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DISTRIBUTIONAL PATTERNS OF MAMMALS IN UTAH

David M. Armstrong

ABSTRACT.—Based on a synthesis of recent work on distribution of mammals in Utah, the hierarchy of eco-geographic distributional units proposed by Durrant (1952) is reevaluated by numerical methods. Areographic faunal elements, distinguished on the basis of shapes of distributional ranges in North America, are identified. Relationships are shown between ecogeographic faunal units and areographic faunal elements, and their historical implications are discussed.

Biogeography seeks to describe patterns in the landscape and to understand their evolution. Utah provides a study area of considerable interest to the zoogeographer interested in faunal movements and effects of corridors, barriers, and isolation. The state is large (nearly 85,000 sq mi or 220,000 km²) and includes a wide range of ecological conditions, from hot desert to alpine tundra. Mean elevation is roughly 6100 ft (1860 m) and the range of relief is from about 2000 ft (610 m where Beaverdam Wash leaves the state in the southwest) to nearly 13,500 ft (4115 m at the summit of Kings Peak in the Uinta Mountains). A north-south “archipelago” of mountains and high plateaus divides Utah roughly in half. The eastern part is drained by the Colorado River and its tributaries, which have carved horizontal sedimentary formations into an intricate landscape of basins and canyons. West of the central highlands lies the Great Basin, a complex area of minor mountain ranges and internal drainage, dominated by the vast bed of Pleistocene Lake Bonneville.

The only previous zoogeographic analysis of mammals of Utah is that of Durrant (1952), who distinguished “faunal areas” in the state. These were ecogeographic units, roughly comparable to the biotic provinces of Dice (1943). Faunal areas were recognized subjectively, by the coincidence between mammalian distributions and physiographic units. Durrant (1952: 480) pointed out that faunal areas tended to be centers of differentiation for subspecies. Kelson (1951) discussed the influence of the Colorado River and its major tributaries on differentiation and distribution of rodents, refining Durrant’s work on faunal areas. Marshall (1940) studied ecological biogeography of mammals on islands in the Great Salt Lake. Lee (1960) investigated the montane mammals of several mountain ranges in southeastern Utah in an effort to understand faunal relationships among the highland faunas and the effects of Pleistocene climatic change on the patterns observed. Brown (1971, in press) studied montane mammals of Utah as an example of insular biogeography. Armstrong (1973) discussed zoogeographic relationships of mammals in Canyonlands National Park, which lies astride the confluence of the Colorado and Green rivers. This work in southeastern Utah suggested some intriguing local patterns of ecological and historical biogeography, but the existing literature was inadequate to place the area in a broader context. The present paper is meant as a partial answer to this need. Its purpose is to refine ecogeographic analyses of previous authors and to provide an areographic analysis of the mammals of Utah.

METHODS

Analyses of range limits in Utah were based on maps of 92 species. Seventeen species range essentially statewide in suitable

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habitat and hence were not mapped: *Myotis lucifugus*, *Myotis volans*, *Myotis evotis*, *Myotis leibii*, *Lasionycteris noctivagans*, *Epitesicus fuscus*, *Lasiorus cinereus*, *Plecotus townsendii*, *Peromyscus maniculatus*, *Erethizon dorsatum*, *Canis latrans*, *Bassariscus astutus*, *Mustela frenata*, *Taxidea taxus*, *Mephitis mephitis*, *Spilogale putorius*, and *Lynx rufus*. (These species are included in analyses of faunal areas.) Twelve species are known from too few localities to allow their ranges in Utah to be outlined with any confidence: *Sorex merriami*, *Sorex nanus*, *Notiosorex crawfordi*, *Myotis velifer*, *Euderma maculatum*, *Idionycteris phyllotis*, *Tadarida macrotis*, *Onodatra zibethicus*, *Procyon lotor*, *Martes pennanti*, *Lutra canadensis*, *Odocoileus virginianus*. Three species (*Canis lupus*, *Ursus arctos*, and *Bison bison*) have been extirpated in Utah over the last 125 years; limits of their former ranges are unknown. In addition, the natural ranges of *Antilocapra americana* and *Ovis canadensis* have been altered to an unknown extent since the advent of European civilization in Utah.


Maps of continental ranges were based on those in Hall and Kelson (1959) with limits in Utah and adjacent states refined on the basis of more recent publications (Cockrum 1960, Long 1965, Armstrong 1972a, Findley et al. 1975) and maps of ranges in Utah prepared for the present paper.

Nine species have been documented in Utah since Durrant’s (1952) checklist was published: *Sorex cinereus* (Durrant and Newey 1953), *Sorex nanus* (Durrant and Lee 1955), *Notiosorex crawfordi* (Wauer 1966), *Myotis thysanodes* (Krutsch and Heppenstall 1955), *Idionycteris phyllotis* (Black 1970), *Spermophilus richardsonii* (Hansen 1953), *Perognathus penicillatus* (Stock 1970), *Perognathus fasciatus* (Hayward and Killpack 1956), and *Odocoileus virginianus* (Miller and Kellogg 1955). Two other kinds, *Eutamias umbinus* (White 1953) and *Thomomys idahoensis* (Thaeler 1972) have been accorded specific status. This brings to 126 the total number of species of recent mammals known from Utah. Most of these species were included by Sparks (1974) in a recent popularized checklist of the mammals of the state. Nomenclature in this paper follows Jones et al. (1975) and Hennings and Hoffmann (in press).

