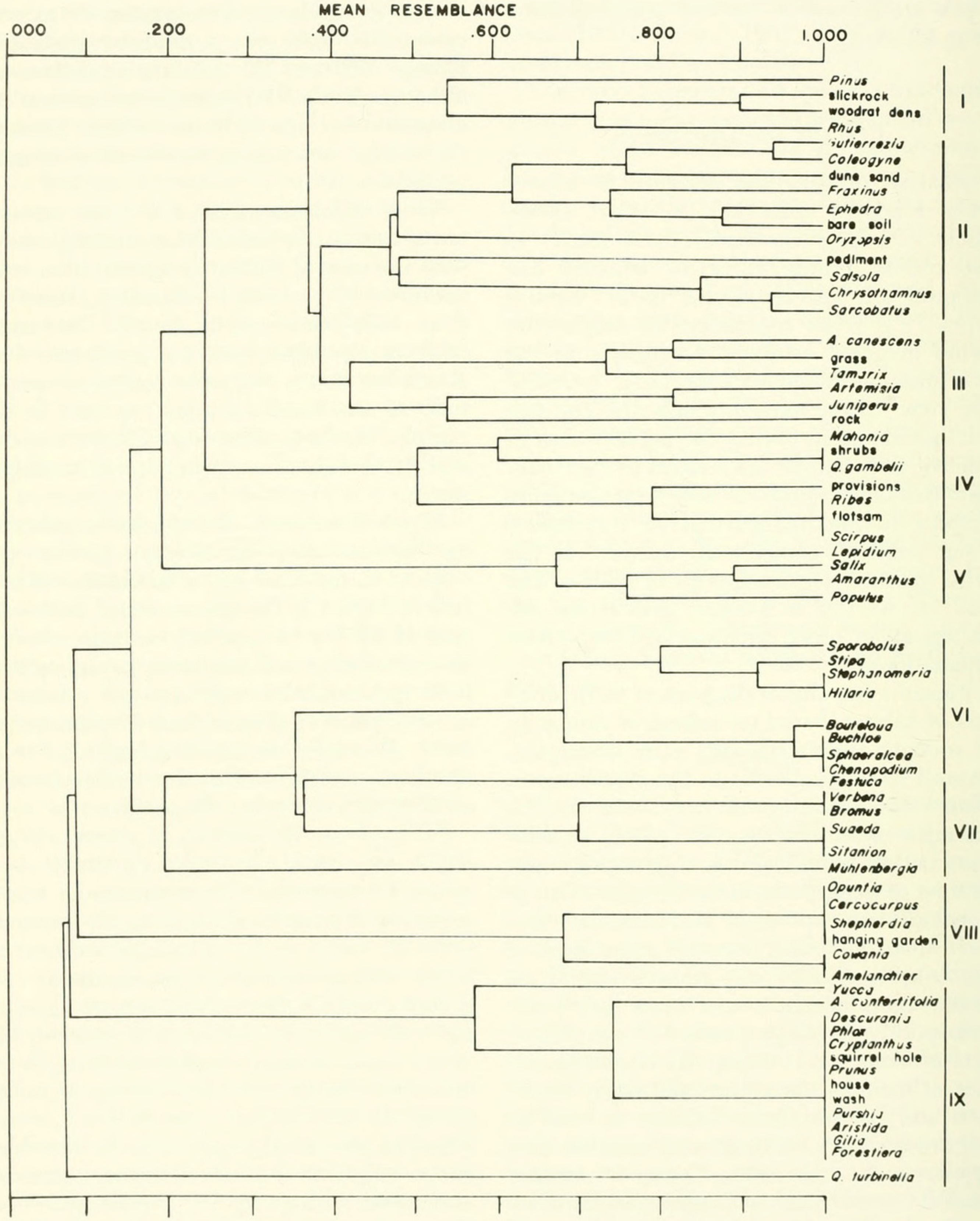

Fig. 1. Cluster diagram of 66 habitat descriptors, based on similarity of associated species of rodents. Abbreviations: A., *Atriplex*, Q., *Quercus* (for explanation of index, see text).

of substrates, from dune sand to cobbly desert pavement). Only *P. apache* shows a primary association with group VI, which describes grassland. The Apache pocket mouse is considerably more stenoecious than its larger congener, *P. parvus*, being closely restricted to bunchgrass flats on sandy to silty soils.

