OCCASIONAL PAPERS

Museum of Texas Tech University

Number 212 6 March 2002

BIOGEOGRAPHY OF HETEROMYID RODENTS ON THE CENTRAL GREAT PLAINS

ROBERT S. DEBACA AND JERRY R. CHOATE

The Heteromyidae is a New World family of rodents with a range west of the Mississippi River from southwestern Canada to coastal Venezuela, Colombia, and Ecuador (Hall, 1981; Schmidly et al., 1993). Five of the species in the family -- *Chaetodipus hispidus, Dipodomys ordii, Perognathus fasciatus, Perognathus flavescens,* and *Perognathus flavus* -- are adapted to arid, semiarid, or temperate grasslands and have ranges that overlap on the central Great Plains (Hall, 1981; Schmidly et al., 1993). These species have some of the widest ecological tolerances and broadest geographic ranges within the Heteromyidae (Schmidly et al., 1993).

Heteromyid rodents of the central Great Plains have been included in a number of regional investigations, but only a few studies have discussed competition or coexistence among these species (Alcoze and Zimmerman, 1973; Maxwell and Brown, 1968; Schmidly et al., 1993). Just one investigation has focused specifically on local interactions of heteromyids in this region (Mohamed, 1989), but the author made conclusions for the area based on only two study sites in Weld County, Colorado. To date, there never has been a comprehensive investigation into local and regional distribution patterns of the Heteromyidae on the central Great Plains.

Much ecological overlap might be expected among *C. hispidus, D. ordii, P. fasciatus, P. flavescens,* and *P. flavus* where they coexist on the central Great Plains. These species closely resemble one another based on diet, physiology, morphology, and activity patterns (Alcoze and Zimmerman, 1973; Bee et al., 1981; Fitzgerald et al., 1994; Flake, 1973; Jones et al., 1983; Jones et al., 1985; Best and Skupski, 1994; Garrison and Best, 1990; Manning and Jones, 1988; Monk and Jones, 1996; Paulson, 1988; Langford, 1983). There also seems to be a broad similarity in use of substrates and habitats by these species as described in published accounts, but these descriptions tend to be anecdotal, contradictory, or over-generalized (Armstrong, 1972; Bee et al., 1981; Cockrum, 1952; Fitzgerald et al., 1994; Jones et al., 1983; Jones et al., 1985; Maxwell and Brown; 1968; Reed and Choate, 1986).

Based on these similarities, the competitive exclusion principle (Gause, 1934) would suggest that *C. hispidus, D. ordii, P. fasciatus, P. flavescens,* and *P. flavus* should locally exclude one another on the central Great Plains. Although this tendency exists within the region, two heteromyid species (one small, the other larger) often coexist at the same location. But the extent of local coexistence has not been quantified.

Likewise, regional distribution patterns seem poorly understood or remain anecdotal. Factors similar to those that shape granivore associations elsewhere might determine these patterns.

Research on granivores that inhabit North American deserts has revealed two categories of factors that determine whether a species will be present or absent from a community. Extrinsic factors ultimately determine which species occur in an area and are independent of other species within the community (Brown, 1987; Brown and Harney, 1993). According to these criteria, a population occurs in areas where a species evolved or dispersed, and it persists where suitable climate, substrate, food, and habitat exist (Brown, 1987; Brown and Harney, 1993; Brown and Kurzius, 1989; Kotler and Brown, 1988; Munger et al., 1983). When these requirements are met, individuals of a species can forage efficiently, find adequate shelter, and survive to reproduce (Kotler and Brown, 1988). Intrinsic factors -- interactions with other species in the community -- secondarily determine which species can coexist among the total species within the region (Brown 1987; Brown and Harney, 1993; Kotler and Brown, 1988; Munger et al., 1983). These interactions include mutualism, competition, and predation, which work together to influence the coexistence of species. Those species with similar extrinsic adaptations should tend to coexist locally if intrinsic factors do not prevent them from doing so.

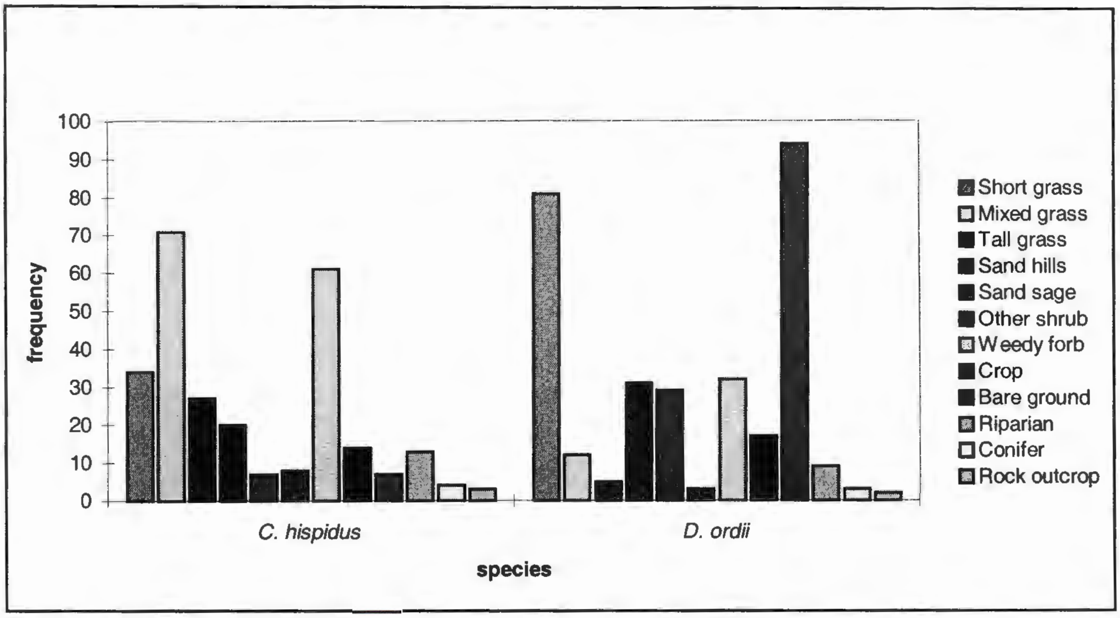
Brown (1987) described six empirically derived patterns, including both extrinsic and intrinsic factors that seem to guide the development of multi-species guilds of granivorous rodents. Two of these patterns were evaluated in this study. One pattern is that species within a guild coexist locally according to a differential of body sizes, and the other is that greater species diversity within a guild can be found in more complex habitats (Brown; 1987). Additionally, the extent of local coexistence and patterns of habitat occurrence were examined in this study, and these collective data were used to discuss regional distribution patterns for the five species on the central Great Plains.

METHODS AND MATERIALS

Study area. The region of investigation included Kansas, Nebraska, and the eastern one third of Colorado. This area encompasses most of the zone of sympatary for the Heteromyidae on the central Great Plains and includes range limits for each of the five species. This region was chosen for these reasons and because mammals there have been well documented in literature and museum collections.

Sampling design. About 3500 museum records for heteromyid rodents in the region of study were obtained from and verified at the University of Colorado Museum, Denver Museum of Nature and Science, Sternberg Museum of Natural History, University of Kansas Natural History Museum, and the University of Nebraska State Museum. These records included field notes, catalog data, and other specimen-based museum data. Approximately 100 additional records from publications or reliable field accounts also were included.

Specimen and environmental data were recorded for each locality of capture. Species presence or absence, location, and date of capture of each specimen were the tabulated variables from museum records. Coexistence at a given site was defined as different species captured in the same habitat and trapping session or captured in the same habitat, on consecutive trapping sessions, and by the same collector. Environmental variables included habitat type; concealment; total depth of soil; degree of rockiness; soil texture of the A, B, and C-horizons; annual precipitation; mean January temperature; mean July temperature; and annual cooling degree-days. Habitat type and concealment were categorized from descriptions in field notes, published accounts, or aerial photographs. The 12 habitat types used for analysis label Figure 1, and the five concealment classes were ranked 1-5 (no concealment to very high concealment). These habitat variables represented the physiognomy of an area, which is the scale at which small mammals seem to perceive habitat (Armstrong, 1977). Lastly, soils data were obtained from county soil surveys (USDA, Soil Conservation Service), and climate data were obtained from 30-year averages published in the NOAA, 1993 annual climate summaries for Colorado, Kansas, and



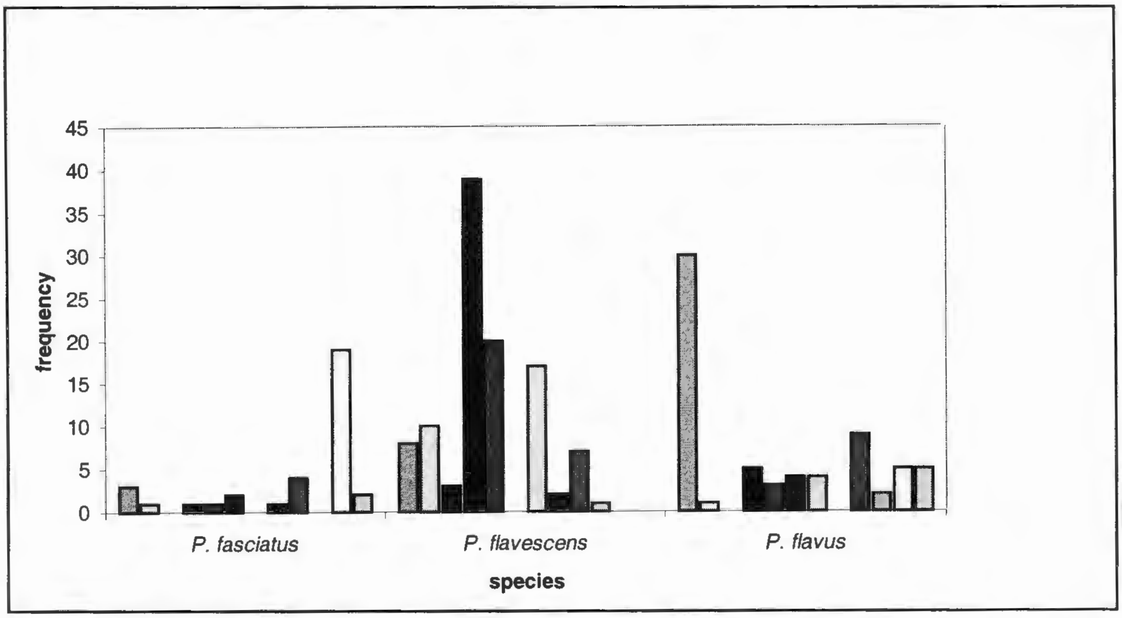


Figure 1. Bar graphs comparing frequency of habitat utilization by heteromyid rodents on the central Great Plains. Medium sized species, *Chaetodipus hispidus* and *Dipodomys ordii,* (top) and small sized species; *Perognathus fasciatus*, *Perognathus flavescens*, and *Perognathus flavus;* (bottom) are compared separately.

