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DISTRIBUTIONAL PATTERNS OF MAMMALS IN THE PLAINS STATES

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The Plains States of North and South Dakota, Nebraska, Kansas, and Oklahoma sometimes are thought of as a monotonous region, but in fact they have an ecology that is sufficiently heterogeneous to provide opportunity for a rich biota of diverse relationships. A number of authors have described zoogeographic patterns of mammals in one or another of the five states. For example, Jones (1964) described what were termed Mammalian Distributional Areas for Nebraska, and Cockrum (1952) did a similar study for Kansas. Bailey (1927) discussed distribution of mammals in North Dakota in terms of Life Zones, and Blair and Hubbell (1938) described mammalian distribution in Oklahoma in terms of Biotic Districts.

Also, part or all of the Plains States have been included in studies of zoogeographic patterns on broader scales. Simpson (1964) and Wilson (1974) discussed patterns of species density, and Hagmeier and Stults (1964) and Hagmeier (1966) described Mammal Provinces of North America, all based on range maps published by Hall and Kelson (1959). Hoffmann and Jones (1970) addressed some effects of Pleistocene events on distributional patterns of Recent mammals on the Northern Great Plains. Jones *et al.* (1983) described zoogeographic patterns of mammals in the Dakotas and Nebraska, and Jones *et al.* (1986) commented briefly on distributional patterns of mammals in the five Plains States treated herein, emphasizing the effects of peripheral species in enriching the fauna of the region.

Recently, we have had occasion to prepare updated range maps for the native mammalian species of the Plains States (Jones *et al.*, 1986). Those maps enable summary description of zoogeographic patterns across the five-state region. The maps were based on the most recent published information and represent the present best estimate of the range of each species. They do, of course, have some limitations. They represent as static and fixed distributional limits that are patently dynamic, advancing or retreating on a variety of time-scales. They ignore shifts resulting from climatic change and the disruptive effects of human influence. They do not depict historical fluctuations or seasonal change due to migration. They map only presence, not density, of species and hence are merely qualitative descriptions of a quantitative reality. They depict gross geographic rather than fine ecological distribution; they map as continuous some patterns that are, in fact, ecologically disjunct among patches of suitable habitat or dendritic along corridors that meet particular resource needs. The scale is small and cannot accommodate the detail of field observation. However, despite all of these drawbacks, the maps probably represent the best data available and they are adequate for our present purposes.

Biogeographic pattern has been described in many different ways at various scales to meet a variety of theoretical and practical goals. Armstrong (1972) distinguished three broad kinds of descriptive biogeographic studies, based on the character of the data base and the nature of the units described or mapped: ecological studies (resulting in systems of community-types, ecosystem-types, and the like), ecogeographic studies (resulting in systems of biotic provinces, faunal provinces, and analogous units), and areographic studies (resulting in description and analysis of faunal elements). These distinctions have not been maintained particularly well in the literature. Areographic and ecogeographic units often appear to be similar, but they should be distinguished carefully. Their observational bases are distinct and their utility in understanding the evolution of environmental pattern is quite different (Armstrong, 1972).

Ball (1975) recognized biogeography as passing through three phases: descriptive (empirical), narrative, and analytical. The latter two phases were said to comprise historical biogeography. Areographic analysis can form a conceptual bridge between descriptive and historical biogeography by suggesting historical scenarios. Those scenarios serve as hypotheses, eventually testable by independent data that may be generated by research in paleozoology, paleobotany, paleoclimatology, and other historical sciences.

Methods

Maps of ranges within the five-state study region were taken from Jones *et al.* (1986). Those maps were based on the most recent available information for each state, including unpublished records. In preparing those maps, the most valuable published references were Jones *et al.* (1983) for Nebraska and the Dakotas and Bee *et al.* (1981) for Kansas. No up-to-date reference on mammals of Oklahoma is available (although one is in preparation); our knowledge of mammalian distribution in that state based on study of the literature and museum collections was supplemented by conversations with Dr. Ronald K. Chesser and Mr. Robert D. Owen, both of Texas Tech University. In those few instances where ranges were not mapped by Jones *et al.* (1986), distribution within the Plains States follows Hall (1981). Methods peculiar to the areographic and ecological analyses beyond are presented in those respective sections. Nomenclature follows Jones *et al.* (1986).

Results and Discussion

Areography is the study of the geographical ranges of species (Rapoport, 1982). The basic data for areographic analysis are range maps. Udvardy (1969:282) observed that "analysis of a local...fauna list will show that the constituent species fall into groups with respect to the shape of their geographical areas." The cohesiveness of such groups may relate to common geographical origin, common routes of movement, or common ecology. The term "faunal element" has been applied to such groups of species with similar areal distributions. For present purposes, we reserve use of the term "faunal element" for patterns on a continental scale; for areographic assemblages within the Plains States themselves we use the informal terms distributional or areographic "groups," or "suites" of species.

Areographic analysis may be of interest and importance because it allows one to sort out historical from ecological factors in zoogeography. The species of a local fauna occur where they do because (1) they could get there or they evolved there and (2) they could establish and maintain populations based on the dynamic resource base of the area in question. The biotic processes involved here are sufficiently complex that zoogeographers need to take considerable care with definition.

Patterns within the Plains States

We first look at patterns of distribution within the Plains States and then provide a larger context for regional patterns. Of the 138 species of mammals native to the Plains States (Jones *et al.*, 1986), all but 18 reach (or formerly reached) distributional limits there. Figure 1 shows the superimposed limits of ranges of 119 species that reach limits in the five-state region (the grizzly bear is excluded for reasons explained beyond). To search for patterns in that seeming chaos of limits, the general method used was that of Polunin (1960), who provided a simple protocol for determining the areographic components of a local flora. First, the 18 eurychores—species present throughout the five-state region—were eliminated. Second, peripheral species (here defined as those species with gross ranges less than one-third the area of the Plains States) were removed and then sorted into groups according to the general shapes of their ranges. (Twelve such peripheral species show disjunct ranges in the Plains States; these were attributed to more than one peripheral group for the analysis.) Third, the remaining species—those with gross ranges occupying greater than one-third the area of the Plains States, but not present throughout the region—were grouped according to the shapes of their ranges into suites with more or less similar limits. (It may be important to reemphasize here that we are considering gross range and not ecological range. Within a mapped distributional range, no species truly is ubiquitous; all reach limits of ecological tolerance and most, in fact, are quite restricted to particular habitats.) Introduced species were not considered, nor were those of accidental occurrence. (Generally speaking, accidental species are far less a problem for mammalian biogeographers than for those who study avian biogeography or phytogeography; however, some species such as game mammals are moved deliberately by humans, others are moved inadvertantly with agricultural products, and a few bats wander as migrants well beyond their normal ranges.)

Data used in the present analysis are from Jones *et al.* (1986) except for the several species not mapped by them. *Canis lupus, C. rufus, Ursus arctos, Gulo gulo, Rangifer tarandus*, and *Ovis canadensis* were not mapped because they have been mostly or quite extirpated from the Plains States. For present purposes,