All four species of *Peromyscus* show their primary association with group III, rocky habitats. Three of the four show strongest secondary association with subcluster II, shrublands; *P. boylii* is the exception, with a strong secondary association with oak brush (Group IV). This analysis is sufficiently crude that it tends to make these species look more similar in ecological distribution than they may actually be. It is not at all uncommon to take three or even four species of *Peromyscus* in adjacent traps, particularly in broken country. Frequently the animals occur in "text-book" fashion: *P. crinitus* on slickrock, *P. maniculatus* in open shrubs, *P. boylii* beneath oakbrush, and *P. truei* with junipers. These relationships are partially obscured in the present analysis by data from localities at which fewer species co-occur or in which environments are too complex for the methods used. It is a seeming paradox that no species of *Neotoma* is related strongly with Group I, which includes the descriptor "woodrat dens." This reflects the fact that woodrats are more difficult to trap in the immediate vicinity of their dens than on their foraging range away from the den. Figure 2 suggests that *N. lepida* is the most euryecious of local species of *Neotoma*, although all species have strong primary associations with subcluster III.

Figure 3 is a cluster diagram of similarity indices of 14 species of rodents with respect to descriptors of habitat. Mean resemblance

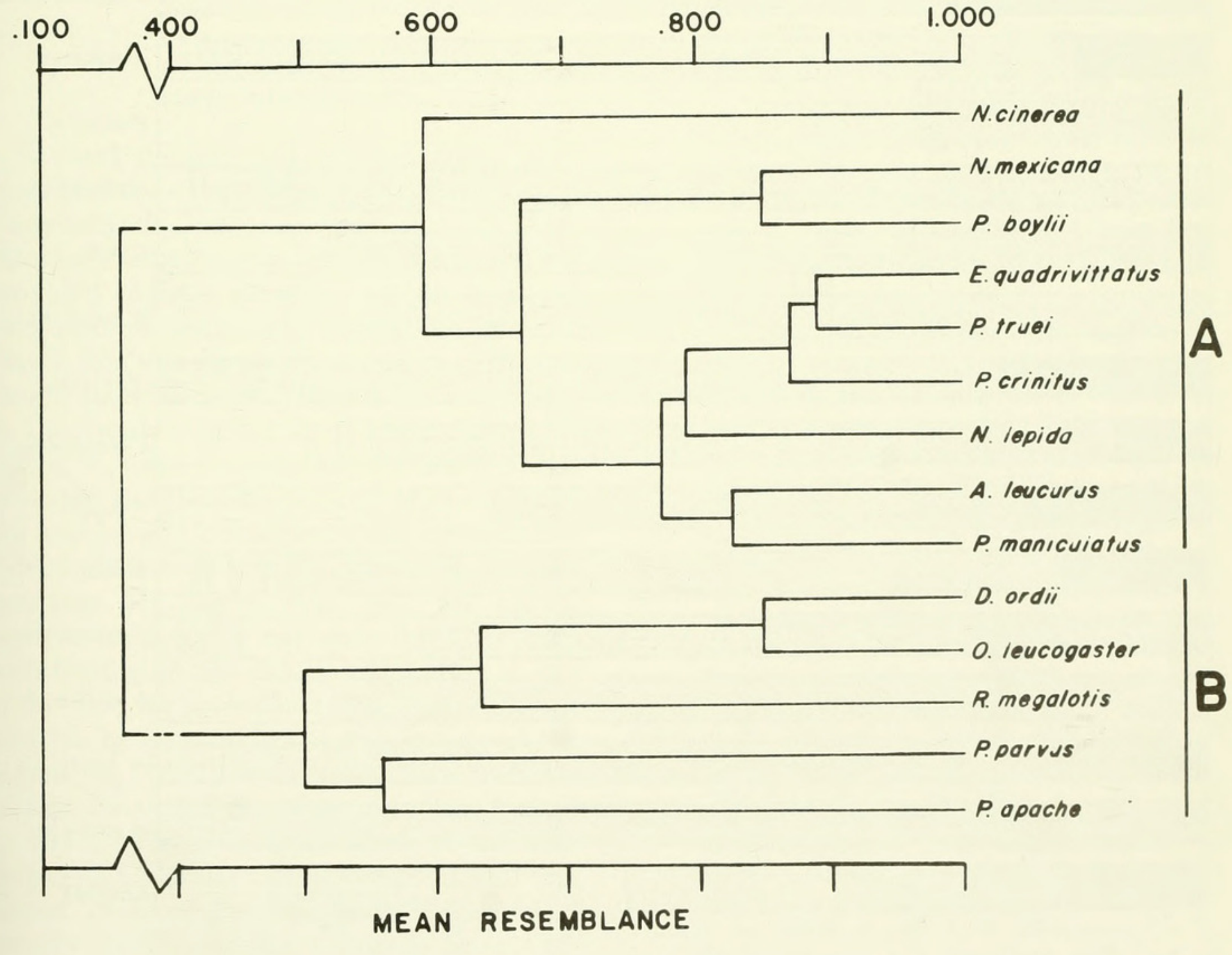