Work on mammals of Canyonlands National Park, of which the present study is a by-product, has been supported by the Society of the Sigma Xi, the Penrose Fund of the American Philosophical Society, the Council on Research and Creative Work of the University of Colorado, and the Canyonlands Natural History Association. I thank Dr. G. L. Kirkland, Jr., for helpful comments on an earlier draft of this paper. The paper is dedicated to the memory of...
Stephen D. Durrant, late dean of mammalogists of the Intermountain West.

Results and Discussion

Distributional limits of mammalian species form complex but recurring patterns. These patterns may be described at various levels of resolution and by various means. In a local area, for example, one might be interested in the pattern of habitat requirements of a single species' population, in recurring communities of organisms, or in distribution along altitudinal or other gradients. On a broader scale, concern might be with distribution of species through ecological community types, with ecogeographic units (like the biotic provinces of Dice, 1943) that summarize regional ecological pattern, or with the shapes of species' ranges (areographic analysis). Emphasis here is on ecogeographic and areographic analysis, and the relationships between them. Ecogeographic description summarizes broad environmental patterns; areographic analysis may provide historical clues to the evolution of regional faunas (Armstrong 1972a).

Ecogeographic Considerations.—J. A. Allen (1892) pioneered ecogeographic studies of North American mammals, and Kendeigh (1954) reviewed subsequent work. Dice (1943) developed the concept of the Biotic Province to describe coherent units of regional landscape. Hagmeier and Stults (1964) and Hagmeier (1966) derived "mammal provinces" in North America by numerical methods, based on range maps in Hall and Kelson (1959). Hagmeier (1966) included parts of Utah in six mammal provinces, arranged in his hierarchy of ecogeographic units as follows:

I. Coniferan Subregion
   A. Mountain Superprovince
      1. Coloradan Province
   II. Sonoran Subregion
      A. Navajo Superprovince
         1. Navajonian Province
         2. Uintian Province
      B. Mapimi Superprovince
         1. Kaibabian Province
      C. Columbia Superprovince
         1. Columbian Province
         2. Artemisian Province

The fact that the six provinces in Utah were arranged in four different superprovinces underscores the patent faunal heterogeneity in Utah detailed below.

Durrant (1952) outlined "faunal subdivisions" of Utah as follows (also see Fig. 1):

I. Middle Rocky Mountain Faunal Area
   A. Wasatch Mountain Province
   B. Uinta Mountain Province
   C. High Plateau Province
      1. Northern High Plateau Subcenter
      2. Southern High Plateau Subcenter

II. Southern Rocky Mountain Faunal Area
   A. Coloradan Province
      1. La Sal Mountain Subcenter
      2. Abajo Mountain Subcenter

III. Colorado Plateau Faunal Area
   A. Canyonlands Province
      1. Kaiparowits Subcenter
      2. San Rafael Subcenter
      3. Grand Valley Subcenter
      4. San Juan Subcenter
      5. Painted Desert Subcenter
         a. Monument Valley District
         b. Navajo Mountain District
   B. Virgin River Valley Province
      1. Beaverdam Wash Subcenter
      2. St. George Subcenter

Fig. 1. Mammalian faunal subdivisions of Utah (after Durrant, 1952). For key to names of units, see text, p. 461.
IV. Columbia Plateau Faunal Area
V. Great Basin Faunal Area
VI. Northern Great Plains Faunal Area
   A. Bridger Basin Province
   B. Uinta Basin Province
      1. Duchesne Subcenter
      2. Uintah Subcenter

Durrant (1952) recognized these areas as distinctive because (1) certain species were restricted there and (2) because they acted as centers of differentiation for subspecies (p. 480). Boundaries of faunal areas were based on physiography. Although based mostly on distribution of mammals, Durrant’s faunal areas are analogues of L. R. Dice’s “biotic province,” an ecogeographic unit that “. . . covers a considerable and continuous geographic area and is characterized by the occurrence of one or more ecologic associations that differ, at least in proportional area covered, from the associations in adjacent provinces” (Dice 1943: 3). Dice’s units are based on distributional patterns in the biota as a whole, Durrant’s on patterns in distribution and differentiation of mammals. Boundaries between both faunal areas and biotic provinces are zones of relatively rapid biotic change, zones in which limits of species tend to be concentrated (Armstrong 1972a). This fact was used in order to evaluate boundaries between faunal areas proposed by Durrant (1952: 480). A number of quantitative methods have been used in recent years to determine boundaries of faunal units, but faunal change in Utah is so rapid that useful units can be identified by inspection. Limits of ranges of 92 mammalian species were superimposed (Fig. 2). The concurrence between zones of rapid faunal change and ecogeographic boundaries is apparent from comparison of Figures 1 and 2. Each of the boundaries indicated in Durrant’s map is marked by a concentration of limits in Figure 2. In particular, note the dense cluster of limits which outlines the central highlands and separates the Colorado Plateau on the east from the Great Basin in the west. In the northwestern corner of the state the Raft River Mountains are outlined clearly, as are the La Sal and Abajo Mountains in the southeast. A concentration of limits in the northeast suggests the distinctiveness of mammals of the Bridger Basin. In the west-central part of the state, the Deep Creek Mountains are highlighted by a concentration of limits. Were sufficient data available on mammals of this and other isolated mountain ranges of the Great Basin—comparable to those provided by Lee (1960) for the highlands of southeastern Utah—subdivisions of the Great Basin Faunal Area might be recognizable. It should be reemphasized that this evaluation of the boundaries of Durrant’s faunal units is based on species’ limits, whereas Durrant used two criteria, species’ occurrence and differentiation of subspecies; this difference in technique has little bearing on the faunal units recognized.