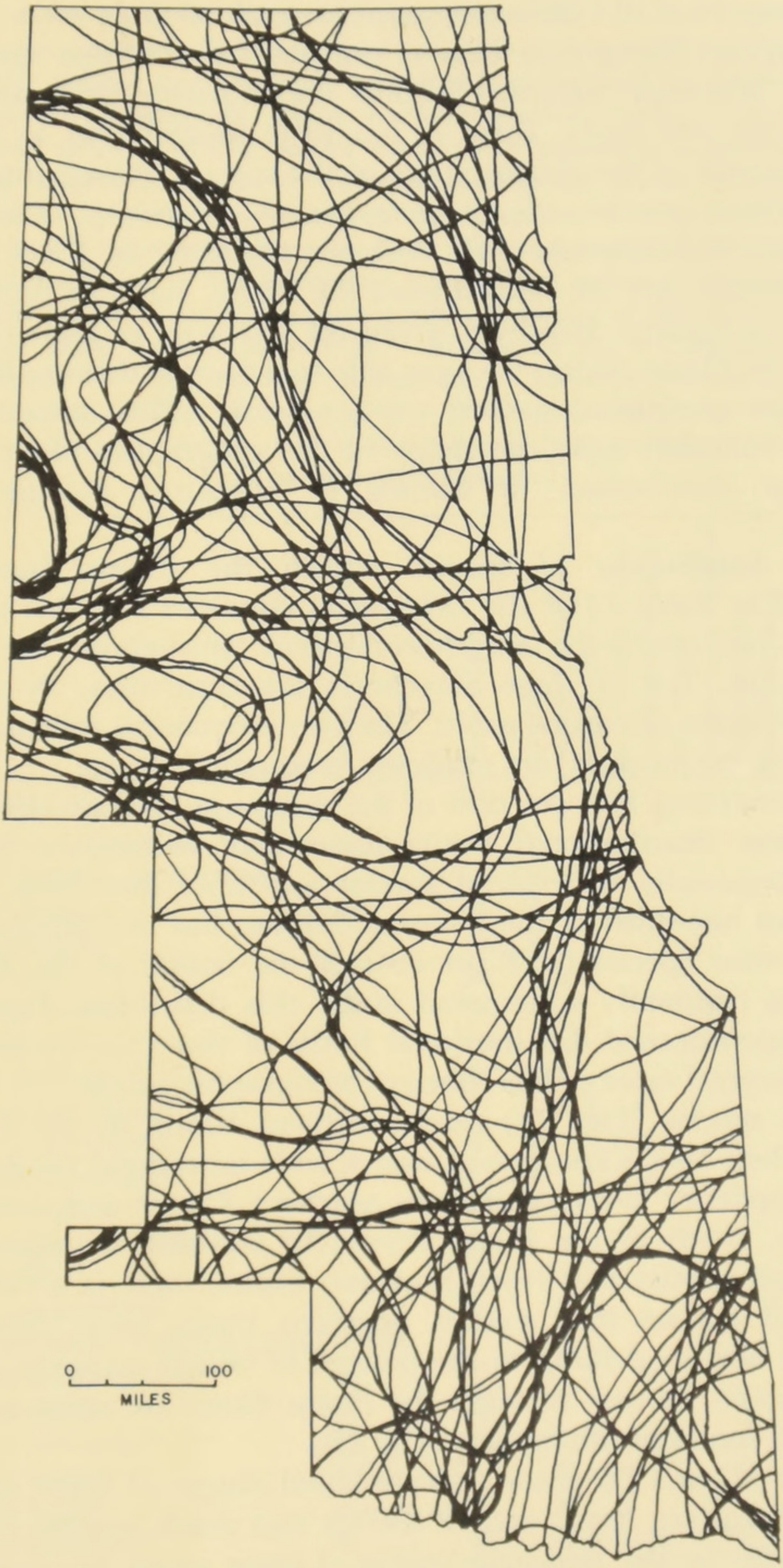

FIG. 1.—Superimposed boundaries of ranges of 119 species of mammals that reach distributional limits in the Plains States.

range maps in Hall (1981) were used for each of those taxa except *Ursus arctos*. The grizzly bear is omitted from further analyses because, although historical records are available from at least four of the five states, there is too little information to allow reconstruction of the former range of the species. Range limits of several other species (*Sorex palustris, S. merriami, Lasiurus seminolus, Tadarida macrotis*) were not indicated by Jones *et al.* (1986) because they are known from the Plains States by only one or a few specimens. However, given the character of their ranges outside the Plains States, we were able to associate them with one or another peripheral pattern unequivocally. This areographic analysis considers only the shape of the geographic range, not ecological distribution or known or suspected evolutionary origins.

Areal distribution of species within the Plains States is indicated in Table 1. Of the 137 species considered in this study, 18 (13.1 per cent)—the eurychores—occur throughout the five-state region. Ten of these eurychores are carnivores, three are bats, and three are artiodactyls. The two eurychoral rodents (the beaver and the muskrat) are restricted to aquatic habitats.

The remaining 86.9 per cent of the species (a total of 119 taxa) reach gross distributional limits somewhere within the Plains States. Regionally widespread species are those that range over more than one-third of the five-state region, but not throughout it. Forty-nine species (35.8 per cent of the fauna) of the Plains States are regionally widespread under this definition. Figure 2 shows superimposed distributional limits of these species broken out into several more or less coherent areographic suites.

Eleven species (Fig. 2A) reach northern limits in the Plains States. These limits are arrayed over a wide latitudinal range, but show a tendency to concentrate in northern Kansas and southern Nebraska, south of the Platte River. (In addition to regionally widespread species that reach northern limits, there is a suite of peripheral species that reaches northern limits also; these are described below.) Adding to the pattern of faunal turnover along a north-south transect through the Plains States are seven species that reach southern limits there (Fig. 2B).

Figures 2C and 2D show superimposed ranges of eight species that reach eastern limits and 12 species that reach western limits, respectively, in the five-state region. Limits along an east-west transect through the Plains States are discussed beyond in some detail, as the efficacy of conditions associated with the 100th

TABLE 1.—*Areographic distribution of mammals of the Plains States. Distributional patterns:* Eu = *eurychore—distributed throughout five Plains States in suitable habitat;* n = *regionally widespread species reaching northern limits;* s = *regionally widespread species reaching southern limits;* e = *regionally widespread species reaching eastern limits;* w = *regionally widespread species reaching western limits;* as = *regionally widespread species absent only in southeast;* se = *peripheral species of southeast;* ne = *peripheral species of northeast;* BH = *peripheral species of Black Hills and associated escarpments;* BM = *peripheral species of Black Mesa;* sw = *peripheral species of southwest;* nw = *peripheral species of northwest;* pe = *peripheral species of east;* ps = *peripheral species of south. Faunal elements:* W = *widespread;* Ch = *Chihuahuan;* Ca = *Campestrian;* E = *Eastern;* A = *Austral;* BC = *Boreo-Cordilleran;* G = *Great Basin;* Co = *Cordilleran;* B = *Boreal;* N = *Neotropical. An asterisk (*) indicates species reaching at least one-third of distributional limit in Plains States between 98° and 102° longitude.*

	Distributional Pattern	Faunal Element	Wetlands	Northern Riparian Forest	Oak-Hickory Forest	Southern Riparian Forest	Oak-Hickory-Pine Forest	Cross Timbers	Pinyon-Juniper Woodland	Coniferous Forest	Sandhills Grassland	Shortgrass Prairie	Mixed Prairie	Tallgrass Prairie	Shrublands
MARSUPIALIA—DIDELPHIDAE															
*Didelphis virginiana**	n	N	X	X	X	X	X	X							
INSECTIVORA—SORICIDAE															
*Sorex arcticus**	ne	B	X	X											
Sorex cinereus	s	BC	X	X											
*Sorex hoyi**	ne	BC	X	X											
Sorex merriami	nw	G									X				
Sorex nanus	BH	Co								X		X			
Sorex palustris	ne	BC	X	X											
*Blarina brevicauda**	w	E	X	X	X									X	
Blarina carolinensis	se	A	X		X	X	X							X	
*Blarina hylophaga**	n	L	X	X	X	X	X							X	
*Cryptotis parva**	n	E	X	X							X		X	X	
Notiosorex crawfordi	ps	Ch							X						X
TALPIDAE															
Scalopus aquaticus	n	E		X							X				
CHIROPTERA—VESPERTILIONIDAE															
Myotis austroriparius	se	A			X		X								
Myotis evotis	as	Ch								X					
Myotis grisescens	se	A			X										
*Myotis keenii**	BH,w	E		X	X					X					
*Myotis leibii**	e,se,sw	W		X		X			X						
*Myotis lucifugus**	w	W		X	X	X	X			X					
Myotis sodalis	se	E			X		X								
Myotis thysanodes	BH	Ch							X	X					X
*Myotis velifer**	sw	Ch		X											X