Nebraska. The ranked, soil texture classes used for analysis appear in Table 1.

Records that had missing or imprecise data were eliminated from subsequent analyses. This removed about half of the original database of localities, leaving 774 unique sites, 5 dependent species variables, and 11 independent environmental variables for analyses.

Coexistence and body size. The null hypothesis that species pairs of heteromyid rodents on the central Great Plains occur randomly and not accord-

Table 1. Categories and ranked values recorded in database for soil texture. Increasing values are ranked by decreasing percentage of sand and increasing percentage of clay.

Soil Texture	Class Code
sand	1
loamy sand	2
sandy loam	3
sandy clay loam	4
sandy clay	5
loam	6
clay loam	7
clay	8
silt loam	9
silt clay	10
silty clay loam	11
silt	12
gravel	13
bedrock	14

ing to different body sizes was evaluated from a subset of 468 records. These were extensively sampled sites from a zone of sympatry where at least two small-sized (<10g) and two medium-sized (35-65g) heteromyid species coexisted. Analysis of sites with just species pairs maintained independence among observations and preserved a conservative χ^2 calculation without using extensive simulations as performed by Bowers and Brown (1982). Species pairs were tabulated in a 2×2 contingency table, and the χ^2 value (ρ=0.05) was calculated using Cochran's correction for continuity.

Coexistence and habitat complexity. The contribution of habitat complexity to multi-species assemblages was evaluated by tabulating physiognomic characteristics from sites with at least three species present in the aforementioned subset of data. Factors that seem to promote coexistence of these close competitors were identified from soil surveys and descriptions in field notes. However, a statistical comparison of this data set to a sample of localities with only one species was impossible because equal sampling effort could not be estimated reliably at most sites.

Habitat occurrence. Descriptive statistics were computed for the environmental variables with the UNIVARIATE procedure in SAS (SAS institute, Inc., 1989), which also screened for normality, linearity, and incorrect data. The rockiness variable (SR) was eliminated from subsequent investigation because it had a Poisson distribution, and the habitat type variable (VT) was evaluated separately because it was a nominal variable. Their inclusion in ordination analyses can make factors incomprehensible (Tabachnick and Fidell, 1996). Consequently, two contingency tables (one 2x12 and one 3x7) were constructed and χ^2 analyses (ρ=0.05) were performed to test the null hypothesis that species of the same body size utilize the same types of habitat on the central Great Plains.

A factor analysis and logistic regression were conducted next. The factor analysis reduced the number of correlated variables into a subset of three factors, and the logistic regression evaluated how strongly each species related to the new factors and how well these predicted the distribution of each species (Cody and Smith, 1997; Tabachnick and Fidell, 1996). These analyses were performed using the FACTOR and VARIMAX functions followed by the LOGISTIC function in SAS (SAS institute, Inc., 1989). A direct logistic regression was used because there was no specificity regarding importance of factors as predictors (Tabachnick and Fidell, 1996).

RESULTS

Coexistence and Body Size. Pairs of species were present at only 19.7% (92) of the 468 extensively sampled sites. Of the 92 localities, six were occupied by two small species, 28 by the two medium-sized species, and 58 by a combination of one small and one medium-sized species. The χ^2 value with Cochran's correction for continuity equaled 6.39. This value exceeded the critical value ($\rho<0.05$); therefore, the null hypothesis was rejected.

Based on this result, it seems that locally co-occurring heteromyids on the central Great Plains pair by a differential of body size. This non-random pairing and the infrequency of multi-species assemblages (25.7%) suggest that *C. hispidus, D. ordii, P. fasciatus, P. flavescens,* and *P. flavus* compete for resources and the extent and pattern of local coexistence is quite limited. However, limited coexistence also could reflect differences in habitat occurrences by the five species, which are explored further.

Coexistence and habitat complexity. Only 6% (28) of the 468 extensively sampled localities had three or more coexisting species. These sites were most common in fencerow vegetation, rock outcrops, alluvial terraces, or combinations thereof (Table 2). To a lesser extent, they were in sand hills prairie, sand sage prairie, grazed habitats, cultivated land, or combinations thereof.

The prevalent pattern of coexistence (Table 2) was for a site to have *D. ordii* (a medium-sized, bipedal, habitat generalist) occupying open areas, *C. hispidus* (a medium-sized, quadrupedal, habitat generalist) occupying more heavily vegetated areas, and a *Perognathus* species (a small, quadrupedal, habitat specialist) also occupying more heavily vegetated areas. This orderly arrangement helped to allow coexistence without the ill effects of displacement or local extinction.

Habitat mosaics and abundant seed resources likely are the other factors that allowed for coexistence of three or more species at these localities. The sites on river deposits and rock outcrops had a variety of soil textures, soil depths, and an array of vegetation types in proximity to one another. Sand hills sites had blowouts with a variety of successional stages in proximity. Windblown seeds typically concentrate in depressions within blowouts, which strongly favor the foraging pattern and presence of *D. ordii* (Bowers, 1982; Munger et al., 1983). Sites with sand sagebrush were disturbed by farming or grazing and had abundant seed resources or high structural complexity. Cropland and fencerow localities had a wide variety of habitat types and great structural complexity in a small area, and they produced vast numbers of seeds (Choate and Terry, 1973; Jones et al., 1985), which are the dietary staple for rodents of the Heteromyidae. Four of the species in this study are known to forage on agricultural crops (Holm, 1984; Jones et al., 1985; Reed and Choate, 1986), eating waste grain, seedlings, or occasionally, planted seeds (Holm, 1984).

Habitat occurrence. Three factors were extracted in the factor analysis. Squared multiple comparisons (SMCs) of the variables for each factor indicated that the first two factors were well defined and internally consistent (Table 3), but the third one was less so, with a value of 0.68. Communality estimates were high for all but two variables (VC and TSD), which indicated that the variables were well defined by the factors overall.

The meaning of each factor was determined by the pattern of loadings for the original variables in the resultant correlation matrix after orthogonal rotation. Only variables that loaded above 0.45 were used to interpret a factor. Soil texture defined the first factor, temperature defined the second one, and annual precipitation defined the third (Table 3). The original variables were simple -- they loaded only on a single factor. Concealment (VC) and soil depth (TSD) failed to load on any factor because concealment could not be estimated adequately and because deep soils were utilized most often by each species.

The logistic regression analysis indicated that soil texture, temperature, and annual precipitation had a significant collective effect in determining the distributions of each species of heteromyid rodent. A χ^2 test ($\rho=0.05$, 3*df*) analyzed for no effect, and significant values ($\rho<0.0001$) were calculated for each of the five species (Table 4).

Table 2. Presence, absence (1, 0) at localities on the central Great Plains with three or more species of heteromyid rodent plotted against habitat physiognomy.

State	County	Location	*Chaetodipus hispidus*	*Dipodomys ordii*	*Perognathus fasciatus*	*Perognathus flavescens*	*Perognathus flavus*	Alluvial	Outcrop	Sand sage	Sand hill	Grazed	Crop	Fencerow
CO	Adams	Rocky Mountain Arsenal PD1 (T3S, R67W, SW sec 12)	1	1	0	1	0					●		●
CO	Adams	Rocky Mountain Arsenal SS2 (T3S, R66W, SW sec 8)	0	1	1	1	0			●		●		
CO	Baca	4.5 mi. S Vilas (T31S, R45W, sec 25)	1	1	0	1	0	●						
CO	Cheyenne	10 mi. S Firstview	1	1	0	0	1							●
CO	Weld	E of Barnesville (T6N, R63W sec 22)	1	1	0	1	0				●			
CO	Weld	E of Cornish (T6N, R62W sec 1)	1	1	0	1	0				●			
CO	Yuma	Bonny Reservoir (T5S, R34W, sec 10)	1	1	0	0	1	●		●		●		
CO	Yuma	Bonny Reservoir (T5S, R34W, sec 27)	1	1	0	1	0	●		●		●		
CO	Yuma	Bonny Reservoir (T5S, R34W, sec14)	0	1	0	1	1	●						
KS	Cheyenne	14.5 mi. N St. Francis	0	1	0	1	1		●					
KS	Clark	4 mi. N, 12 mi. W Ashland (T32S, R24 W, sec 19)	1	1	0	0	1		●					●
KS	Comanche	Swartz Canyon (T34S, R16W, sec 14)	1	0	0	0	1	●	●					
KS	Ellis	1 mi. S, 6 mi. W Antonino (T15S, R20W, sec 11)	1	1	0	1	0	●						
KS	Finney	11.5 mi. S, 3.5 mi. W Holcomb (T26S, R34W, S1/2 sec 4)	1	1	0	1	0			●			●	
KS	Finney	12 mi. S, 3.75 mi. W Holcomb (T26S, R34W, N1/2 sec 8)	1	1	0	1	0			●	●			●
KS	Gove	8 mi. N, 5 mi. W Healy (T15S, R30W, NW1/4 sec 31)	1	1	0	0	1		●			●		●
KS	Morton	7 mi. N, 0.5 mi. W Elkhart (T34S, R42W, sec 8)	1	1	0	1	0	●	●					
KS	Morton	Elkhart, 9 mi. N, 3 mi. E of	0	1	0	1	1	●	●					●
KS	Russell	T13S, R11W, E1/2 sec 10	1	1	0	1	0	●						
KS	Russell	T13S, R11W, NE 1/4 sec 4	1	1	0	1	0	●						●
KS	Seward	Liberal, 3 mi. NE of	1	1	0	1	0	●					●	
KS	Stanton	1 mi. N, 7.5 mi. W Manter (T19S, R43W, sec 9)	1	1	0	0	1	●						●
NE	Arthur	Arapaho Prairie, T18N, R39W, sec32	1	1	0	1	0				●			
NE	Cherry	Valentine, 4 mi. E of	1	1	0	1	0	●	●		●			
NE	Knox	5 mi. S/5.5mi S, 5 mi. W Niobrara, Bohemia Prairie WMA	1	1	0	1	0				●			
NE	Morrill	T18N, R52W, SE1/4 sec 19	1	1	1	0	0		●					
NE	Morrill	T22N, R50W, NE1/4 sec 27	1	1	0	0	1						●	
NE	Morrill	T22N, R50W, NW1/4 sec 15	1	1	0	1	1		●				●	