Fig. 2. Superimposed distributional limits in Utah of 92 mammalian species.
the 19 faunal units recognized by Durrant. Faunal resemblance was calculated by the formula $2C / N_1 + N_2$, where $C$ is the number of species held in common between two units and $N_1$ and $N_2$ are total numbers of species in the two units. Resemblance values (which ranged from 0.438 to 0.964) were clustered by the unweighted pair-group method (Sokal and Sneath 1963: 309). Figure 3 is the result.

In large measure, the dendrogram substantiates the hierarchy of units suggested by Durrant (1952: 481—see p. 00 above), despite wide differences in technique and recent additions to knowledge of Utah mammals. Units of the Colorado Plateau form a tight cluster, with faunas of the Canyons and the Virgin River Valley separating into distinct subclusters, and units within the Canyons forming further subclusters east and west of the Colorado River. In the central mountainous core, two subclusters are evident. The Wasatch and Uinta mountains are more closely related than all but one other pair of faunal units, and the Northern High Plateaus and Southern High Plateaus form a distinct, albeit weaker, subcluster. The isolated La Sal and Abajo mountains form a distinct unit, allied (on average) more closely with the Colorado Plateau than with the central highlands of Utah. Their nearest contact with a well-developed highland fauna is via the high plateaus of western Colorado, not the Middle Rocky Mountains in Utah. The Duchesne and Uintah units of the Uinta Basin form a tight cluster and are distinct from faunal units of the Colorado Plateau south of the Tavaputs Plateaus, but they are more closely related to the Bridger Plateau. The Great Basin and the Columbia Plateau (Raft River Mountains) tend to be faunally distinct from each other and from the rest of the state.

Comparison of Durrant's faunal units with the diagram in Figure 3 suggests that levels of the hierarchy (faunal area, province, subcenter, district) are not used quite consistently, at least at the specific level of analysis employed here. In particular, faunas of the Wasatch and Uinta Mountains are more closely related than most other pairs of units, yet they are distinguished as provinces. Recent studies (e.g., Durrant and Dean 1959) suggest that the Navajo Mountain and Monument Valley units are more distinctive than Durrant (1952) supposed. Indeed, Monument Valley seems to be more closely related to the San Juan area (which lies north of the San Juan River) than to the Navajo Mountain unit. Based on relationships in the dendrogram (Fig. 3), I suggest the following rough guidelines for levels of the hierarchy of ecogeographic units: average resemblance between faunal areas, less than 0.800; average resemblance between provinces within faunal areas, 0.800 to about 0.900; average resemblance between subcenters within provinces, greater than about 0.900. Using these criteria, the following slightly revised list of faunal subdivisions in Utah is suggested:

I. Central Highlands Faunal Area
   A. Middle Rocky Mountains Province
      1. Wasatch Mountains Subcenter
      2. Uinta Mountains Subcenter
   B. High Plateaus Province
      1. Northern High Plateaus Subcenter
      2. Southern High Plateaus Subcenter

![Fig. 3. Mean resemblance among mammalian faunal subdivisions of Utah. (For explanation of index, see text.)](image-url)
Changes in names of two faunal areas (Middle Rocky Mountains to Central High-
lands, Northern Great Plains to Wyoming Basin) follow Durrant’s lead in naming faun-
al units to correspond with physiographic units (here following Fenneman, 1931).

Areographic Patterns.—Having considered distributional patterns of mammals in Utah
and arrived at a set of ecogeographic faunal areas, let us turn to broader, continental
patterns of distribution. The pattern of spe-
cies’ ranges, irrespective of extant ecologic
pattern, may suggest historic affinities of
the fauna. Udvardy (1969:282) noted that
the constituent species of a faunal list “...fall into groups with respect to the shapes
of their geographic areas.” These groups of
species may be called “faunal elements.”
Polunin (1960:212) suggested sorting out elements in a local flora as follows: (1) re-
move exotic and occasional species; (2) re-
move widespread species; (3) remove en-
demic species; and (4) sort out the remain-
der according to the shapes of their ranges. Such a procedure was used here, re-
sulting in nine distinctive, areographic faun-
al elements and a group of widespread spe-
cies.