TABLE 1.—*Continued.*

*Myotis volans**	BH	G							X					
Myotis yumanensis	BM	Ch						X						
Lasionycteris noctivagans	Eu	W	X	X	X	X			X					
*Pipistrellus hesperus**	sw	Ch						X						X
*Pipistrellus subflavus**	w	E	X	X	X	X	X							
Eptesicus fuscus	Eu	W	X	X	X	X	X		X					
Lasiurus borealis	w	E	X	X	X	X	X							
Lasiurus cinereus	Eu	W	X	X	X	X			X					
Lasiurus seminolus	se	A			X									
*Nycticeius humeralis**	w	E	X	X	X	X	X							
Plecotus rafinesquii	se	A				X								
*Plecotus townsendii**	se,BH,sw	Ch			X			X	X					X
*Antrozous pallidus**	BM,sw	Ch						X						X
MOLOSSIDAE														
Tadarida brasiliensis	n	N		X										
Tadarida macrotis	ps	Ch						X						
EDENTATA—DASYPODIDAE														
*Dasypus novemcinctus**	n	N	X			X	X							X
LAGOMORPHA—LEPORIDAE														
Sylvilagus aquaticus	se	A			X	X								
*Sylvilagus audubonii**	e	Ch									X	X		X
Sylvilagus floridanus	w	E	X	X	X	X	X							X
Sylvilagus nuttallii	BH,nw	G							X					X
Lepus americanus	ne	BC	X						X					
Lepus californicus	n	Ch						X		X	X			X
Lepus townsendii	s	Ca								X	X	X		X
RODENTIA—SCIURIDAE														
Tamias minimus	ne,BH	BC	X						X					X
Tamias quadrivittatus	BM	Co						X						
Tamias striatus	pe	E		X										
Marmota flaviventris	BH	Co							X					
Marmota monax	pe	B		X	X	X	X							
Spermophilus elegans	nw	G									X			
*Spermophilus franklinii**	w	Ca											X	
*Spermophilus richardsonii**	ne	Ca										X		X
*Spermophilus spilosoma**	sw	Ch								X	X			X
Spermophilus tridecemlineatus	as	Ca								X	X	X		
Spermophilus variegatus	BM	Ch						X						
Cynomys ludovicianus	e	Ca								X	X	X		
*Sciurus carolinensis**	se,ne	E		X	X	X								
Sciurus niger	w	E	X	X	X	X	X							
Tamiasciurus hudsonicus	ne,BH	BC	X						X					
Glaucomys sabrinus	ne,BH	BC	X						X					
Glaucomys volans	se	E		X	X	X	X							
GEOMYIDAE														
Thomomys talpoides	nw	Co							X		X			X
Geomys breviceps	se	L				X						X	X	
Geomys bursarius	as	Ca								X		X	X	
*Cratogeomys castanops**	BM	Ch									X			

TABLE 1.—*Continued.*

HETEROMYIDAE															
Perognathus fasciatus	e	Ca										X			X
Perognathus flavescens	as	Ch									X	X			
*Perognathus flavus**	sw	Ch										X	X		X
Perognathus hispidus	n	Ca									X	X	X		X
Dipodomys elator	ps	L													X
*Dipodomys ordii**	e	Ch									X	X	X		X
CASTORIDAE															
Castor canadensis	Eu	W	X	X		X									
CRICETIDAE															
Oryzomys palustris	se	A	X				X								
Reithrodontomys humulis	se	A					X								
Reithrodontomys fulvescens	se	Ch	X	X		X	X							X	X
Reithrodontomys megalotis	as	Ch		X									X	X	X
Reithrodontomys montanus	as	Ca										X	X		X
Peromyscus attwateri	se	L					X	X							X
Peromyscus difficilis	BM	Ch							X						
Peromyscus gossypinus	se	A	X			X	X								X
Peromyscus leucopus	w	W		X	X	X	X	X							X
Peromyscus maniculatus	as	W		X	X	X	X	X	X	X	X	X	X	X	X
Peromyscus pectoralis	ps	Ch						X							
Peromyscus truei	BM	Ch							X						
Ochrotomys nuttalli	se	A				X	X								
Onychomys leucogaster	as	Ca									X	X	X		X
Sigmodon hispidus	n	N	X	X		X							X	X	
Neotoma albigula	BM	Ch							X						
*Neotoma cinerea**	BH	Co								X					
*Neotoma floridana**	n	A		X		X	X	X							
Neotoma mexicana	BM	Ch							X						
Neotoma micropus	sw	Ch										X			X
Clethrionomys gapperi	ne,BH	BC								X					
Microtus longicaudus	BH	Co								X					
Microtus ochrogaster	s	Ca						X			X			X	
Microtus pennsylvanicus	s	BC	X								X			X	
Microtus pinetorum	se	E			X	X	X	X							
*Lemmiscus curtatus**	k	G									X				X
Ondatra zibethicus	Eu	W	X	X		X									
*Synaptomys cooperi**	w	E	X												
ZAPODIDAE															
*Zapus hudsonius**	s	B	X												
Zapus princeps	ne	Co	X												
ERETHIZONTIDAE															
Erethizon dorsatum	as	W		X	X				X	X					
CARNIVORA—CANIDAE															
Canis latrans	Eu	W		X	X		X	X	X	X	X	X	X	X	X
Canis lupus	as	W		X	X	X	X	X	X	X	X	X	X	X	X
Canis rufus	se	A				X	X								
Vulpes velox	e	Ca									X	X			

TABLE 1.—*Continued.*

Vulpes vulpes	Eu	W	X	X	X	X	X	X		X	X				
*Urocyon cinereoargenteus**	w	N		X	X	X	X	X	X					X	
URSIDAE															
Ursus americanus	Eu	W		X	X	X	X	X		X					
Ursus arctos	?	?													
PROCYONIDAE															
Procyon lotor	Eu	W	X	X	X	X	X								
Bassariscus astutus	ps	Ch						X	X					X	
MUSTELIDAE															
Martes americana	ne	BC		X						X					
Martes pennanti	ne	B		X						X					
Mustela erminea	ne,BH	BC	X	X	X					X				X	
Mustela frenata	Eu	W	X	X	X	X	X	X	X	X	X	X	X	X	X
Mustela nigripes	e	Ca										X	X		X
*Mustela nivalis**	s	B	X	X										X	
Mustela vison	Eu	W	X	X		X									
*Gulo gulo**	ne,BH	BC	X	X						X					
Taxidea taxus	as	W									X	X	X	X	X
Spilogale gracilis	BM	Ch							X						X
Spilogale putorius	n	A		X	X	X	X	X					X	X	X
Mephitis mephitis	Eu	W	X	X	X	X	X	X	X	X	X	X	X	X	X
Lutra canadensis	Eu	W		X		X									
FELIDAE															
Felis concolor	Eu	W		X	X	X	X	X	X	X	X				X
Felis lynx	s	BC								X					
Felis rufus	Eu	W		X	X	X	X	X	X	X	X				X
ARTIODACTYLA—CERVIDAE															
Cervus elaphus	Eu	W		X	X			X		X				X	
Odocoileus hemionus	as	W		X					X	X	X	X	X		X
Odocoileus virginianus	Eu	W		X	X	X	X	X					X	X	
*Alces alces**	ne	B	X							X					
Rangifer tarandus	ne	B		X						X					
ANTILOCAPRIDAE															
*Antilocapra americana**	e	Ca										X	X		X
BOVIDAE															
Bison bison	Eu	W									X	X	X	X	X
Ovis canadensis	BH	Co								X					

Meridian in determining patterns of mammalian distribution are evaluated.