Table 3. Rotated factor loadings, communalities (h^2), squared multiple comparisons (SMC's), percent of variance, and percent of covariance for principal factor analysis on environmental variables. [a]Factor labels: F_1 Soil texture, F_2 Temperature, F_3 Precipitation.

Item	F_1[a]	F_2	F_3	h^2
Soil texture of A horizon (SA)	**0.89**	0.13	0.20	0.86
Soil texture of B horizon (SB)	**0.89**	0.13	0.15	0.84
Soil texture of C horizon (SC)	**0.84**	0.08	0.12	0.73
Total depth of soil (TSD)	-0.18	0.06	0.38	0.18
Concealment (VC)	0.19	-0.01	0.29	0.12
January mean temperature (MN)	-0.01	**0.61**	-0.39	0.52
July mean temperature (MX)	0.16	**0.70**	0.19	0.55
Cooling degree-days (CDD)	0.12	**0.84**	0.33	0.83
Annual precipitation (PPT)	0.24	0.24	**0.70**	0.61
SMC's of variables with each factor	0.91	0.81	0.68	
Percent of variance	0.27	0.18	0.12	
Percent of covariance	0.47	0.32	0.19	

Although soil, temperature, and precipitation contributed significantly to the distributions of the five species as a whole, association and concordance values indicated that *C. hispidus, D. ordii, P. fasciatus, P. flavescens,* and *P. flavus* varied in their response to these factors. *Perognathus fasciatus* had the highest concordance and association values (was the best classified species per set of environmental factors), whereas *D. ordii* had the lowest (was the worst classified). The remaining three species had intermediate values (Table 4). Overall, a species was better classified in the proper environment if it had a smaller geographic range and if it occupied a smaller range of soil textures and climatic conditions.

Individual evaluation of the three factors also fared well. Wald χ^2 values appear in table 4. Soil texture was a significant predictor ($\rho<0.05$) of the distributions of *C. hispidus, D. ordii, P. flavescens,* and *P. flavus*, but it failed to be significant for *P. fasciatus* ($\chi^2=3.55$; $p=0.059$). Too few records for this species were responsible for the marginal failure of the test. Temperature significantly predicted ($\rho<0.05$) the distributions of all five species, but precipitation failed to significantly predict the distribution of *P. flavescens* (Table 4) ($\chi^2=1.34$, $\rho=0.25$), which was attributable to this species being uniformly distributed across all precipitation levels between 34 and 91 cm per year. Overall, individual factors typically predicted distributions of the species.

Standardized estimate and odds ratio values determined how the distribution of each species was affected by individual factors. Odds ratios indicated the likelihood of a species being absent per unit of change within a factor, and standardized estimates showed the polarity of the relationship (Table 4). Standardized estimates for *C. hispidus* were negative in each factor, thus, specifying a distribution on loamy to silt soils (Fig. 2) in a warm, wet climate in the region. Odds ratios revealed that none of the factors defined well its range limit in the region. *Dipodomys ordii* had positive standardized estimates for soil texture and precipitation but a negative one for temperature, specifying a distribution on sandy soils (Fig. 2) in a warm, dry climate in the region. Odds ratios indicated that soil texture and precipitation but not temperature defined well its range limit in the region. All standardized estimates for *P. fasciatus* were positive, meaning it was distributed on sandy soils (Fig. 2) in a cool, dry climate in the region. Odds ratios indicated that each of the three factors affected its range limit in the region. *Perognathus flavescens* had positive standardized estimates for soil and temperature, which indicated that this species associated with sandy soils (Fig. 2) and a cool climate in the region. Odds ratios showed that

Table 4. Logistic regression analysis of distributions of heteromyid rodents on the central Great Plains as a function of soil texture (F_1)*, temperature* (F_2)*, and precipitation* (F_3)*.*

	d.f.	*Chaetodipus hispidus*	*Dipodomys ordii*	*Perognathus fasciatus*	*Perognathus flavescens*	*Perognathus flavus*
-2 log L	3	224.35 ***	114.11 ***	126.22 ***	116.86 ***	98.73 ***
Score	3	201.97 ***	106.44 ***	128.58 ***	102.08 ***	98.77 ***
Wald Chi-square						
F_1	1	79.20 ***	54.82 ***	3.55	55.88 ***	7.66 *
F_2	1	07.14 **	9.60 **	51.34 ***	21.29 ***	8.98 *
F_3	1	90.92 ***	44.76 ***	11.93 **	1.34	68.56 ***
Odds ratio[1]						
F_1	1	0.45	1.88	2.18	4.17	0.63
F_2	1	0.78	0.77	11.02	1.68	0.57
F_3	1	0.31	1.98	3.34	0.83	4.52
Standardized Estimate						
F_1	1	-0.43	0.33	0.41	0.75	-0.24
F_2	1	-0.13	-0.13	1.19	0.26	-0.28
F_3	1	-0.54	0.31	0.55	-0.09	0.69
Concordant		78.7 %	70.2 %	94.1 %	79.8 %	82.8 %
Disconcordant		21.1 %	29.4 %	5.6 %	19.7 %	16.6 %
Tied		0.2 %	0.4 %	0.3 %	0.5 %	0.6 %
Somers' D		0.58	0.41	0.89	0.60	0.66
Gamma		0.58	0.41	0.89	0.60	0.67
Tau-a		0.28	0.20	0.08	0.15	0.11
c		0.78	0.70	0.94	0.80	0.83

* $p<0.05$, ** $p<0.001$, *** $p<0.0001$

[1] probability = odds/1+odds

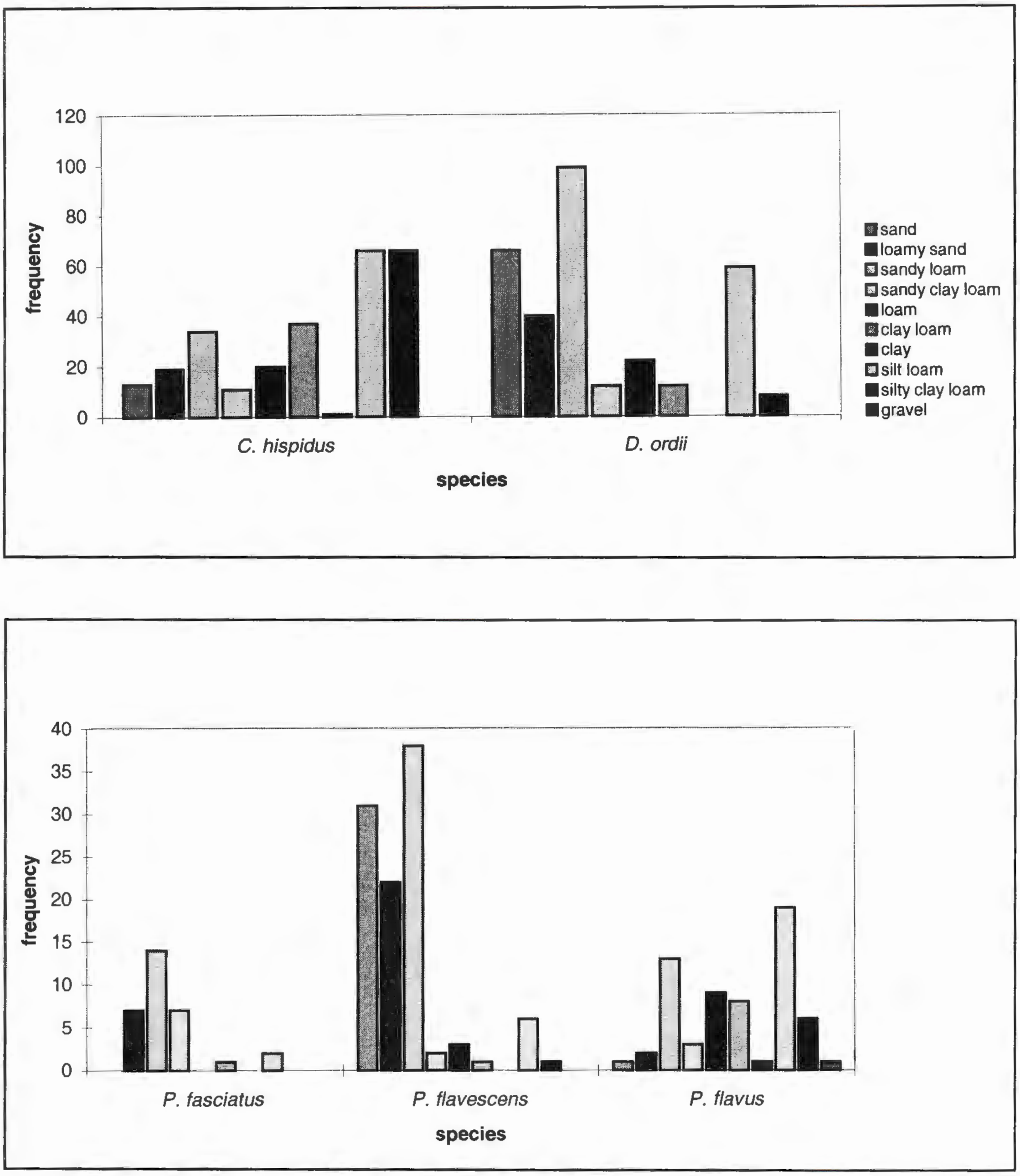


Figure 2. Bar graphs comparing frequency of soil texture utilization by heteromyid rodents on the central Great Plains. Medium sized species, *Chaetodipus hispidus* and *Dipodomys ordii,* (top) and small sized species; *Perognathus fasciatus*, *Perognathus flavescens*, and *Perognathus flavus;* (bottom) are compared separately.