Fig. 2. Cumulative percentage distribution of 14 species of rodents with respect to nine subclusters of habitat descriptors.

in the similarity matrix on which the diagram was based is 0.5297. The diagram shows two different "habitat groups" of rodents, one (group A) occupying broken, rocky habitats, the other (group B) restricted to flats with relatively well-developed soils. The strongest associations are between *N. mexicana* and *P. boylii*, *E. quadrivittatus*, *P. truei*, and *P. crinitus*, *A. leucurus* and *P. maniculatus*, and *D. ordii* and *O. leucogaster*. *Neotoma mexicana* and *P. boylii* co-occur regularly in saxicoline oakbrush and *Mahonia* thickets in the Needles District. *Eutamias quadrivittatus*, *P. truei*, and *P. crinitus* occur in rough, broken terrain, *P. truei* most often in scattered juniper woodland, *P. crinitus* more frequently in more open situations. *Peromyscus maniculatus* and *A. leucurus*, which are related closely to the saxicolous group, are species that occupy the ecotone between the two broad habitats; they seem to be about equally likely to be captured among rocks or in open country. *Dipodomys ordii* and *O. leucogaster* occur in open shrub- or grassland on sandy soils. The pattern of dispersion across groups of descriptors in Figure 2 suggests that *P. truei* and *P. maniculatus* are the most euryecious of local rodents. They also are the species with the highest mean habitat similarity to all other species, 0.702 and 0.672, respectively.

Perhaps the most striking feature of the foregoing analyses is the strong microhabitat similarities among the saxicoline rodents.