Seven regionally widespread species range across the Plains States except for southeastern Oklahoma and in some cases extreme southeastern Kansas (see Fig. 2E). The ranges of these taxa generally complement those of a large group of peripheral species confined to the general area of the Ozarks (Fig. 2F). Four additional species nearly share the same pattern: *Reithrodontomys megalotis* and *R. montanus* reach both southeastern and

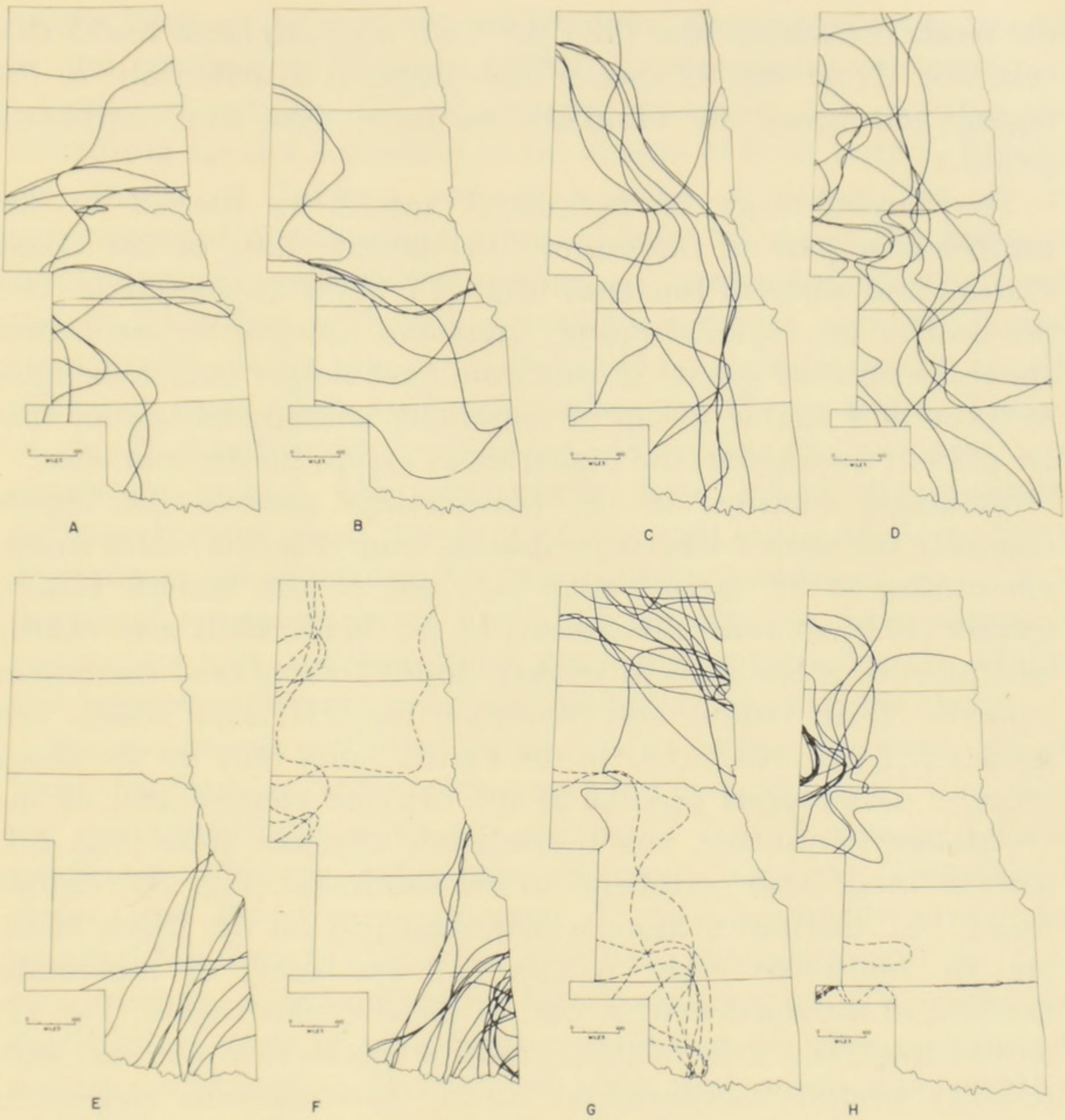

FIG. 2.—Superimposed distributional limits of species of several areographic suites of species: A, 11 species reaching northern limits; B, seven species reaching southern limits; C, eight species reaching eastern limits; D, 12 species reaching western limits; E, seven species widespread in the region but reaching southeastern limits; F, 20 species peripheral on the southeast (solid lines), and six species peripheral in the northwest (dashed lines); G, 17 species peripheral in the northeast (solid lines), and eight species peripheral on the southwest (dashed lines); H, 15 species peripheral on the Black Hills and nearby areas (solid lines), and 10 species peripheral on the Black Mesa and nearby areas (dashed lines).

northeastern limits, the former species being absent from northeastern North Dakota and the latter being limited to south and west of the Missouri River; *Perognathus flavescens* and *Geomys bursarius* reach northwestern as well as southeastern limits.

Peripheral species are those with gross ranges covering less than one-third of the area of the Plains States. Seventy species of the fauna considered here (51.1 per cent) are peripheral under that criterion. (Note that 12 species have disjunct distributions in the region and hence are tabulated in more than one peripheral group.)

The largest suite of peripheral species is limited to the southeastern part of the region, the general area of the Ozark Plateau and adjacent lowlands (Fig. 2F). Some 20 mammals (15.3 per cent of the regional fauna) share this pattern. As mentioned above, peripheral species in this suite have ranges complementary to those of a sizable group of regionally widespread species that are present throughout the Plains States except for the southeast.

Mammals confined to the northeastern part of the region comprise the second largest peripheral suite (Fig. 2G, solid lines), amounting to 17 species (12.3 per cent of the fauna). Fifteen species (10.9 per cent) are limited to the Black Hills and nearby escarpments or badlands in western South Dakota (and sometimes adjacent North Dakota and Nebraska; Fig. 2H, solid lines). Ten species (7.2 per cent) occur in the Plains States only on the Black Mesa, a lava-topped upland at the extreme western end of the Oklahoma Panhandle, and immediately adjacent areas (Fig. 2H, dashed lines). Also peripheral in the southwest (Fig. 2G, dashed lines), but distributed more widely than just on the Black Mesa, are an additional eight species (5.8 per cent) of mammals. Limited to the northwestern part of the five-state region (Fig. 2F, dashed lines) is a suite of six peripheral species (5.1 per cent) with roughly similar distributional limits. *Spermophilus elegans* is included in this suite for want of a closer association; it occurs (or at least once occurred) in the Plains States only in part of the Nebraska Panhandle. Two species (1.4 per cent, not mapped), *Marmota monax* and *Tamias striatus,* occupy the eastern periphery of the region, but unlike a number of other eastern taxa, they have not become widespread by following riparian corridors westward. Finally, five species (3.6 per cent, not mapped) occupy the southern periphery of the region, reaching limits in Oklahoma or extreme southern Kansas.

The Plains States in Context: Faunal Elements

Patterns of areal distribution in the Plains States are a subset of patterns on a larger scale. As with the regional distributional groups discussed above, our approach is strictly areographic, that is, based strictly on shapes of mapped ranges. Continental ranges of species were taken from Hall (1981), and some were modified on the basis of more recent information. Range maps were sorted by the protocol of Polunin (1960): (1) eliminating faunistically widespread species; (2) eliminating endemics; (3) sorting the remaining species according to the shapes of their ranges. Results are shown in Table 1 and in a series of maps (Fig. 3) of superimposed distributional limits. Figure 3A shows the limits of 26 faunistically widespread species, so categorized because none can be identified with any particular coherent regional faunal element. Of species that are widespread on a continental scale, 18 (69.2 per cent) reach no limits within the Plains States. Twelve of the 26 faunistically widespread mammals (46.2 per cent) are carnivores, which characteristically have broad distributions, perhaps because most are at least one step removed from direct dependence on vegetation for nourishment and hence occur in a variety of ecosystem types. Five (19.2 per cent) of the widespread species are bats and four (15.4 per cent) are artiodactyls. Flight and large size often are associated with broad geographic ranges.

No species are endemic to the Plains States, but four are of local distribution, sufficiently restricted geographically that they are not identifiable with any particular faunal element. These species are *Blarina hylophaga, Geomys breviceps, Dipodomys elator,* and *Peromyscus attwateri.* It may be worth a note in passing that three of these taxa have been elevated to specific rank only recently, based on careful biosystematic work. This suggests that further study of peripheral populations of other widespread species could lead to discovery of additional populations worthy of specific recognition.

With widespread and local species eliminated, distinct faunal patterns begin to emerge. We recognize eight regional areographic faunal elements, each characterized by ranges of generally similar shape and a center of coincidence where all members of the faunal element occur. Centers of coincidence are indicated in Figure 3J. The center of coincidence encompasses environmental conditions suitable to all members of the faunal element, and it seems reasonable to suppose that such a center may represent the conditions under which members of the faunal element evolved their present genetic limits of tolerance. In many cases, it seems quite certain that places now meeting the common resource needs of members of the faunal element have been located elsewhere in the past, so we should not confuse "centers of coincidence" with "centers of origin."