The implications of these areographic faunal elements are complex. The area oc-
cupied summarizes the interaction of spe-
cies’ limits of tolerance with the mosaic of
regional landscapes; both are subject to
change over time. Hultén (1937) argued
strongly that areographic analysis leads to
historical insights in plant geography, pro-
mulgating the concept of “progressive equi-
formal areas,” the common centers of which
point to areas of origin (or refugia from en-
vironmental perturbations). Broad areo-
graphic studies of animals (e.g., Dunn 1931, for
North American amphibians and reptiles,
Mayr 1946, for birds, and Simpson 1947,
and Burt 1958, for mammals) have used
ranges—usually of higher taxonomic cate-
gories—as a basis for historical conclusions.
A few studies have sought to use areogra-
phic patterns of species as clues to local
faunal history. For example, Miller (1951:582) recognized four avifaunal ele-
ments in California, “... on the basis of
strong or repeated associations of species
which have similar centers of distribution
and probably also similar areas of origin.”
Armstrong (1972a:333) discussed areogra-
phic patterns of Coloradan mammals, draw-
ing tentative historical conclusions. Clearly,
faunal elements may have a degree of his-
toric integrity, reflecting centers of origin
and dispersal, although recent ecologic his-
tory may have distorted older patterns.
Despite problems in interpretation, the at-
tempt to sort out areographic faunal ele-
ments is important. In the absence of a
fossil record, such an exercise may provide
the only clues to the development of the
extant fauna.

Seventeen species (14 percent of the Utah-
han mammalian fauna) have ranges center-
ing on the Middle Rocky Mountains (see Fig.
4A) and are called Cordilleran species. These are:

Sorex vagrans—Vagrant Shrew
Sorex monticolus—Dusky Shrew
Sorex usius—Dwarf Shrew
Ochotona princeps—Pika
Eutamias amoena—Yellow-pine Chipmunk
Eutamias umbrinus— Uinta Chipmunk
Marmota flaccata—Yellow-bellied Marmot
Spermophilus armatus— Uinta Ground Squirrel
Spermophilus lateralis—Golden-mantled Ground Squirrel
Thomomys talpoides—Northern Pocket Gopher
Neotoma cinerea—Bushy-tailed Woodrat
Fig. 4 A-D. Superimposed continental distributions of species of four areographic faunal elements.
Ranges of most of these species extend from the Canadian Rockies southward, often in an increasingly insular pattern, to Arizona and New Mexico. They are restricted at their southern limits to mountainous country. Habitat of many of the species is mountain meadows, stream sides, and forest-edge situations. Two of the species (Sorex obscurus and Spermophilus lateralis) have isolated montane populations in Mexico. However, four other species (Sorex vagrans, Eutamias amoenus, Spermophilus armatus, and Arvicola richardsonii) do not extend farther south than the Middle Rocky Mountains, and they do not reach Colorado. The American bison of Utah were members of the subspecies Bison bison athabascae (see Hall and Kelson 1959:1025) and hence are included as Cordilleran rather than widespread species.

The following 15 species of Utahan mammals (12 percent of the fauna) share a distributional pattern that may be called Boreo-Cordilleran:

- Sorex cinereus—Masked Shrew
- Sorex palustris—Water Shrew
- Lepus americanus—Snowshoe Hare
- Eutamias minimus—Least Chipmunk
- Tamiasciurus hudsonius—Red Squirrel, or Chickaree
- Glaucomys sabrinus—Northern Flying Squirrel
- Clethrionomys gapperi—Southern Red-backed Vole
- Phenacomys intermedius—Heather Vole
- Microtus pennsylvanicus—Meadow Vole
- Martes americana—Marten
- Martes pennanti—Fisher
- Mustela erminea—Ermine
- Gulo gulo—Wolverine
- Felis lynx—Lynx
- Alces alces—Moose

These species are distributed in mountainous parts of western North America and also eastward across the continent, mostly in forested areas (Fig. 4B). In an areographic sense, these species contrast markedly with those of the Cordilleran Faunal Element. Unlike Cordilleran species, many Boreo-Cordilleran mammals range throughout forested parts of Alaska and several species (including Sorex cinereus, Mustela erminea, Gulo gulo, Felis lynx, Alces alces) occur on both sides of Bering Strait. In addition, there is a tendency for Boreo-Cordilleran mammals to be associated with heavy forest. There is some suggestion that Eutamias minimus, perhaps the most euryecious mammal in this faunal element, may include more than a single species (Sutton and Nadler, 1969).

Thirty species (24 percent of the fauna) comprise the Chihuahuan Faunal Element:

- Notiosorex crawfordi—Desert Shrew
- Myotis californicus—California Myotis
- Myotis yumanensis—Yuma Myotis
- Myotis velifer—Cave Myotis
- Myotis eremicus—Long-eared Myotis
- Myotis thysanodes—Fringed Myotis
- Pipistrellus hesperus—Western Pipistrelle
- Plecotus townsendii—Townsend’s Big-eared Bat
- Idionycteris phyllotis—Allen’s Big-eared Bat
- Antrozous pallidus—Pallid Bat
- Tadarida brasiliensis—Brazilian Free-tailed Bat
- Tadarida macrotis—Big Free-tailed Bat
- Sylviulus audubonii—Desert Cottontail
- Lepus californicus—Black-tailed Jackrabbit
- Eutamias dorsalis—Cliff Chipmunk
- Spermophilus sciureus—Spotted Ground Squirrel
- Spermophilus variegatus—Rock Squirrel
- Perognathus flavus—Silky Pocket Mouse
- Dipodomys ordii—Ord’s Kangaroo Rat
- Reithrodontomys megalotis—Western Harvest Mouse
- Peromyscus boylii—Brush Mouse
- Peromyscus truiei—Pinyon Mouse
- Peromyscus difficilis—Rock Mouse
- Neotoma albicella—White-throated Woodrat
- Neotoma mexicana—Mexican Woodrat
- Microtus mexicanus—Mexican Vole
- Vulpes macrotis—Kit Fox
- Urocyon cinerargentus—Gray Fox
- Bassariscus astutus—Ringtail
- Spilogale gracilis—Western Spotted Skunk