only soil texture determined its distributional limit in the region. Standardized estimates for *P. flavus* indicated that this species was distributed on loamy to silt loam soils (Fig. 2) in a warm, dry climate in the region. Odds ratios indicated that precipitation was the factor that defined well its distributional limit in the region. Overall, each of the five species seemed to respond differently to environmental conditions in the region. It also needs to be noted that climate itself does not directly affect the distributions of these rodents; instead, it influences the development of major vegetation types, which in turn affects their distributions.

Habitat type. The results of the x^2 analysis indicated that similarly sized species do not occur in the same habitats. Habitat type frequencies appear in appendix B as separate contingency tables, and highly significant probabilities were calculated in each instance.

Although distinct differences existed among a primary group of habitat types, there was overlap among the array of habitat types frequented by these species. Among the five species, *C. hispidus* and *D. ordii* frequented all twelve recognized habitat types, *P. flavus* occurred in ten, and *P. fasciatus* and *P. flavescens* utilized nine each (Fig. 1). *Chaetodipus hispidus* was a habitat generalist, utilizing most often (including 80% of the observations) mixed-grass prairie, weedy forb, short-grass prairie, tall-grass prairie, sand hills grassland, and cropland. *Dipodomys ordii* and *P. flavus* were more specialized. *Dipodomys ordii* occurred most often in bare ground, short-grass prairie, weedy forb, sand hills grassland, and sand sage grassland, whereas *P. flavus* occurred most often in short-grass prairie, bare ground, sand hills grassland, rock outcrop, and pinion-juniper woodland. *Perognathus flavescens* occurred most often in sand hills grassland, sand sage grassland, weedy forb, and mixed-grass prairie. Lastly, *P. fasciatus* occurred most often in coniferous woodland, bare ground, short-grass prairie, and other shrub; however, more than half the sites were located in a specific type of coniferous woodland -- ponderosa pine savanna. Overall, these rodent species seemed to share an affinity for moderately disturbed sites that were dominated by grasses or herbaceous vegetation, but each species responded uniquely to broad environmental regimes within the region.

DISCUSSION

The distributions of *C. hispidus, D. ordii, P. fasciatus, P. flavescens,* and *P. flavus* on the central Great Plains are largely individualistic (Gleason, 1926). This is evident because the five species are largely allopatric and use different habitats at a local scale. However, the species are adaptable and overlap in their associations with habitat type, substrate, and climate in the region. These wide tolerances allow for local coexistence where habitat mosaics and microhabitat diversity exist or where abundant food resources are available, but where the species coexist, they assemble according to a size differential and a regular pattern, which is indicative of interspecific competition affecting these associations.

Numerous authors have found that locally sympatric, granivorous rodents in desert communities also assembled in local habitats by a size differential, and they concluded that this was evidence of interspecific competition structuring this portion of the community (Bowers and Brown, 1982: Brown, 1975; Brown and Harney, 1993; Price and Brown, 1983). The prevailing hypothesis is that this non-random pairing reduces competition and allows for local coexistence by combining species that will partition similar scarce resources in the most efficient manner possible (Brown and Harney, 1993).

These kinds of studies offer only indirect evidence of interspecific competition, but direct experiments have indicated that resource or interference competition indeed exists among species of the Heteromyidae. Alcoze and Zimmerman (1973) measured significant overlap in the diets of *C. hispidus* and *D. ordii* in the mesquite plains of Texas, but they found that these similarly sized species avoided competitive exclusion by foraging in different areas with different soil textures. In New Mexico, Lemen and Rosenzweig (1978) discovered that *P. flavus* and *D. ordii* avoided competitive exclusion by utilizing different microhabitats according to their mode of locomotion. The quadrupedal *P. flavus* confined its foraging to well-vegetated areas, whereas the bipedal *D. ordii* foraged in open areas. These foraging patterns are consistent with those found throughout the family (Kotler and Brown; 1988, Thompson, 1982a). Additional studies, in which the largest or most behaviorally dominant competitor was removed, showed a significant increase in the abundance of subordinate heteromyid species or altered their patterns of habitat use (Bowers and Brown, 1992; Heske et al., 1994; Lemen and Freeman, 1983; Rebar and Conley, 1983). Interspecific competition seems to influence similarly local distributions of the species of Heteromyidae on the central Great Plains.

Species rich areas in this study did support the assemblage rule proposed by Brown (1987) in that they appeared to be extremely productive or had a mosaic of structural types and vegetation types in proximity. These factors likely allowed for coexistence by effectively eliminating resource competition (Rosenzweig and Winakur, 1969; Brown and Lieberman, 1973). It is not understood how increased primary productivity increases species diversity, rather than simply promoting larger populations of fewer species (Brown and Harney, 1993), but increased food resources might decrease time and space required for foraging, thus decreasing encounters with individuals of all species. With fewer encounters, interspecific aggression would lessen and normally competitive species could coexist without expulsion of one or more of the competitors. On the other hand, it is better understood how habitat heterogeneity affects diversity. Brown and Harney (1993) suggested that heterogeneous habitats provide greater microhabitat divergence, which increases diversity by allowing coexistence of ecologically related species of different functional groups. They based their supposition on empirical studies in which manipulation of vegetation structure altered species composition and abundance of heteromyids (Price, 1978; Rosenzweig, 1973; Thompson, 1982b). Kotler and Brown (1988) presented observational evidence that species similar in size and morphology coexist by macrohabitat selection and habitat selection within a mosaic. It seems likely that a combination of these factors is operative with respect to multi-species assemblages of heteromyids on the central Great Plains. However, this does not explain why most sites within the region had only one species.

Distinct primary habitat use by the five species and structurally simple habitats overall may account for this. North American deserts typically have a dichotomously structured microhabitat of clusters of dense vegetation spaced by open, unvegetated substrate (Brown and Harney, 1993; Kotler and Brown, 1988) in which larger bipedal species frequent open areas and smaller quadrupedal species frequent brushy areas without competitive exclusion of either species (Kotler and Brown, 1988). Temperate grasslands, on the other hand, typically have a structural uniformity (Boone, 1995; Kaufman and Kaufman, 1990), with habitats usually being open or vegetated but not both. Therefore, a given grassland site ordinarily can support only one species of heteromyid rodent. However, heterogeneity exists at a macrohabitat level within these grasslands (Boone, 1995; Grant and Birney, 1979), which allows for regional coexistence (but not necessarily local coexistence) of the five heteromyids on the central Great Plains. Conditions that bring a variety of macrohabitats in proximity or that produce a dichotomously structured microhabitat would permit local coexistence as well.

Grazed sand sagebrush grassland is an example in which the structurally uniform habitat of mixed-grasses and shrubs is transformed it into microhabitats of shrubs spaced by open substrate (Moulton et al., 1981; Mutel and Emerick, 1984). Such sites often have an increased number of species of heteromyid rodents. For example, Boone (1995) captured only *P. flavescens* in undisturbed sand sage grassland in Adams County, Colorado. But grazed sand sage grassland in Yuma County, Colorado supported three heteromyid species: *D. ordii,* which typically occupies open habitats; *P. flavus*, which is common in short-grass habitats; and *P. flavescens*, which is a denizen of sand sage grassland (Moulton et al., 1981). Ecological and geographical distributions on the central Great Plains are discussed in further detail for each species in this investigation.

Chaetodipus hispidus. — The hispid pocket mouse is a habitat generalist that utilizes almost any habitat and substrate on the central Great Plains, given that herbaceous rather than woody plants dominate the locality. It occurred in all habitat types studied but was most common within mixed-grass, weedy forb, short-grass, and tall-grass vegetation (Fig. 1). This species commonly associated with sunflower (*Helianthus sp.*), western ragweed (*Ambrosia psylostachia*), Russian thistle (*Salsola iberica*), Kochia (*Kochia scoparia*), big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), blue grama (*Bouteloua gracilis*), buffalograss (*Buchloe dactyloides*), cheat grass (*Bromus mollis*), and western wheat grass (*Agrypogon smithii*) at these sites. This was the only species of the five that was captured in introduced stands of smooth brome (*Bromus inermis*) and a cultivated cedar forest (Manning and Geluso, 1989). Prairie dog towns and rock outcrops were among the more unique habitats that could support populations of *C. hispidus*. The hispid pocket mouse occurred most often on deep silt loam and silty clay loam soils (Fig. 2) with less than 35% clay. The hispid pocket mouse often coexisted with *D. ordii* and *P. flavescens* in disturbed, sand sagebrush, and sand hills habitats.

Chaetodipus hispidus is distributed throughout the central Great Plains, but it seemed most common in the mixed-grass and tall-grass regions in Kansas and Nebraska (Fig. 3). It was present but less common in the short-grass region, but the species was uncommon in sand hills regions of Nebraska, the Denver Basin, and along the Arkansas River in Kansas. Overall, the range of *C. hispidus* probably is not limited by any of the heteromyids in this region, but it could be limited locally by competition with the similarly sized *D. ordii* in some habitats. The distribution of the hispid pocket mouse is limited along the Front Range by unsuitable habitat at the foot of the Rocky Mountains. Its eastern limit in Kansas likely is determined by the presence of oak woodland in the Chautauqua Hills and oak-hickory forest near the state's eastern border (Fig. 3).