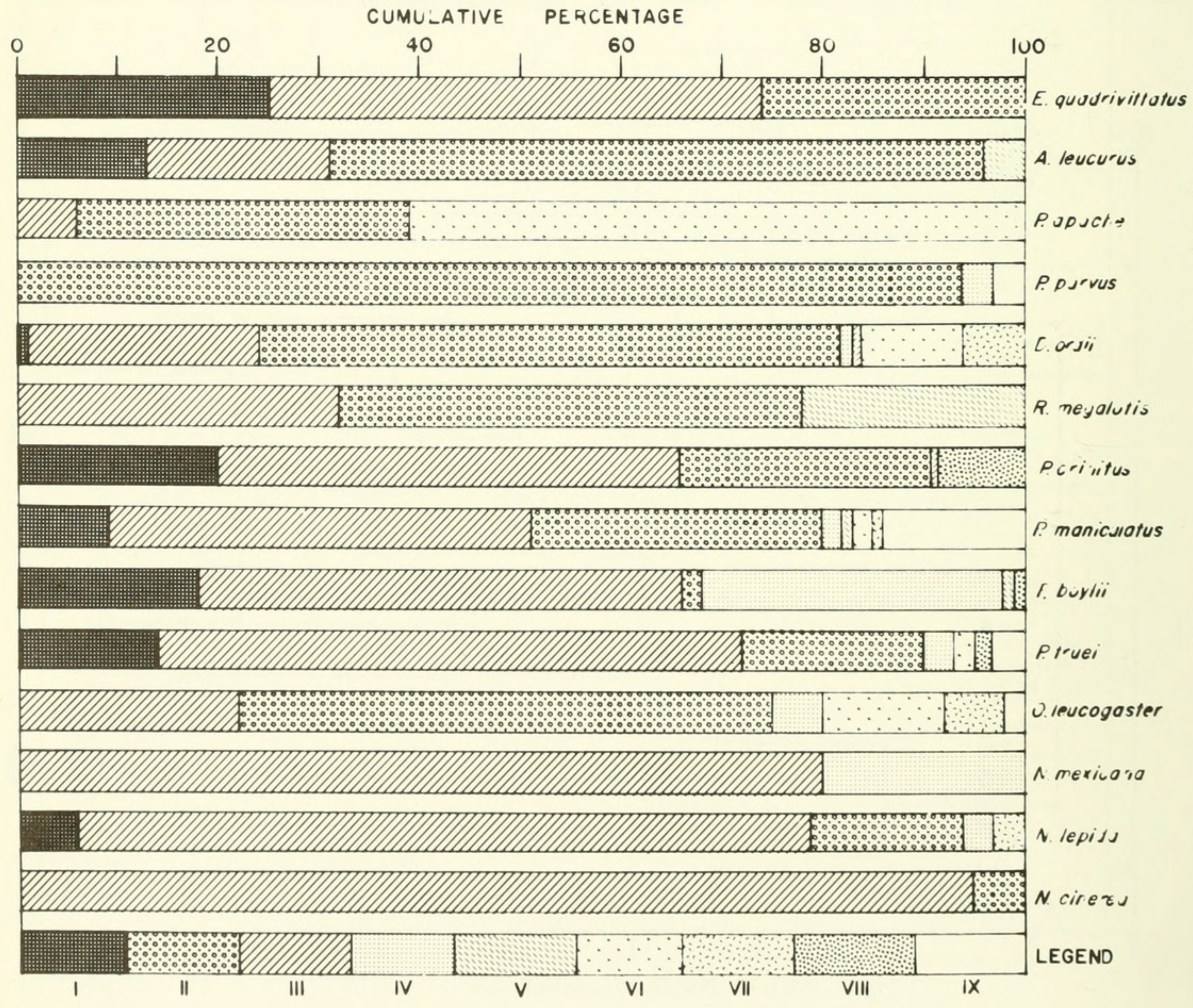

Fig. 3. Cluster analysis of indices of similarity of 14 species of rodents with respect to descriptors of habitat (for explanation of index, see text).

This is especially noteworthy among closely related species of cricetines, *Peromyscus* and *Neotoma*. Other criteria by which these species assort resources to allow coexistence are under study.

The only previous study of ecological distribution of rodents in the general vicinity of Canyonlands National Park was that by Hayward et al. (1958), who reported on Arches National Monument as one of several study areas. The suite of species considered was slightly different (*Thomomys bottae* was included, but neither *P. parvus* nor *N. mexicana* was) and the approach was geographically broader and more anecdotal. Still, correspondence with results of the present study is close. Hayward et al. (1958:32, Fig. 16) showed *E. quadrivittatus*, *A. leucurus*, and *P. truei* as considerably more stenoecious than they are in Canyonlands. They pointed out that *N. lepida* is more broadly distributed ecologically than is *N. cinerea*, a fact suggested by our data.

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