These species mostly occur in arid to semiarid grasslands or in rocky, broken brushlands or woodlands. They share a center of coincidence in the basin and range region of Chihuahua and Coahuila, Mexico, and Trans-Pecos Texas (Fig. 4C). Of this faunal element, four species (Plecotus townsendii, Tadarida brasiliensis, Reithrodontomys megalotis, and Urocyon cinerargentus) range east of the Mississippi River. However, their identification in the southwest with this faunal element is clear. The two species of free-tailed bats, Tadarida brasiliensis and T. macrotis, occur widely in South America, as does Urocyon cine-
reorganizes. These might have been segregated as a Neotropical Faunal Element, inasmuch as only four of the remaining Chihuahuan species (Myotis velifer, Peromyscus boylii, Neotoma mexicana, Spilogale gracilis) range farther south than the Isthmus of Tehuantepec. Note that 12 of the Chihuahuan species (40 percent) are bats. Despite their capacity for flight these species are of restricted distribution, present patterns perhaps reflecting the historical integrity of this faunal element.

A Nevadan Faunal Element (Fig. 4D), comprised of the following 14 species, with a center of coincidence in Nevada, contributes 11 percent of the Utahan fauna:

*Sorex merriami*—Merriam's Shrew  
*Myotis volans*—Long-legged Myotis  
*Euderma maculatum*—Spotted Bat  
*Sylvilagus idahoensis*—Pygmy Rabbit  
*Sylvilagus nuttallii*—Nuttall’s Cottontail  
*Lepus townsendii*—White-tailed Jackrabbit  
*Spermophilus townsendii*—Townsend’s Ground Squirrel  
*Spermophilus beldingi*—Belding’s Ground Squirrel  
*Perognathus parvus*—Great Basin Pocket Mouse  
*Microdipodops megacephalus*—Dark Kangaroo Mouse  
*Dipodomys microps*—Chisel-toothed Kangaroo Rat  
*Onychomys leucogaster*—Northern Grasshopper Mouse  
*Lagurus curtatus*—Sagebrush Vole  
*Antilocapra americana*—Pronghorn

This is a complex distributional element. At a finer level of analysis it might be subdivided profitably. Some species are restricted to arid interior basins of the western United States (e.g., *Spermophilus townsendii, Microdipodops megacephalus, Dipodomys microps*), whereas others inhabit sagebrush steppe (e.g., *Sorex merriami, Sylvilagus idahoensis, Sylvilagus nuttallii, Lagurus curtatus*). *Lepus townsendii, Onychomys leucogaster*, and *Antilocapra americana* have an additional center of occurrence on the central Great Plains and might be considered a part of a Campestrian Faunal Element (Armstrong 1972a: 356), although this designation would not be particularly meaningful with respect to these species as they occur in Utah, inasmuch as communication with the Great Plains is indirect.

Twelve species (10 percent of the fauna) have continental distributions that might be called “Yuman,” for their center of coincidence is in the Mojave Desert and along the Lower Colorado River in California, Arizona, Sonora, and Baja California (Fig. 4F). These species are:

*Ammospermophilus leucurus*—White-tailed Antelope Squirrel  
*Thomomys bottae*—Botta’s Pocket Gopher  
*Perognathus longimembris*—Little Pocket Mouse  
*Perognathus formosus*—Long-tailed Pocket Mouse  
*Perognathus penicillatus*—Desert Pocket Mouse  
*Perognathus intermedius*—Rock Pocket Mouse  
*Dipodomys deserti*—Desert Kangaroo Rat  
*Dipodomys merriami*—Merriam’s Kangaroo Rat  
*Peromyscus eremicus*—Cactus Mouse  
*Peromyscus crinitus*—Canyon Mouse  
*Onychomys torridus*—Southern Grasshopper Mouse  
*Neotoma lepida*—Desert Woodrat

In the vicinity of the center of coincidence, *Ammospermophilus leucurus* and *Perognathus formosus* only occur west of the Colorado River, and *Perognathus intermedius* is known only east of the river. Yuman mammals generally do not range southward in Mexico as far as Chihuahuan species, with only five reaching Jalisco, Guanajuato, and San Luis Potosi. On the north, most species reach no farther than southeastern Oregon and southwestern Idaho, and several reach limits in Nevada and Utah. Note that half the species in this faunal element are heteromyid rodents, whereas the predominant rodents in the Chihuahuan element are cricetids. This fact underscores the historical integrity of these faunal elements.