The eastern limit of *C. hispidus* in Nebraska seemingly is not related to abiotic factors. Suitable climate, habitat, and soils exist beyond its present range limit in the Missouri River lowlands. Furthermore, *P. flavescens* occurs (but is extremely rare) beyond that limit, and *C. hispidus* occurred 660 km farther to the east during the late Wisconsinan-early Holocene (Schmidly et al., 1993; Wilson et al., 1996). Therefore, the Missouri River itself is not an insurmountable barrier. It is possible that competition with a non-heteromyid rodent, *Zapus hudsonius,* prevents the hispid pocket mouse from dispersing to the east. *Zapus hudsonius*, a semi-quadrupedal representative of the family Dipodidae, has similar habits, a comparable diet, and is of similar (albeit slightly smaller) size (Krutzsch, 1954; Quimby, 1951). Accordingly, these two species likely are close competitors, and *Z. hudsonius*, a species best adapted to utilizing mesic grassland habitats (Choate et al., 1991; Tester et al., 1993), may out compete in the region *C. hispidus*, a species best adapted to utilizing xeric grassland habitats (Kaufman and Fleharty, 1974; Kaufman et al., 1993).

Jones (1964) was of the opinion that the influences of man on the Missouri River are the present factors that prevent the hispid pocket mouse from ranging eastward. Specifically, efforts to channel, straighten, and dam this river makes it more of an impenetrable barrier to dispersal.

Dipodomys ordii.— Ord's kangaroo rat also is a habitat generalist that occurred in all habitat types studied and on all soil textures except pure clay. Nonetheless, this species was most common in bare ground, short-grass, weedy forb, sand hills, and sand sage habitats (Fig. 1) and utilized almost exclusively deep sandy substrates (Fig. 2) with less than 20% clay and more than 50% sand. Bare ground sites included blowouts, dry washes, sandbars, unpaved roads, and plowed fields. Ord's kangaroo rat typically utilized sparsely vegetated parts of other habitat types that it frequented, which is consistent with its bipedal mode of locomotion (Bartholomew and Caswell, 1951; Brylski, 1993), but this study could not resolve always this scale of habitat use given that it was limited to habitat descriptions in field notes. For example, the first author has captured *D. ordii* in dense stands of needle and thread grass (*Stipa comata*) but only along the runways of thirteen-lined ground squirrels. Such a site was recorded as sand hills grassland, but Ord's kangaroo rat was utilizing only unvegetated portions of the habitat. Clearly, *D. ordii* is an opportunistic species that can widely utilize its surrounding environment: Testament to this statement, the species has been captured even among rock outcrops or boulder fields on the central Great Plains. This adaptability may explain why this species was found often in seemingly unsatisfactory habitats and indicates that habitat type is of little consequence to this species. Instead, substrate and habitat structure are most important.

Ord's kangaroo rat was captured with each of the remaining heteromyid species in this region. It occurred most often with *C. hispidus* and *P. flavescens* in disturbed sand sage and sand hills grassland, and it occurred less often with *P. flavus* in short-grass habitats.

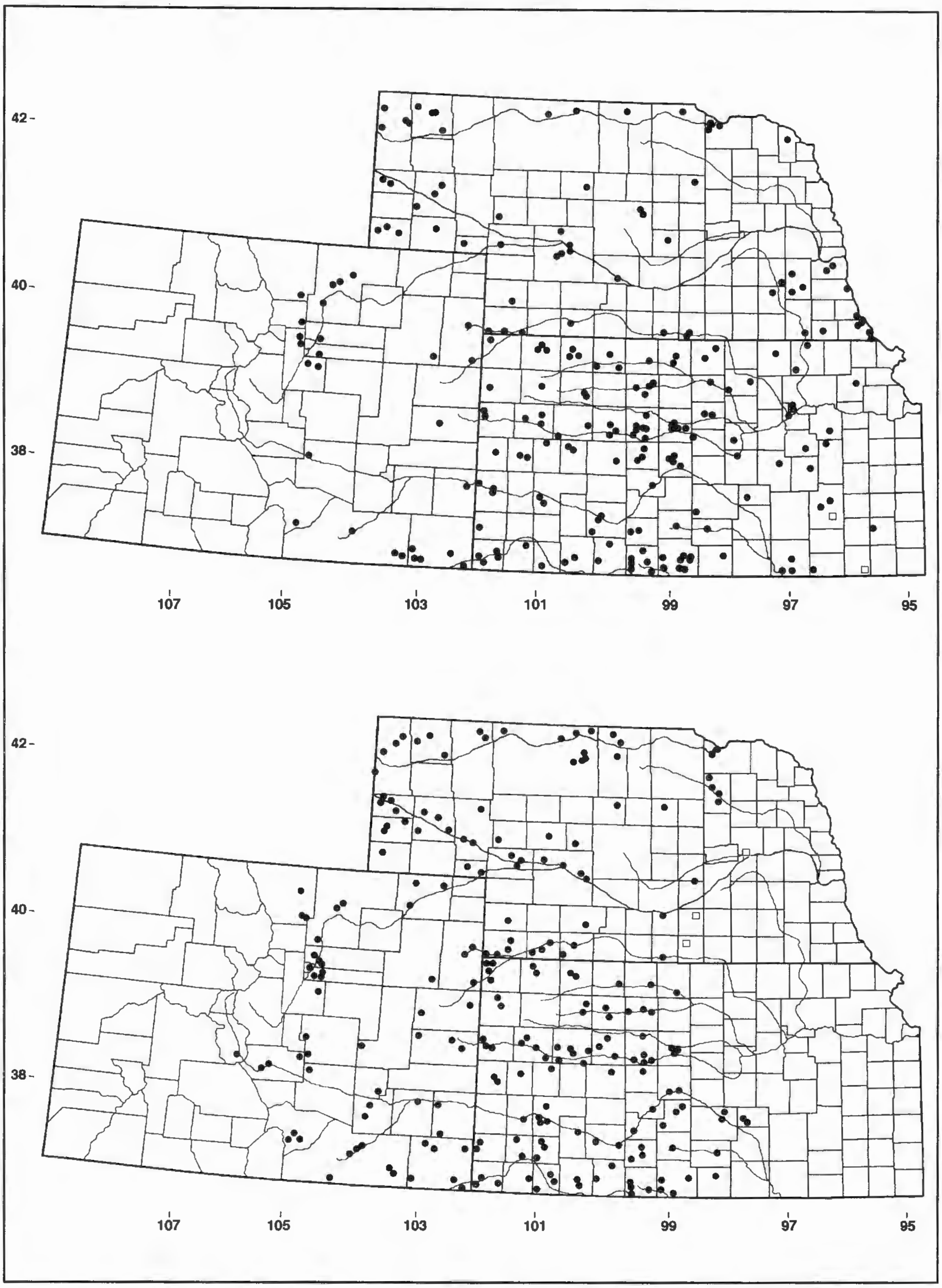


Figure 3. Distribution maps of *Chaetodipus hispidus* (top) and *Dipodomys ordii* (bottom) on the central Great Plains. Closed circles represent examined records, and open squares represent unexamined records.

Ord's kangaroo rat is distributed throughout most of the central Great Plains (Fig. 3). *Dipodomys ordii* is the largest and behaviorally dominant species of the five studied, and no evidence indicated that its range is limited by other heteromyid species in the region. Its western boundary is limited by unsuitable habitat at the Front Range and upper Arkansas River valley in Colorado. It was common in the Nebraska Sand Hills and its limit there coincides with the eastern limit of this region, where soil and vegetation both become inhospitable. This species is common throughout the short-grass region in Kansas but is increasingly confined to alluvial deposits in the mixed-grass prairie. The Flint Hills and eastern Smoky Hills seem to form impenetrable barriers to *D. ordii* where rocky uplands, woody vegetation in riparian areas, or soils with high clay content prevail. Both soil texture and low precipitation predicted distribution of Ord's kangaroo rat within the region. These variables are coincidental and indicative of the prevalence of aeolian and alluvial sands (the substrate utilized most often by *D. ordii*) in the more arid western, central Great Plains.

Perognathus fasciatus. — Within the region of investigation, the olive-backed pocket mouse was closely associated with ponderosa pine savanna (figure 1), but it apparently has a wider ecological distribution in Wyoming (Clark and Stromberg, 1987; Maxwell and Brown, 1968). On the central Great Plains, *P. fasciatus* utilized substrates with both shallow and deep sandy soils composed of less than 20% clay and more than 60% sand (Fig. 2). On the central Great Plains, stands of ponderosa pine (*Pinus ponderosa)* grow on outcrops of sandstone with a thin mantle of sandy soil, and grassland grows nearby where soils are more developed. Sand specialists, montane species, and short-grass species dominate the grassland part of this habitat in Colorado. In Nebraska, sand specialists and tall grass species dominate (Keeler et al., 1980). As this habitat becomes more disturbed, short-grass species and yucca dominate, and annual and exotic species overtake the most highly disturbed sites (Keeler et al., 1980; Mutel and Emerick, 1984). *Perognathus fasciatus* usually was found in undisturbed or slightly disturbed habitat but also was caught in cropland and along unpaved roads.

Only four examined records of *P. fasciatus* in Colorado occurred more than 9 km from the nearest stand of ponderosa. Two specimens were captured about 20 km east of Fort Collins (Armstrong, 1972); and the first author captured and released two individuals in southern Adams County. Both sites are approximately 30 km from the nearest stand of ponderosa, and they are at the periphery of the sand hills of the South Platte River where substrate is more variable and *P. flavescens* is less common.