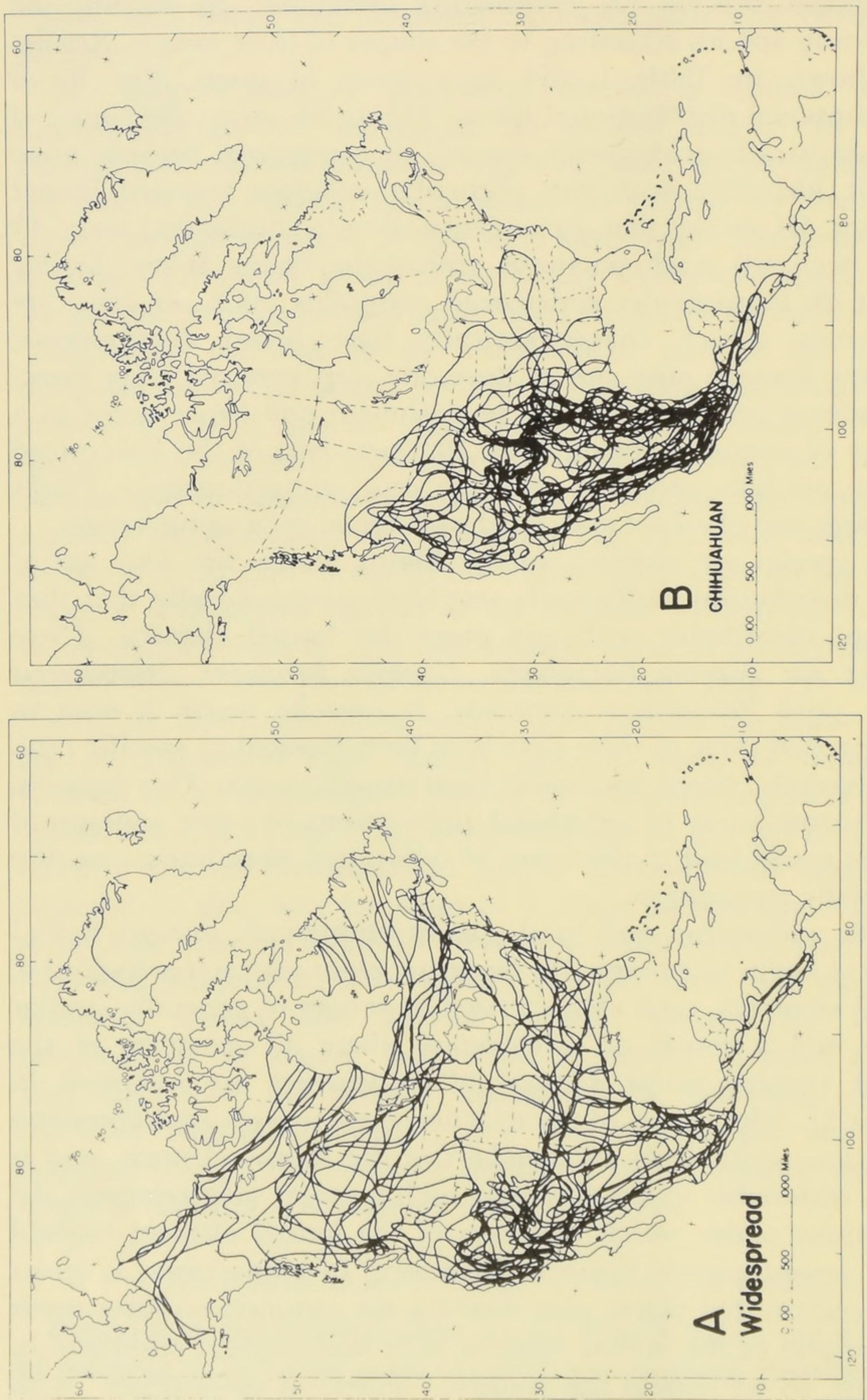

FIG. 3.—Superimposed continental ranges of 26 widespread species (A), species of eight distinctive faunal elements (B-I), and centers of coincidence (J) of the several faunal elements (labelled as on the several separate maps in this figure).