Five species, comprising 4 percent of the Utahan mammalian fauna, constitute an Arizonan Faunal Element (Fig. 4F). These are:

*Eutamias quadricittatus*—Colorado Chipmunk  
*Cynomys gunnisoni*—Gunnison’s Prairie Dog  
*Sciurus aberti*—Abert’s Squirrel  
*Perognathus apache*—Apache Pocket Mouse  
*Neotoma stephensi*—Stephens’ Woodrat

These are species of the Four Corners area (although *Neotoma stephensi* is as yet unknown from Colorado, Armstrong 1972a: 312). In Utah, Arizonan species generally
are restricted to the southeastern part of the state; all but *E. quadricivittatus* occur only east of the Colorado and Green rivers.

Three mammals of the Great Plains (*Spermophilus tridecemlineatus*, *Perognathus fasciatus*, *Mustela nigripes*) have limited

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Fig. 4 E-H. Superimposed continental distributions of species of four areographic faunal elements.
ranges in Utah and constitute a Camp-strian Faunal Element (Fig. 4G). All occur in grasslands of the eastern part of the state. Another three species (Cynomys leucurus, Thomomys idahoensis, and Spermophilus richardsonii) share a center of coincidence in the Bridger Basin of southwestern Wyoming (Fig. 4H) and are herein called the Bridgeran Faunal Element. Armstrong (1972a: 354) placed S. richardsonii as a member of the Cordilleran Faunal Element, but its range is somewhat discordant with that group of species. Recent studies (Nadler et al. 1971) suggest that the population in Wyoming, Utah, and Colorado, known as S. r. elegans, is in fact specifically distinct from S. richardsonii. The range of elegans fits closely with the Bridgeran Faunal Element.

A single species of the mammalian fauna of Utah is obviously endemic there, Cynomys parvidens, the Utah Prairie Dog. According to Pizzimenti and Collier (1973), C. parvidens is more closely related to C. leucurus (a species of the Bridgeran Faunal Element) than to other prairie dogs; Collier and Spillett (1975) concluded that the range of the C. parvidens once covered large portions of the Great Basin.

Of mammals of Utah, the following 26 kinds (21 percent of the state’s fauna) are sufficiently widespread (Fig. 4I) that they cannot be identified with any one areographic faunal element:

- Myotis lucifugus—Little Brown Bat
- Myotis leibii—Small-footed Bat
- Lasiomycteris noctivagans—Silver-haired Bat
- Eptesicus fuscus—Big Brown Bat
- Lasiusurus cinereus—Hoary Bat
- Lasiusurus borealis—Red Bat
- Castor canadensis—Beaver
- Peromyscus maniculatus—Deer Mouse
- Ondatra zibethicus—Muskrat
- Erethizon dorsatum—Porcupine
- Canis latrans—Coyote
- Canis lupus—Gray Wolf
- Vulpes vulpes—Red Fox
- Ursus americanus—Black Bear
- Ursus arctos—Grizzly Bear
- Procyon lotor—Raccoon
- Mustela frenata—Long-tailed Weasel
- Mustela vison—Mink
- Mephitis mephitis—Striped Skunk
- Taxidea taxus—Badger

Many of these species are rather large in size and many have broad habitat tolerances. It is perhaps noteworthy that half of these eurychores are members of a single order, Carnivora; carnivores are at least one step removed from direct dependence on the vegetation for food and generally are less narrowly restricted to particular habitats than are herbivores. Thirteen of the 23 carnivores known to occur in Utah are widespread species. In addition, three of four Utah cervids are widespread on a continental scale. Three highly specialized aquatic species, the beaver, the muskrat, and the mink, appear on the list. This is hardly surprising, since aquatic habitats provide corridors of uniform habitat for dispersal through otherwise highly distinctive regions. Fewer than one-third of Utah’s bats are widespread species; nearly 60 percent

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**Fig. 4 I.** Superimposed continental distributions of 26 widespread species.
are Chihuahuan kinds. Were distribution of bats better known, they might provide quite useful data for zoogeographers, contrary to the conventional wisdom.

The least broadly distributed species on the above list are the small-footed myotis (Myotis leibii) and the grizzly bear (Ursus arctos). The range of the former species is similar to that of those labelled “Nevadan,” but it extends also across the Great Plains to the Ohio Valley and the East Coast. The former range of the grizzly bear extended eastward across the Northern Great Plains and Central Great Plains; otherwise the range is that of a Cordilleran species.

Figure 5 indicates cumulative percentage composition of the mammalian faunas of 19 ecogeographic faunal units by species of the 10 faunal elements identified by areographic analysis. Also indicated, for comparison, is the composition of the fauna of Utah as a whole, based on a total of 126 species. Only 109 species were tabulated in the faunal units, because of inadequate distributional data on 17 species (see Methods, above). Those species too poorly known to map represent five faunal elements: Cordilleran (three species), Boreo-cordilleran (one), Chihuahuan (four), Nevadan (three), and widespread (six). Thus, poorly known species are sufficiently well distributed across the major faunal elements that they do not bias the remarks that follow.

Note first in Figure 5 the consistent importance of widespread species at about 35 percent (28 to 38) through each of the faunal elements. It is the differential occurrence of species of well-defined areographic elements that makes the faunal units distinctive. Cordilleran species are most important in faunal units of the central mountain core of the state, somewhat less important in the La Sal Mountains and the Raft River Mountains of the Columbia Plateau. In other faunal units, their contribution falls to 10 percent or less. Boreo-cordilleran species are even more narrowly restricted to mountainous areas, although one species, Eutamias minimus, is sufficiently euryecious that it occurs in most faunal areas. “Boreal” mammals of Utah discussed by Brown (in press) mostly are Cordilleran and Boreo-cordilleran species as defined here.