Local coexistence is rare between the olive-backed pocket mouse and the other heteromyid species on the central Great Plains. The species has been recorded with *P. flavescens* at just three localities; Jones (1964) described two of these in Nebraska and the other in Adams County, Colorado is described above. Interspecific competition may maintain local allopatry and sharp range limits between the two because they are sister species (Schmidly et al., 1993) that share exceedingly similar habitat proclivities. Ecological separation is, perhaps, the main factor that governs local allopatry between *P. fasciatus* and the three remaining species.

The olive-backed pocket mouse is at its absolute southern and eastern limit within this region. Its range in Colorado is restricted to a narrow band along the Front Range, south to the Wet Mountains, and in Nebraska, *P. fasciatus* occurs along and near the Wildcat Hills, the Pine Ridge, and the Crookston Table, (Fig. 4). Its western limit in Colorado is determined by unsuitable soil and vegetation in the transition zone. Climate and substrates that limit the development of ponderosa savanna and competition with *P. flavescens* and *P. flavus* probably regulate its range limits in Nebraska and its eastern boundary in Colorado.

Although the olive-backed pocket mouse is rare in Nebraska, conservation of the species is probably adequate because most of its available habitat lies in preserves, urban development is not prevalent within its range, and much of the habitat it utilizes is unsuitable for farming. But the habitat of *P. fasciatus* in Colorado is protected poorly, and most of it is being lost irreplaceably and rapidly to urban development along the Front Range. Further study of this species and protection of its habitat in Colorado are needed urgently. Conservation status of the other four heteromyid species is probably adequate at this time.

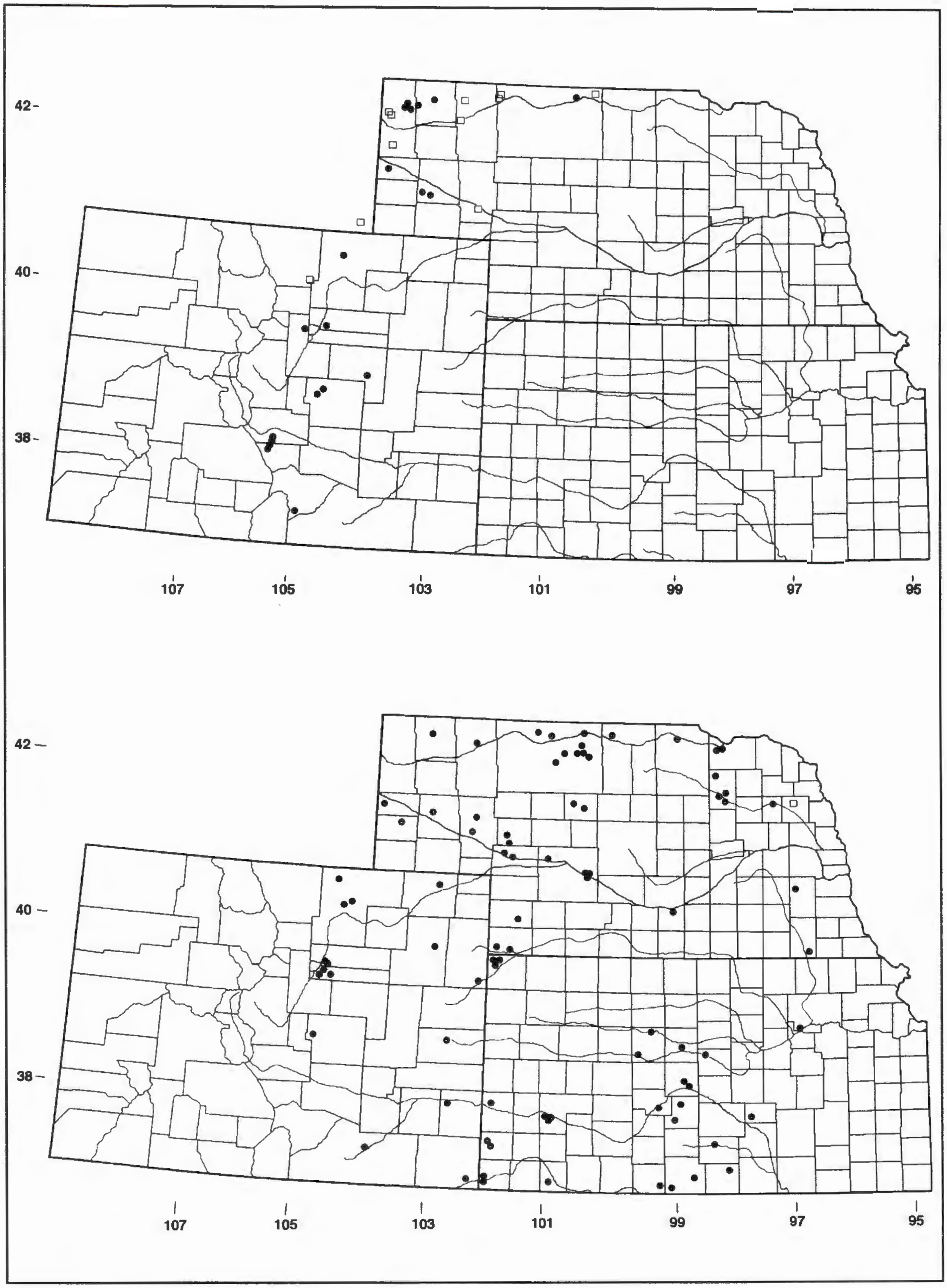


Figure 4. Distribution maps of *Perognathus fasciatus* (top) and *Perognathus flavescens* (bottom) on the central Great Plains. Closed circles represent examined records, and open squares represent unexamined records.

***Perognathus flavescens*.**— The plains pocket mouse occurred in most of the habitat types in this study, but it overwhelmingly utilized sand hills and sand sagebrush grasslands (Fig. 1) with deep sandy soils (Fig. 2) composed of less than 20% clay and more than 60% sand. *Perognathus flavesces* coexisted with *D. ordii* and *C. hispidus* in disturbed versions of these habitats. The plains pocket mouse also was common in mixed-grass and disturbed herbaceous vegetation. Recent publications support these apparent preferences (Baumann, 1982; Manning and Geluso, 1989; Reed and Choate, 1986), yet this is the first quantification of its habitat use.

Distribution of the plains pocket mouse was similar to that of *D. ordii* (Fig. 4). It was most common along the sand hills of the Arkansas River in Kansas and in the Nebraska Sand Hills; however, unlike *D. ordii,* it ranged into the loess hills and scattered sand hills of eastern Nebraska, Missouri, and Iowa (Wilson et al, 1996). The western limit of *P. flavescens* in Colorado and western Nebraska likely is determined by competition with *P. fasciatus* and unsuitable soils near the Front Range. This species, is widespread in Colorado but becomes confined to alluvial deposits in the mixed-grass region of Kansas. A decrease in the prevalence of aeolian sand from west to east seems responsible for this range constriction on the central Great Plains. The easternmost record in Kansas is on sandy alluvium near the confluence of the Smoky Hill and Republican rivers in Riley County (Pitts and Choate, 1987). As for *D. ordii*, the Flint Hills beyond this locality were an absolute barrier to dispersal because of a lack of deep sandy soils. Soil texture effectively predicted distribution, but climate did not.

***Perognathus flavus*.**— The silky pocket mouse is a moderate habitat specialist and a soils generalist that utilized most of the habitat types and a wide array of shallow and deep, loamy soils composed of less than 35% clay (Fig. 2) in this study. But *P. flavus* most often occupied short-grass prairie sites (Fig. 1) dominated by buffalograss (*buchloe dactyloides*), grama grasses (*Bouteloua sp.*), western wheat grass (*Agropyron smithii*), and occasionally cholla cactus *(Opuntia imbricata)* or yucca (*Yucca glauca*). It was captured to a lesser extent in mixed-grass prairie, sand sagebrush, weedy forb, and bare ground habitats. This species occurred infrequently in rock outcrops and piñon juniper habitats. Low precipitation was a good predictor of regional distribution but soil texture was not, which reflects the distribution of short-grass prairie and the occurrence of the silky pocket mouse on a wide variety of substrates.

Perognathus flavus commonly was captured only with *D. ordii* and occasionally was found with *C. hispidus*. They coexisted in short-grass prairie, sagebrush grasslands, and habitats with sparse vegetation. Utilization of largely different habitat, substrates, and interspecific competition probably made this species locally allopatric with *P. fasciatus* and *P. flavescens*.

The silky pocket mouse was distributed throughout the short-grass zone, but it was most common south of the Arkansas River (Fig. 5). *Perognathus flavus* also was common along the chalk bluffs (badlands) of western Kansas and Wildcat Hills in Nebraska. This species occurred but was uncommon in the western half of the Nebraska Sand Hills. Its presence there might be a recent event influenced by intense grazing and increased development of croplands in the last 50 years. There were no records of the silky pocket mouse in the Nebraska Sand Hills before the late 1950's, and these disturbances may have altered vegetation structure and species composition throughout large parts of that region to a pattern more similar to short-grass prairie (Moulton et al., 1981; Mutel and Emerick, 1984). This may have expanded the range of *P. flavus* by making portions of the region less suitable for *P. flavescens* (Reynolds, 1958), or increased the likelihood of coexistence by creating a greater structural diversity among microhabitats (Kotler and Brown, 1988).