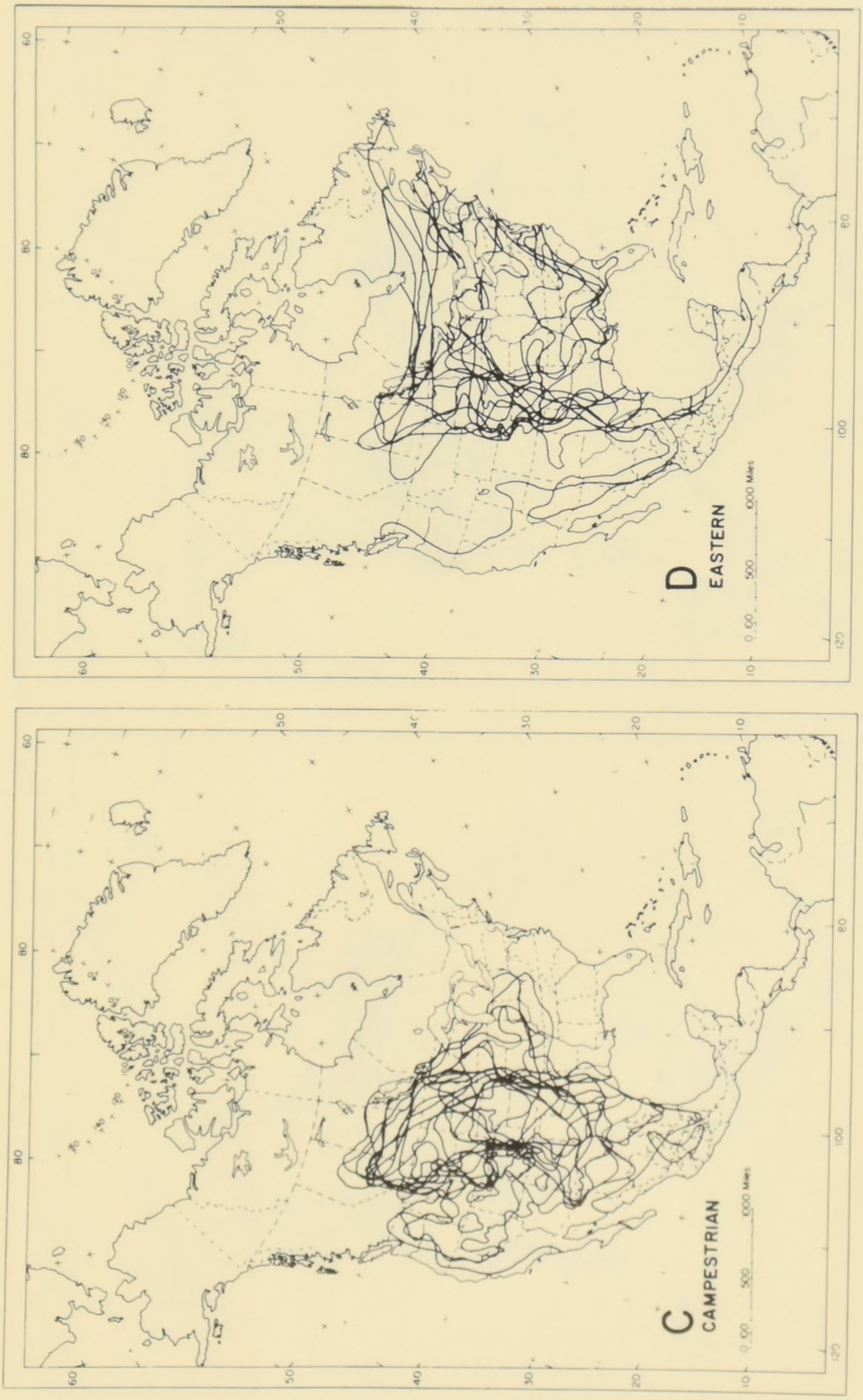

FIG 3.—*Continued.*

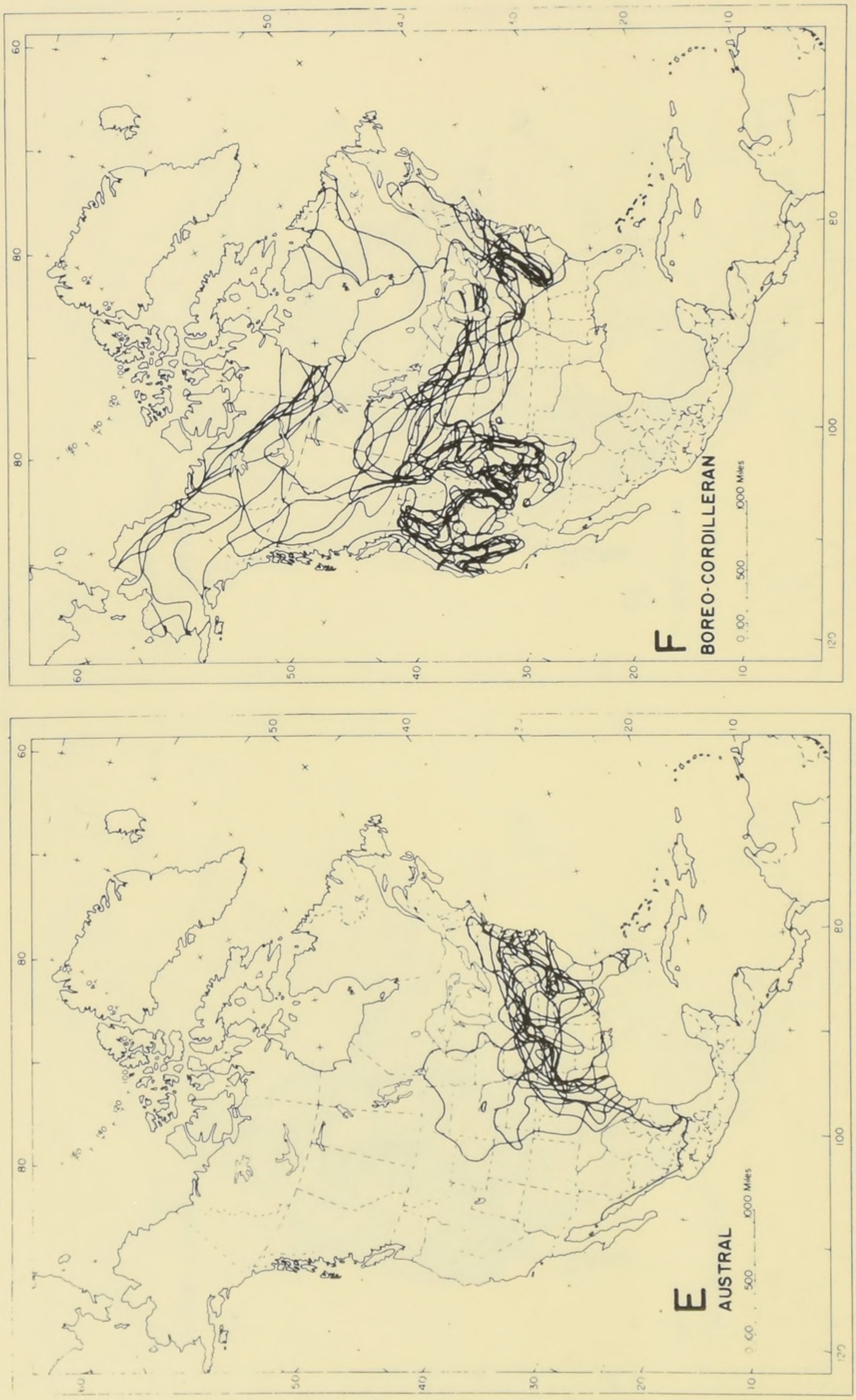

Fig 3.—*Continued.*

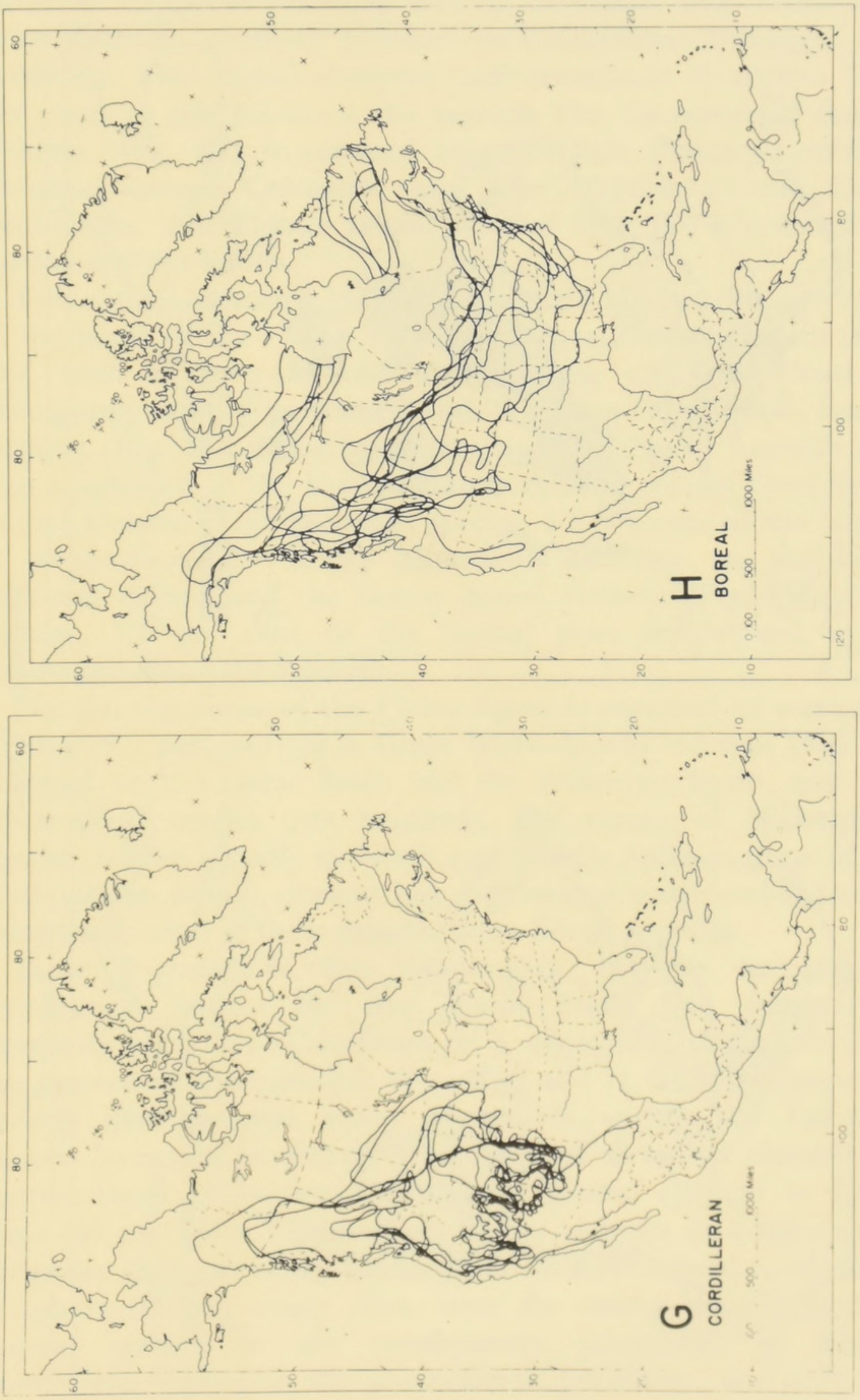

FIG 3.—*Continued.*

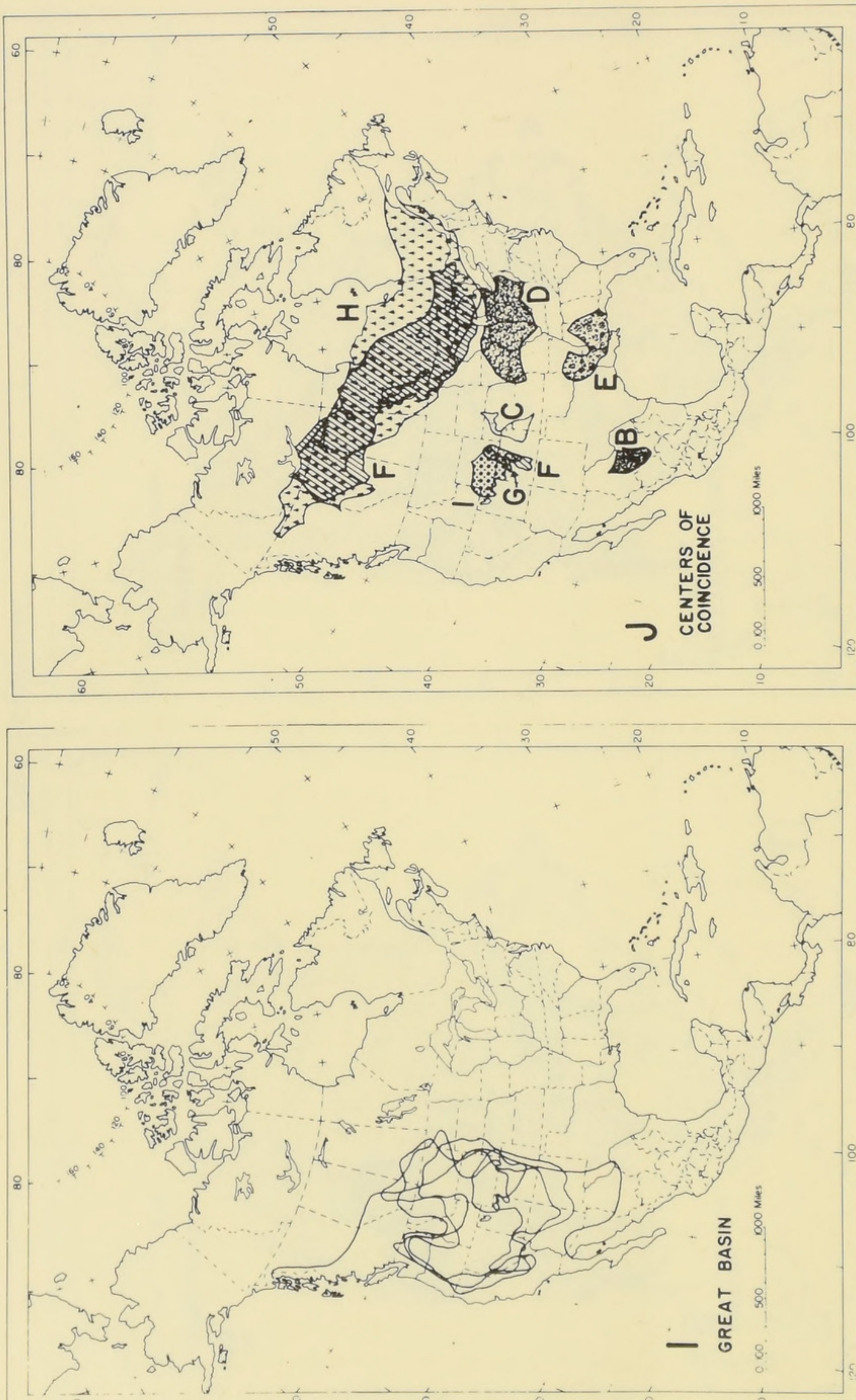

Fig 3.—*Continued.*

The largest single areographic faunal element contributing to the fauna of the Plains States is the Chihuahuan (Fig. 3B), a group of 26 species (19.0 per cent of the fauna) with a center of coincidence in northern Mexico—in Chihuahua, Durango, and Coahuila. Two faunal elements each contribute 15 species (10.9 per cent) to the fauna of the region. The Campestrian faunal element (Fig. 3C) is centered on the High Plains of western Kansas, eastern Colorado, and the Oklahoma and Texas panhandles. The Eastern faunal element (Fig. 3D) is centered on the lower Ohio Valley.

Two faunal elements each contribute 13 species (9.5 per cent) to the fauna of the Plains States: an Austral faunal element (Fig. 3E), with a center of coincidence along the Gulf Coast in Mississippi and Louisiana, and a Boreo-Cordilleran faunal element (Fig. 3F), occurring across northern North America and also southward in the Rocky Mountains. The related Cordilleran faunal element (Fig. 3G; eight species, 5.8 per cent of the fauna) is centered on the Rocky Mountains and has no particular northern extent, and the Boreal faunal element (Fig. 3H; seven species, 5.1 per cent of the fauna) does not extend much southward along the Rockies.

Finally, the fauna of the Plains States is enriched by some five species (3.6 per cent) of a Great Basin faunal element (Fig. 3I) centered on the Great Basin and the Wyoming Basin, and five Neotropical species (not mapped). The ranges of Neotropical species overlap broadly in North and Middle America those of the Chihuahuan faunal element but they extend considerably farther southward, most of them into northern South America.

Table 2 indicates the relationship between areographic distribution within the five Plains States and areographic distribution of faunal elements on a continental scale, showing the percentage contribution of each of the 11 faunal elements to various distributional suites of species within the five-state region. Strongest percentage contributions of faunal elements to distributional suites are: Chihuahuan faunal element to Black Mesa (90 per cent); Chihuahuan faunal element to southwestern periphery (87.5 per cent); Chihuahuan faunal element to southern periphery (80 per cent). Also, note the strong contribution of Austral species to the southeastern periphery, of Boreo-Cordilleran species to the northeastern periphery, and of Great Basin species to the northwestern periphery. Boreo-Cordilleran species contribute strongly to the suite of regionally widespread taxa with southern limits, Eastern species contribute strongly to the suite of regionally widespread mammals with western limits, and Campestrian species are strongly represented in the suite of widespread species with eastern limits. All of the species that occur throughout the Plains States also are faunistically widespread; that is, none can be associated with any particular faunal element. Faunistically widespread species also contribute strongly to the pattern of southeastern limits. These associations suggest that areographic faunal elements may, indeed, have some historico-ecological integrity, and also that areographic patterns in the Plains States are consistent with areographic patterns on a continental scale.