The Chihuahuan Faunal Element is the largest distinctive areographic element in Utah, constituting about one quarter of the fauna. Given this prominence statewide, the element is under-represented in the central highlands faunal areas and on the Columbia Plateau. Over most of the Colorado Plateau south of the Tavaputs Plateaus, the Chihuahuan element contributes some 40 percent of the fauna. North of the Tavaputs Plateaus, in the southeastern mountains, and in the Great Basin, the importance of Chihuahuan species is diminished. Yuman mammals are most important on the southern Colorado Plateau, especially in the Virgin River Valley. They are absent from the Middle Rocky Mountain Province and from the Northern High Plateaus. Nevadan species, on the other hand, are most important in the Great Basin, with modest representation over most of the rest of the state (except on the Colorado Plateau, where they tend to be under-represented). The minor faunal elements tend to show rather narrow distribution across the state. Campestrian species occur in eastern Utah. Arizonan species occur mostly in the Canyonlands Province of the Colorado Plateau and in the Uinta Basin. Bridgerian species occur only in northeastern and east-central parts of the state.

Having considered the composition of the faunas of the ecogeographic units, it might be useful (if only as a check on the integrity of the faunal elements) to look briefly at the extent to which members of the 10 faunal elements occupy the various units (Table 1). Most of the units include 60 to 70 percent of the widespread species, with highest percentages occurring in mountainous areas. As might be expected, the units of the Central Highlands Faunal Area accommodate most members of the Cordilleran and Boreo-cordilleran elements, with occurrence attenuating southward. The Colorado Plateau includes the ranges of the highest proportion of Chihuahuan species. Yuman species, by contrast, occur strongly only in the Virgin River Valley, and Neva-
dan mammals are well represented only in the Great Basin. The minor faunal elements also are strongly represented only in local areas—Campestrian species in the northeast, Arizonan species east of the Colorado River (and south of its confluence with the Green River), the Bridgeran species in the Bridger Basin.

Fig. 5. Cumulative percentage composition of mammalian faunas of ecogeographic faunal areas by members of ten areographic faunal elements.
Historical Implications.—One of the major goals of zoogeographic analysis is to gain some insight into the evolution of local or regional faunas. Indeed, in the absence of an adequate fossil record, extant patterns of distribution and differentiation provide the only historical data that we have to work with. Durrant (1952) looked at patterns of subspecific differentiation in fossorial rodents as a clue to the Pleistocene history of the Bonneville Basin. Lee (1960) studied the distribution and differentiation of montane mammals of southeastern Utah and drew inferences about past faunal movements. Findley (1969) presented a strong argument on historical implications of such patterns in New Mexico and adjacent areas. Brown (1971, in press) analyzed distribution on several mountain ranges in Utah of mammals typical of woodland (and higher elevation) biotic communities, arguing convincingly that extant distributional patterns stem from local extinction of populations that reached the montane islands during the late Pleistocene. Armstrong (1972a) relied on evidence at both the specific and subspecific level to reach tentative historical conclusions about Coloradoan mammals, and hypothesized access to the state by several faunal components under a diversity of environmental conditions which prevailed at various times in the past.

Extant zoogeographic patterns in western North America are a post-Pleistocene development. The Pleistocene Epoch was marked by pronounced climatic fluctuations. Warm, dry periods were interrupted by cool, moist glacio-pluvial intervals. Evidences of zoogeographic patterns in the earlier Pleistocene were obliterated by the last major glacial interval, the subsequent Hypsithermal Interval (Deevey and Flint 1957), and the development of the existing climatic regime (Armstrong 1972a). Extant patterns may provide clues to these most recent events. In the absence of a coherent or extensive fossil record, distributional patterns of recent species are the only clues available to

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us. This is the case in Utah. Conspicuously lacking from the abundant literature on Pleistocene environments of Utah is any record of a mammalian local fauna. Even fragmentary fossils are few. When a nearly adequate fossil local fauna does become available (the Hogup Cave deposits from Box Elder County described by Durrant, 1970, and dated at 8500 years B.P.) the mammals that are present are those that would be expected in the vicinity of the cave today.

For purposes of discussion of Pleistocene conditions, Utah is conveniently divisible into three broad sections: the Great Basin, the central mountainous core, and the Colorado Plateau. The Great Basin records evidence of a series of pluvial periods separated by intervals of dessication (for details, see Morrison 1965). Lake levels fluctuated in synchrony with alpine glaciers in the higher mountains of central and northern Utah. This glaciation strongly influenced the modern landscape, lowering regional snowlines some 4000 ft, and producing summer temperatures perhaps 16 F cooler than today (Richmond 1965). On the Colorado Plateau, glacial intervals were marked by erosion, and warmer, drier periods produced sedimentary deposition (Kottlowski, Cooley, and Ruhe 1965). These events and conditions set an environmental baseline against which present distributional patterns of mammals have developed. During the last glacio-pluvial stage, conditions probably prevailed that were beyond the tolerance of many species in the fauna today. Previous patterns of distribution would have been obscured. With a depression of zonal biotic communities, forested situations that are highly disjunct today would have been more nearly continuous, and semidesert and desert community-types would have seen concomitant restriction and fragmentation.