Range limits elsewhere more likely are determined by environmental conditions rather than interspecific competition. Distribution of *P. flavus* in Colorado is limited by unsuitable habitat at the transition zone along the Front Range and Sangre de Cristo Mountains. *Perognathus flavus* occurs to the eastern limit of the short-grass prairie in Kansas. The easternmost records are confined to two peninsulas of short-grass prairie along the Saline River in Ellis County (Choate and Fleharty, 1975) and along the Smoky Hill River in Trego County. Shale and limestone outcrops on bluffs above these rivers have drainage and water availability regimes that presently support short-grass species. The

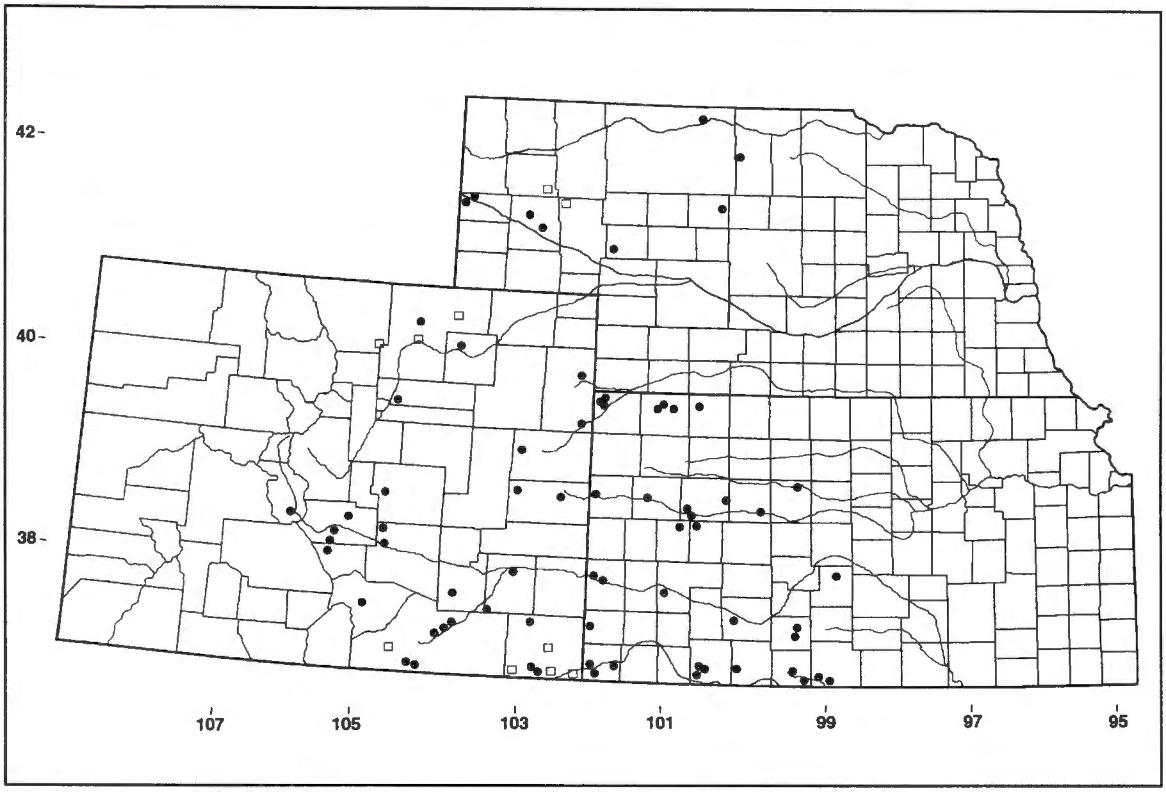


Figure 5. Distribution map of *Perognathus flavus* on the central Great Plains. Closed circles represent examined records, and open squares represent unexamined records.

silky pocket mouse occurred in Riley County (200 km farther east) in the late 19th century (Bee et al., 1981), but the suppression of fire and extirpation of bison has allowed eastern deciduous forest to encroach upon the area and eliminate eastern populations of the species. Prior to settlement, under the influence of heavy grazing by bison and natural fires, peninsular shortgrass prairie extended almost to Missouri (Fleharty, 1995) and populations of silky pocket mice may have persisted for several decades after settlement of northeastern Kansas.

While utmost care was taken throughout this investigation, some errors may have affected results. Some of the sites where animals were trapped may not realistically measure habitat use; the individual may have been passing through rather than foraging or living in that habitat (Kotler, 1985). Furthermore, habitat descriptions were difficult to standardize because many individuals made them. Additional field sampling could have resulted in better classification of habitat use, and field sampling in distribution gaps would have had the greatest effect in improving the overall data analysis (Eberhardt and Thomas, 1991). Despite these shortcomings, the large sample size minimized sources of error overall.

These results hopefully will inspire additional investigations into the distributions of the species of Heteromyidae on the central Great Plains. Most importantly, the conservation status of *P. fasciatus* urgently needs direct investigation in Colorado, and a conservation plan for the species needs to be developed there. Furthermore, experiments involving diversity patterns in complex versus simple habitats should be undertaken, and gaps in collections need to be addressed in northwestern Nebraska and eastern Colorado for Ord's kangaroo rat and the hispid pocket mouse and for the *Perognathus* species throughout the region.

ACKNOWLEDGMENTS

We are indebted to a number of people for the fruition of this project. T. Wenke, E. Fleharty, and R. Nicholson provided numerous, helpful comments. J. Boone assisted with the multivariate statistical analyses. We also thank the museum personnel who gave access to their collections and field records. Tom Labedz at the University of Nebraska State Museum was especially helpful in this regard.

LITERATURE CITED

Alcoze, T.M., and E.G. Zimmerman. 1973. Food habits and dietary overlap of two heteromyid rodents from the mesquite plains of Texas. Journal of Mammalogy, 54:900-908.

Armstrong, D.M. 1972. Distribution of mammals in Colorado. Monograph of the Museum of Natural History, The University of Kansas, 3:1-415.

Armstrong, D.M. 1977. Ecological distribution of small mammals in the upper Williams Fork Basin, Grand County, Colorado. Southwestern Naturalist, 22:289-304.

Bartholomew, G.A., and H.H. Caswell. 1951. Locomotion in kangaroo rats and its adaptive significance. Journal of Mammalogy, 32:155-169.

Baumann, W.L, Jr. 1982. Microhabitat use in three species of rodent on a Nebraska Sandhills prairie. M.S. thesis, University of Nebraska, Lincoln, 80 pp.

Bee, J.W., G. Glass, R.S. Hoffmann, and R.R. Patterson. 1981. Mammals in Kansas. Public Education Series, University of Kansas Museum of Natural History, 7:1-300.

Best, T.L., and M.P. Skupski. 1994. *Perognathus flavus*. Mammalian Species, 471:1-10.

Boone, J.D. 1995. Contingencies in the habitat relationships of prairie rodents: indirect effects, interspecific competition, and spatial scale. Ph.D. thesis, the University of Colorado, Boulder, 122 pp.

Bowers, M.A. 1982. Foraging behavior of heteromyid rodents: field evidence for resource partitioning. Journal of Mammalogy, 63: 361-367.

Bowers, M.A., and J.H. Brown. 1982. Body size and coexistence in desert rodents: chance or community structure? Ecology, 63:391-400.

Bowers, M.A., and J.H. Brown. 1992. Structure in a desert rodent community: use of space around *Dipodomys spectabilis* mounds. Oecologia, 92:242-249.

Brown, J.H. 1975. Geographical ecology of desert rodents. Pp.315-341, *in* Ecology and evolution of communities (M.L. Cody and J.M. Diamond, eds.). Belknap Press, Cambridge, Massachusetts, 545 pp.

Brown, J.H. 1987. Variation in desert rodent guilds: patterns, processes, and Scales. Pp. 181-197, *in* Organization of communities: past and present (J. Gee and P. Giller, eds.). 27th Symposium of the British Ecological society, Oxford, Blackwell Scientific Publications, 576 pp.

Brown, J.H., and B.A. Harney. 1993. Population and community ecology of heteromyid rodents in temperate habitats. Pp. 618-651, *in* Biology of the Heteromyidae (H.H. Genoways and J.H. Brown, eds.). Special Publication, American Society of Mammalogists, 10:1-719.

Brown, J.H., and M. Kurzius. 1989. Spatial and temporal variation in guilds of North American granivorous desert rodents. Pp. 71-89, *in* Patterns in the structure of mammalian communities (D.W. Morris, Z. Abramsky, B.J. Fox, and M.R. Willig, eds.). The Museum, Texas Tech University, 28:1-266.

Brown, J.H., and G.A. Lieberman. 1973. Resource utilization and coexistence of seed-eating desert rodents in sand dune habitats. Ecology, 54:789-797.

Brylski, P. 1993. The evolutionary morphology of heteromyids. Pp. 357-385, *in* Biology of the Heteromyidae (H.H. Genoways and J.H. Brown, eds.). Special Publication, American Society of Mammalogists, 10:1-719.

Choate, J.R., and E.D. Fleharty. 1975. Synopsis of native, Recent mammals of Ellis County, Kansas. Occasional Papers, Museum, Texas Tech University, 37:1-79.

Choate, J.R., D.W. Moore, and J.K. Frey. 1991. Dispersal of the meadow jumping mouse in northern Kansas. Prairie Naturalist, 23:127-130.

Choate, J.R., and D.M. Terry. 1974. Observations on habitat preference of *Onychomys leucogaster* (Rodentia: Muridae) on the central Great Plains. Transactions of the Kansas Academy of Science, 76:263-266.

Clark, T.W., and M.R. Stromberg. 1987. Mammals in Wyoming. Public Education Series, University of Kansas Museum of Natural History, 10:1-314.

Cockrum, E.L. 1952. Mammals of Kansas. University of Kansas Publications, Museum of Natural History, 7:1-303.

Cody, R.P., and J.K. Smith. 1997. Applied statistics and the SAS programming language. Simon and Schuster, Upper Saddle River, New Jersey, 445 pp.

Dalquest, W.W., F.B. Stangl, Jr., and J.K. Jones, Jr. 1990. Mammalian zoogeography of a Rocky Mountain-Great Plains interface in New Mexico, Oklahoma, and Texas. Special Publications, Museum, Texas Tech University, 34:1-78.

Eberhardt, L.L., and J.M. Thomas. 1991. Designing environmental field studies. Ecology, 61:53-73.

Flake, L.D. 1973. Food habits of four species of rodent on a short grass prairie in Colorado. Journal of Mammalogy, 54:636-647.

Fitzgerald, J.P., C.A. Meaney, and D.M. Armstrong. 1994. Mammals of Colorado. Denver Museum of Natural History and University Presses of Colorado, 467 pp.