Importance of the 100th Meridian to Mammalian Distribution

A number of authors have suggested that there is an important biogeographic boundary on the Great Plains, roughly coincident with the 100th Meridian. Jones *et al.* (1983) commented briefly on environmental changes across the plains, noting that the physiographic boundary between the Central Lowlands and Great Plains physiographic provinces is generally coincident with the 20-inch isopleth of precipitation. That isopleth is roughly the point of equivalence between precipitation and evapotranspiration, and thus is the boundary between humid and dry climates. The 100th Meridian is also more or less coincident with the transition from shortgrass prairie to mixed prairie (although that pattern is greatly complicated on the Great Plains by the presence of the Nebraska Sandhills—which allow the extension of mesic communities westward, by exposures of Pierre Shale in the Dakotas—which allow the extension of bunchgrasslands eastward, and by outcrops of the Ogallala formation in Kansas—which have been dissected by headward cutting rivers). These environmental factors are associated with patterns of human settlement and land use that are readily apparent from even superficial perusal of such references as *The National Atlas*.

Bock *et al.* (1977, 1978) provided numerical analyses of the distribution of some wintering birds in North America, based on Audubon Society Christmas Count data. They noted a strong turnover of species across the 100th Meridian, especially on the southern Great Plains. Bock and Smith (1982) identified a major biogeographic transition at about the 100th Meridian in a numerical study of the distribution of North American amphibians. They noted that many eastern amphibians reach

TABLE 2.—*Percentage contribution of faunal elements to distributional groups within Plains States.*

Distributional Group (*N*)	Neotropical	Austral	Boreal	Boreo-Cordilleran	Great Basin	Cordilleran	Eastern	Campestrian	Chihuahuan	Widespread	Local
Eurychores (18)										100	
Regionally Widespread Species											
Northern limits (8)	36.4	18.2					18.2		18.2		9.1
Southern limits (7)			28.6	42.9				28.6			
Eastern limits (8)								62.5	25.0	12.5	
Western limits (12)	8.3						66.7	8.3		16.7	
Absent southeast (11)								45.5	9.1	45.5	
Peripheral Species											
Southeast (20)		55.0					20.0		10.0	5.0	10.0
Northeast (16)			25.0	56.3		6.2	6.2	6.2			
Black Hills (14)				28.6	14.3	35.7	7.1		14.3		
Black Mesa (10)						10.0			90.0		
Southwest (8)									87.5	12.5	
Northwest (6)					66.7	16.7			16.7		
East (2)			50.0				50.0				
South (5)									80.0		20.0

their western limits at about 100° west, and that there are many fewer species to the west of that line. They noted, also, that some groups have complementary distributions about the boundary. They noted further—following the work of Hagmeier (1966)—that mammals appear not to show such a biogeographic boundary, speculating that perhaps the majority of mammals of the plains are grassland specialists whereas many amphibians (and birds as well) are confined to aquatic and associated riparian habitats.