The present-day fauna of the highlands of Utah provides better evidence of past environmental change than do faunas of the Colorado Plateau and the Great Basin. Today, a number of the state’s mountain ranges and high plateaus appear as “islands” in a “sea” of nonmontane habitats. Communication among them by nonvolant mammals restricted to forested habitats is probably impossible. Nonetheless, some of the highlands have reasonably complete highland faunas (Brown 1971, in press). Altitudinal depression of zonal biotic communities by 2000 to 4000 ft would unite many of these areas with corridors of suitable habitat. The La Sal Mountains would have been connected with the Uncompahgre Plateau and the San Juan Mountains (and nearby ranges), and the Abajo Mountains probably would have been joined with the La Sals by more-or-less continuous forest or woodland corridors. Navajo Mountain, south of the San Juan River, and the Henry Mountains probably have been isolated (or nearly so) throughout Pleistocene times (although Lee, 1960, noted some affinity of mammals of the Henrys with those of the Aquarius Plateau). The distribution of forest-dwelling mammals along the mountains of central Utah suggests that Pleistocene conditions there provided a continuous corridor for movement. Isolated ranges of the Great Basin generally support depauperate highland faunas (Brown 1971, in press), although the definitive study of mammals of the minor ranges of southwestern Utah (House Range, Wah Wah Mountains, etc.) remains to be made.

The fact that faunas of the more isolated ranges on either side of the central highlands corridor have variously depauperate faunas probably reflects local extinction rather than selective or chance dispersal across barriers. The fact that such extinction has been more pronounced on the smaller uplifts may reflect the greater susceptibility of small populations to extinction (Brown 1971, in press). Such small populations would have been constricted still further by the climatic changes of the Hypsithermal Interval (warmer and effectively or absolutely drier than at present) which would have resulted in upward movement of zonal biotic communities with consequent restriction of the higher zones.

At lower elevations in Utah, extant distributional patterns strongly reflect present-day physiography, suggesting the efficacy of
existing boundaries throughout the period of development of the fauna. Ranges of many Chihuahuan and Yuman species, for example, are limited on the Colorado Plateau by the major rivers and their canyons, despite the fact that seemingly suitable habitat often exists on the other side of the barrier. On a north-south axis, the Wasatch Mountains and the high plateaus today form an effective barrier to communication between the Great Basin and the Colorado Plateau. This barrier seems to have been generally effective throughout the period of evolution of the fauna. If the Hypsithermal Interval had significantly reduced its effectiveness, one would expect to find several Nevadan species on the Colorado Plateau. However, only the most euryecous species are found on both sides of the mountains. The Uinta Mountains also seem to have persisted as an effective barrier as faunal patterns have evolved. Bridgeran species are not found on the Colorado Plateau to any significant extent, and most Chihuahuan species are limited south of the Uintas.

A barrier to one faunal element or species may well be a corridor for the movement of another. The central mountainous corridor has been discussed in this context. The river systems of the Colorado Plateau seem generally to have been ineffective as corridors. Often they are entrenched deeply; riparian habitats tend to be fragmented or nonexistent. Species adapted to the broken habitats of the canyons seem to have found the river systems more effective corridors than have species of desert grasslands (such as several Yuman species).

Kelson (1951) suggested that the Colorado-Green system becomes an increasingly less effective zoogeographic barrier northward. East of the Colorado River and north of the San Juan, there is no strong barrier to northward faunal movement until one reaches the Book Cliffs. West of the Colorado, the Kaiparowits Plateau and the canyon of the Escalante River may constitute major barriers, but the mammals of this area remain poorly known except in the immediate vicinity of Lake Powell.

In summary, scrutiny of broad patterns of distribution of mammalian species provides few clues to the conditions of the past that influenced the composition of the extant fauna. Ranges of montane mammals suggest the occurrence of more continuous highland biotic communities in late Pleistocene time, and the depauperate faunas of isolated ranges may reflect the efficacy of the Hypsithermal Interval in constricting highland communities more severely than at present. In the lowlands, distributions correspond to extant barriers. Truly relict populations of lowland, xeric-adapted species are lacking. The overall conclusion must be that barriers to distribution in the present also were barriers to distribution in the past.

**Summary**

Distributional patterns of the 126 mammalian species native to Utah were analyzed and discussed. Ecogeographic faunal areas, proposed by Durrant (1952), were reevaluated. These correspond strongly with physiographic subdivisions of Utah. Areographic analysis indicated that several faunal elements contribute to the total mammalian assemblage within the political confines of Utah. These faunal elements contribute differentially to the several ecogeographic units, and they differ in their response to barriers and corridors for dispersal. With the exception of the montane fauna of the highlands of the state—which reflects both a cooler, moister late Pleistocene climate, and a warmer, effectively drier Hypsithermal climate—clues are lacking to suggest the vagaries of Quaternary history. Data still are inadequate to allow a satisfactory picture of some aspects of mammalian zoogeography in Utah. Areas of particular interest are the south-central part of the state (Kaiparowits Subcenter) and the isolated basins and ranges of the southern part of the Great Basin Faunal Area.

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