Flehearty, E.D. 1995. Wild animals and settlers on the Great Plains. University of Oklahoma Press, Norman and London, xvii+316.

French, A.R. 1993. Physiological ecology of heteromyids: economics of energy and water utilization. Pp. 509-538, *in* Biology of the Heteromyidae (H.H. Genoways and J.H. Brown, eds.). Special Publication, American Society of Mammalogists, 10:1-719.

Garrison, T.E., and T.L. Best. 1990. *Dipodomys ordii*. Mammalian Species, 353:1-10. Gause, G.F. 1934. The struggle for existence. Macmillan (Hafner Press), New York. (Reprinted 1964).

Gleason, H.A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Club, 53:7-26.

Grant, W.E., and E.C. Birney. 1979. Small mammal community structure in North American grasslands. Journal of Mammalogy, 60:23-36.

Hall, E.R. 1981. The mammals of North America. 1981. John Wiley & Sons, 2nd ed., 1:1-600 + 90, 2:601-1181 + 90.

Heske, E.J., J.H. Brown, and S. Mistry. 1994. Long-term experimental study of a Chihuahuan Desert rodent community: 13 years of competition. Ecology, 75:438-445.

Holm, K.E. 1984. Small mammal populations and rodent damage in Nebraska no-tillage crop fields. M.S. thesis, University of Nebraska, Lincoln, 56 pp.

Jones, J.K., Jr. 1964. Distribution and Taxonomy of Mammals of Nebraska. University of Kansas Publications, Museum of Natural History, 6:1-356+4.

Jones, J.K., Jr., D.M. Armstrong, and J.R. Choate. 1985. Guide to the mammals of the Plain States. University of Nebraska Press, Lincoln, 371 pp.

Jones, J.K., Jr., D.M. Armstrong, R.S. Hoffmann, and C. Jones. 1983. Mammals of the northern Great Plains. University of Nebraska Press, Lincoln, 379 pp.

Karl, M.G 1986. Control methods and management for black-tailed prairie dogs (*Cynomys ludovicianus*) in northwestern Kansas. M.S. thesis, Fort Hays State University, 59 pp.

Kaufman, D.W., and E.D. Fleharty. 1974. Habitat selection by nine species of rodents in north-central Kansas. Southwestern Naturalist, 18:443-452.

Kaufman, D.W., B.K. Clark, and G. A. Kaufman. 1990. Habitat breadth of nongame rodents in the mixed-grass prairie region of north central Kansas. Prairie Naturalist, 22:19-26.

Kaufman, D.W., and G. Kaufman. 1982. Effect of moonlight on activity and microhabitat use by Ord's kangaroo rat (*Dipodomys ordii*). Journal of Mammalogy, 63:309-312.

Kaufman, D.W., and G. A. Kaufman. 1990. Influence of plant litter on patch use by foraging *Peromyscus maniculatus* and *Reithrodontomys megalotis*. American Midland Naturalist, 124:195-198.

Kaufman, D.W., and G. A. Kaufman, and E.J. Fink. 1993. Small mammals of wooded habitats of the Konza Prairie Research Natural Area, Kansas. Prairie Naturalist, 25:27-32.

Keeler, K.H., A..T. Harrison, and L.S. Vescio. 1980. The flora and sandhills prairie communities of Arapaho Prairie, Arthur County, Nebraska. Prairie Naturalist, 12:65-78.

Kotler, B.P., and J.S. Brown. 1988. Environmental heterogeneity and the coexistence of desert rodents. Annual Review of Ecology and Systematics, 19:281-307.

Kotler, B.P. 1985. Microhabitat utilization in desert rodents: a comparison of two methods of measurement. Journal of Mammalogy, 66:374-378.

Krutzsch, P.H. 1954. North American jumping mice (genus *Zapus*). University of Kansas Publications, Museum of Natural History, 7:349-472.

Langford, A. 1983. Pattern of nocturnal activity of male *Dipodomys ordii* (Heteromyidae). Southwestern Naturalist, 28:341-346.

Lemen, C., and P.W. Freeman. 1983. Quantification of competition among coexisting heteromyids in the Southwest. Southwestern Naturalist, 28:41-46.

Lemen, C.A., and M.L. Rosenzweig. 1978. Microhabitat selection in two species of heteromyid rodents. Oecologia, 33:127-135.

Manning, R.W., and K.N. Geluso. 1989. Habitat utilization of mammals in a man-made forest in the sand hill region of Nebraska. Occasional Papers, Museum, Texas Tech University, 131:1-34.

Manning, R.W., and J.K. Jones, Jr. 1988. *Perognathus fasciatus*. Mammalian Species, 303:1-4.

Maxwell, M.H., and L.N. Brown. 1968. Ecological distribution of rodents on the High Plains of eastern Wyoming. Southwestern Naturalist, 13:143-158.

Mohamed, R.M. 1989. Ecology and biology of *Perognathus* species in a grassland ecosystem in northeastern Colorado. Unpublished Ph.D.

dissertation, University of Northern Colorado, Greeley, 177 pp.Monk, R.R., and J.K. Jones, Jr. 1996. *Perognathus flavescens*. Mammalian Species, 525:pp. 1-4.

Moulton, M.P., J.R. Choate, S.J. Bissell, and R.A. Nicholson. 1981. Associations of small mammals on the central High Plains of eastern Colorado. Southwestern Naturalist, 26:53-57.

Munger, J.C., M.A. Bowers, and W.T. Jones. 1983. Desert rodent populations: factors affecting abundance, distribution, and genetic structure. Great Basin Naturalist Memoirs, 7:91-115.

Mutel, C.F., and J.C. Emerick. 1984. From grassland to glacier: the natural history of Colorado. Johnson Publishing Company, Boulder, CO, 238 pp.

Paulson, D.D. 1988. *Chaetodipus hispidus*. Mammalian Species, 320:1-4. Pitts, R.M., and J.R. Choate. 1987. The plains pocket mouse in eastern Kansas. Prairie Naturalist, 19:263.

Price, M.V. 1978. The role of microhabitat specialization in structuring desert rodent communities. Ecology, 68:1393-1399.

Price, M.V., and J.H. Brown. 1983. Patterns of morphology and resource use in North American desert rodent communities. Great Basin Naturalist Memoirs, 7:117-134.

Quimby, D.C. 1951. The life history and ecology of the jumping mouse. Ecological Monographs, 21:62-95.

Rebar, C., and W. Conley. 1983. Interactions in-microhabitat use between *Dipodomys ordii* and *Onychomys leucogaster*. Ecology, 64:984-988.

Reed, K.M., and J.R. Choate. 1986. Natural History of the plains pocket mouse in agriculturally disturbed sandsage prairie. Prairie Naturalist, 18:79-90.

Reynolds, H.G. 1958. The ecology of Merriam's pocket mouse (*Dipodomys merriami* Mearns) on the grazing lands of Arizona. Ecological Monographs, 28:111-127.

Ribble, D.O., and F.B. Samson. 1987. Microhabitat associations of small mammals in southeastern Colorado, with special emphasis on *Peromyscus* (Rodentia). Southwestern Naturalist, 32:291-303.

Rosenzweig, M.L. 1973. Habitat selection experiments with a pair of coexisting heteromyid species. Ecology, 62:327-335.

Rosenzweig, M.L., and J. Winakur. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. Ecology, 50:559-572.

SAS Institute, Inc. 1989. SAS user's guide: statistics. Fifth ed. SAS Institute, Inc., Cary North Carolina, 846 pp.

Schmidly, D.J., K.T. Wilkins, and J.N. Derr. 1993. Biogeography. Pp. 319-356, *in* Biology of the Heteromyidae (H.H. Genoways and J.H. Brown, eds.). Special Publication, American Society of Mammalogists, 10:1-719.

Tabachnick, B.G., and L.S. Fidell. 1996. Using multivariate statistics. Third edition. New York, Harper Collins, 880 pp.

Tester, J.R., S. Malchow, C. Mclain, and J.B. Lehrer. 1993. Movements and habitat use by meadow jumping mice in northwestern Minnesota. Prairie Naturalist, 25:33-37.

Thompson, S.D. 1982a. Microhabitat utilization and foraging behavior of bipedal and quadrupedal heteromyid rodents. Ecology, 63: 1303-1312.

Thompson, S.D. 1982b. Structure and species composition of desert heteromyid rodent species assemblages: effects of a simple habitat manipulation. Ecology, 63:1313-1321.

Wilson, G.M., J.B. Bowles, and J.W. Van Zee. 1996. Current status of the plains pocket mouse, *Perognathus flavescens*, in Iowa. The Journal of the Iowa Academy of Science, 103:52-55.

Addresses of Authors:

ROBERT S. DEBACA

Texas Tech University
Department of Biological Sciences and Museum
Lubbock, TX 79409-3191
e-mail: bio67@mindspring.com

JERRY R. CHOATE

Department of Biological Sciences
Fort Hays State University
600 Park Street, Hays, KS 67601
e-mail: jchoate@fhsu.edu

PUBLICATIONS OF THE MUSEUM OF TEXAS TECH UNIVERSITY

It was through the efforts of Horn Professor J Knox Jones, as director of Academic Publications, that Texas Tech University initiated several publications series including the Occasional Papers of the Museum. This and future editions in the series are a memorial to his dedication to excellence in academic publications. Professor Jones enjoyed editing scientific publications and served the scientific community as an editor for the Journal of Mammalogy, Evolution, The Texas Journal of Science, Occasional Papers of the Museum, and Special Publications of the Museum. It is with special fondness that we remember Dr. J Knox Jones.

Institutional subscriptions are available through the Museum of Texas Tech University, attn: NSRL Publications Secretary, Box 43191, Lubbock, TX 79409-3191. Individuals may also purchase separate numbers of the Occasional Papers directly from the Museum of Texas Tech University.

museum
texas tech university

ISSN 0149-175X

Museum of Texas Tech University, Lubbock, TX 79409-3191