It may be of interest to look briefly at the importance of the 100th Meridian to the distribution of mammals using our areographic analysis—an indirect test of previous comments by Bock and Smith. We expect to provide a numerical analysis comparable to theirs in a subsequent paper. To get some idea of the importance of the 100th Meridian as a boundary in mammalian distribution, we superimposed upon the range map of each species an overlay showing the 98th, 100th, and 102nd meridians. All species for which one-third or more of the distributional limit in the Plains States lay between 98° and 102° West were tabulated. This tabulation was deliberately generous. Nonetheless, the list included only 37 species (27 per cent of the native mammalian fauna). These species are indicated with an asterisk in Table 1. Their distributions in terms of distributional groups within the Plains States and in terms of areographic faunal elements are of some interest.

Table 3 indicates the number of species of each areographic distributional suite reaching at least one-third of their distributional limits between 98° and 102° W. Consider first regionally widespread species. None of the species reaching only southeastern limits—mostly grassland mammals—is limited between 98° and 102° W. Each of the other distributional suites of widespread species includes some taxa that reach limits at about the 100th Meridian. Of regionally widespread species (that is, species that occupy greater than one-third of the area of the Plains States, but do reach limits there), those reaching northern, eastern, and western limits are most likely to reach such limits in the vicinity of the 100th Meridian. From an ecological standpoint, it is species of the tallgrass prairie and riparian woodland that are so limited, reaching the transition zone from the east and southeast. Species that reach eastern limits in the vicinity of the 100th Meridian mostly are those of the shortgrass prairie. Species that reach only western limits are species of a

TABLE 3.—*Species in each areographic distributional group reaching at least one-third of their distributional limits between 98° and 102° W longitude.*

Areographic distributional group	Number in group	Number with limits	Percentage with limits
Eurychores	18	0	0.0
Regionally Widespread Species			
Northern limits	8	5	62.5
Southern limits	7	2	28.6
Eastern limits	8	4	50.0
Western limits	12	8	66.7
Absent southeast	11	0	0.0
Peripheral Species			
Southeast	20	0	0.0
Northeast	16	6	37.5
Black Hills	14	2	14.3
Black Mesa	10	1	10.0
Southwest	8	6	75.0
Northwest	6	1	16.7
East	2	0	0.0
South	5	0	0.0

variety of mesic habitats—riparian forest, wetlands, tallgrass prairie; other eastern species of riparian forest range well to the west of 102° along watercourses.

Suites of peripheral species differ quite markedly in the degree to which they reach limits across the 100th Meridian. In three suites (southeastern periphery, eastern periphery, southern periphery) no species reaches such limits; they do not extend westward to 98°. Peripheral species centered on the Black Hills, Black Mesa, and in the northwest also show a low incidence of such limits, and for an analogous reason—they reach their limits in specialized habitats to the west of the 102nd Meridian. That suite showing the highest incidence of species reaching limits near the 100th Meridian is the southwestern periphery; these mostly are species of semidesert grassland or rocky, broken terrain.

Table 4 indicates the number of species in each areographic faunal element reaching distributional limits between 98° and 102° W longitude. Some 24 per cent of the species are so limited. Considering the weighted percentage allows one to compare one faunal element against another although absolute numbers of species in each element differ widely. The average weighted percentage contribution of elements to the total number of species with limits between 98° and 102° is 2.67 (SD = 2.097). Using a criterion of the mean ± SD, Chihuahuan species are over-

TABLE 4.—*Number of species in each faunal element, number of those species reaching at least one-third of their distributional limits between 98° and 102° W longitude, and weighted percentage (calculated as the product of the percentage of the total fauna in element times the percentage of the element so limited).*

Faunal element	In element		Limited		Weighted
	Number	(%)	Number	(%)	(%)
Widespread	26	18.8	2	7.6	1.42
Chihuahuan	30	20.8	10	33.3	6.92
Eastern	17	11.8	6	35.3	4.16
Boreo-Cordilleran	16	11.1	2	12.5	1.39
Campestrian	15	10.4	3	20.0	2.08
Austral	13	9.0	1	7.7	0.69
Boreal	7	4.9	4	57.1	2.80
Cordilleran	7	4.9	1	14.3	0.70
Great Basin	6	4.2	2	33.3	1.40
Neotropical	5	3.5	3	60.0	5.16
TOTALS/MEANS	144	$\bar{Y}$=9.94	34	$\bar{Y}$=28.06	$\bar{Y}$=2.67

represented among species with such limits. With weighted percentages arc-sine transformed and using the same criterion, no elements are over-represented.

Consider the ecological distribution of species reaching limits around the 100th Meridian (Table 1). The mean percentage of mammalian species that reach such limits within each ecological community-type is 22.15 (SD = 6.68). Mammals of wetlands (40.7 per cent) and those of northern riparian forests (29.3 per cent) are somewhat over-represented among species reaching limits, and species of coniferous forest (17.5 per cent), sandhills grassland (14.2 per cent), and tallgrass prairie (14.2 per cent) are somewhat under-represented. A number of mammalian species are narrowly restricted in the Plains States to coniferous forest; such forest in the region occurs mostly in the extreme northeast and on the Black Hills.

Our concern in this paper has been with shapes of geographical ranges. We have noted that geographical ranges of species change over time. At any given point in time, however, the ranges of some species are likely to be static whereas those of other species are relatively dynamic. Static distributions may be relict, remnants of past distributions of greater extent, or they may represent a state of general equilibrium with broader environmental patterns (for example, vegetation) that are similarly static. Dynamic ranges may be expanding or retracting. Such changes may be in response to broad, regional climatic change, or to local change due to human influences, or to any one or a combination of a spectrum of natural or anthropogenic causes between those extremes.

Insofar as current changes are concerned, members of the several faunal elements tend to differ. Widespread species show no major trend toward areographic change within the Plains States. Campestrian species tend to be more or less stable regionally, but there has been local retraction of some ranges (for example, *Lepus townsendii*) as native upland habitats have been converted to agricultural uses; however, other more broadly tolerant species (for example, *Perognathus flavescens* and *Geomys bursarius*) utilize croplands as habitat. Often Campestrian species of well-developed prairie (for example, *Spermophilus franklinii*) are restricted to railroad rights-of-way, rural cemeteries, and other relict patches of native habitat.

Members of the Neotropical faunal element are expansive, perhaps in response to secular climatic amelioration in the region. Ranges of species of the Boreal element, by contrast, are static or retracting. We have noted that Boreal and Boreo-Cordilleran species are relict on the Black Hills and on the northeastern periphery of the Plains States. Land-use changes in the latter area have led to local retraction of ranges and even to extirpation of species.

The Chihuahuan faunal element is in part relict on the mesas of the Oklahoma Panhandle. Chihuahuan species not restricted to rocky habitats, however, may be expanding in response to climatic change or to man-induced habitat alteration; *Lepus californicus* is an example of a species with such a dynamic range. Some members of both Eastern and Austral elements are expansive due to stabilization of riparian corridors (through control of fire and flooding) and the augmentation of native deciduous forest habitat elements by artificial landscaping, including urban plantings and rural shelterbelts; the well-known expansion of *Sciurus niger* is a case in point.

Frequently it is difficult to know in a given instance whether apparent changes in ranges of species are due to natural or anthropogenic change, to random fluctuations, or simply to increasingly complete observations. However, it may be useful to try to identify the causes behind range dynamics. The fauna of a locality may be a sensitive indicator of the effects of land-use practices.

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