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Cohesion and survivorship of a rodent community during the past 4 million years in southwestern Kansas

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ABSTRACT

Preliminary studies of rodent community evolution in the Meade Basin of southwestern Kansas do not support the hypothesis that all organismal communities are tightly bound, highly co-evolved units. With the Jaccard Index as a measure of similarity, rodent community composition appears to change continually through the 4.2 million year study period, thus supporting the classic 'open' community concept of Gleason (1926) and Whittaker (1975). This also logically suggests that many predator–prey systems are opportunistic, although larger predators and prey may co-exist for longer periods if their species lifespans are longer. Survivorship analyses show that extinction rates are statistically similar for much of late Pliocene time, but escalate rapidly during the middle Pleistocene. Survivorship data are best fit by a linear model, providing empirical support for the idea that rodent community structure is determined primarily by the interplay of stochastic climatic and biotic influences. An exponential distribution (straight line) on a semi-log survivorship plot in real time may indicate either a dynamic (Red Queen) or stable (evolutionarily stable strategy) equilibrium. The 'smoking gun' for Red Queen competitive co-evolution in a study system will be data demonstrating that species in a community evolve in the presence of guild associates, combined with independent climatic data identifying a pacemaker for continual, albeit stochastic, environmental change during the study period. Preliminary data from the Meade Basin rodent community support a 'weak' version (Ridley, 1993) of the Red Queen hypothesis.

Keywords: carnivore, community similarity, extinction, immigration, Pleistocene, Pliocene, Quaternary, Red Queen, survivorship.

INTRODUCTION

> . . . the chasm between evolutionary biology and ecosystem science is a wide one, and there is little overlap between the two in journals or scientific meetings. (Levin, 1992, p. 1944)

One of the continuing important problems in ecological theory is the extent to which modern animal and plant communities are tightly co-evolved entities. Do guilds, for example, have a long history and dependency similar to parasite–host relationships? How long has it taken for modern predator–prey relationships to develop? Do entire

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Fig. 1. Location of the Meade Basin, southwestern Kansas, and a photograph showing characteristic outcrops in the Borchers Badlands (reprinted with permission from Bayne, 1976).

mammal communities evolve as a unit, tracking environmental changes, or do mammal species respond individually along environmental gradients as proposed by Gleason (1926), Whittaker (1975), Graham (1986) and Graham *et al.* (1996) in the 'open' community concept? The answers to these questions require information from the fossil record, and the late Pliocene and Pleistocene, or the last 4.5 million year period, is the logical interval to examine for resolution of these questions for a variety of reasons, including the following: (1) modern species are often represented in deposits of this age, and their physiological and habitat tolerances can be used to infer past environmental conditions; (2) species can be identified with greater certainty; (3) there are likely to be more specimens from more localities available for statistical testing; and (4) there is a large body of neontological literature available for consultation. One of the special needs of an inquiry of this type is to find a depositional setting that spans a long period of time, including the transition to a modern fauna in the same geographical region. Such locations are rare, and in the New World we are aware of only one that satisfies these conditions, the Meade Basin of southwestern Kansas (Fig. 1). This study examines rodent community integrity and turnover over approximately the last 4.2 million years, and is part of a long-term project to investigate the dynamics of rodent community evolution in southwestern Kansas.

To test the relative cohesion of an assemblage, expectations from the fossil record must be clearly delineated. That is, what kinds of patterns would we expect to see in fossil materials and what statistical tests would we use to confirm them? Community stability would be suggested by continuity of the same species in aggregate over long periods of time. The open community hypothesis would be supported if species were seen to come and go according to a random, or at least stochastic, model. Completely random distributions are rare in nature because of the numerous constraints placed on evolving systems by phylogeny, ontogeny and biogeography (i.e. dispersal probabilities, regional topography, etc.). In this study, we chose to use a modified form of the Jaccard Index (Krebs, 1989) to examine community integrity.

If one establishes that communities are generally fortuitous associations of species that become extinct with some regularity when examined over long intervals, then it is of interest to determine the rate and manner of these disappearances. Are they lost in mass extinctions, in regional episodes as the result of a variety of influences (perhaps including competition and climatic modification), or in a more regular fashion? Do communities, like radioisotopes, senesce at an endogenous rate? Much of our interest in these questions is generated by a model developed by Van Valen (1973), in which he proposed that all organisms go extinct at a rate that is constant for each group. This 'Law of Extinction' has profound consequences for understanding both the evolutionary process and community assembly rules. For one thing, it suggests that organismal adaptations do not ensure long-term species survival. Van Valen expressed this as 'comparability of taxa'. Secondly, in the absence of mass extinctions, the model proposes that communities will change in a stochastically constant manner. A number of authors have criticized the model on statistical as well as heuristic grounds (e.g. Salthe, 1975; McCune, 1982), but data sets for fossil organisms, when examined with modern analytical methods, often support the proposition (e.g. Jaeger, 1994). Nevertheless, there is a possible problem of *scale*: extinctions that appear regular on the multi-million year scale may appear episodic on the scale at which selection is presumed to operate. This is expected from Van Valen's model, but it still must be evaluated for importance and underlying causation. For this reason, we have incorporated a variety of analytical techniques of faunal turnover, from polycohort analysis over the full study period to a more refined examination during briefer intervals of roughly equal duration.

Van Valen (1973) further proposed that constant extinction was powered by two processes, a dynamic competitive co-evolution among related species and guild associates (Root, 1967) and stochastically constant environmental change. The competitive aspect has been termed a 'Rat Race' (Rosenzweig, 1973) and an 'Arms Race' (Dawkins and Krebs, 1979), but the most widespread descriptor is Van Valen's (1973) 'Red Queen' hypothesis. This hypothesis and its alternatives are explored in detail below; suffice for now to say that other equilibrium scenarios are possible that can mimic the Red Queen process (Rosenzweig *et al.*, 1987). Tests to discriminate between the influences of purely abiotic (physical) and

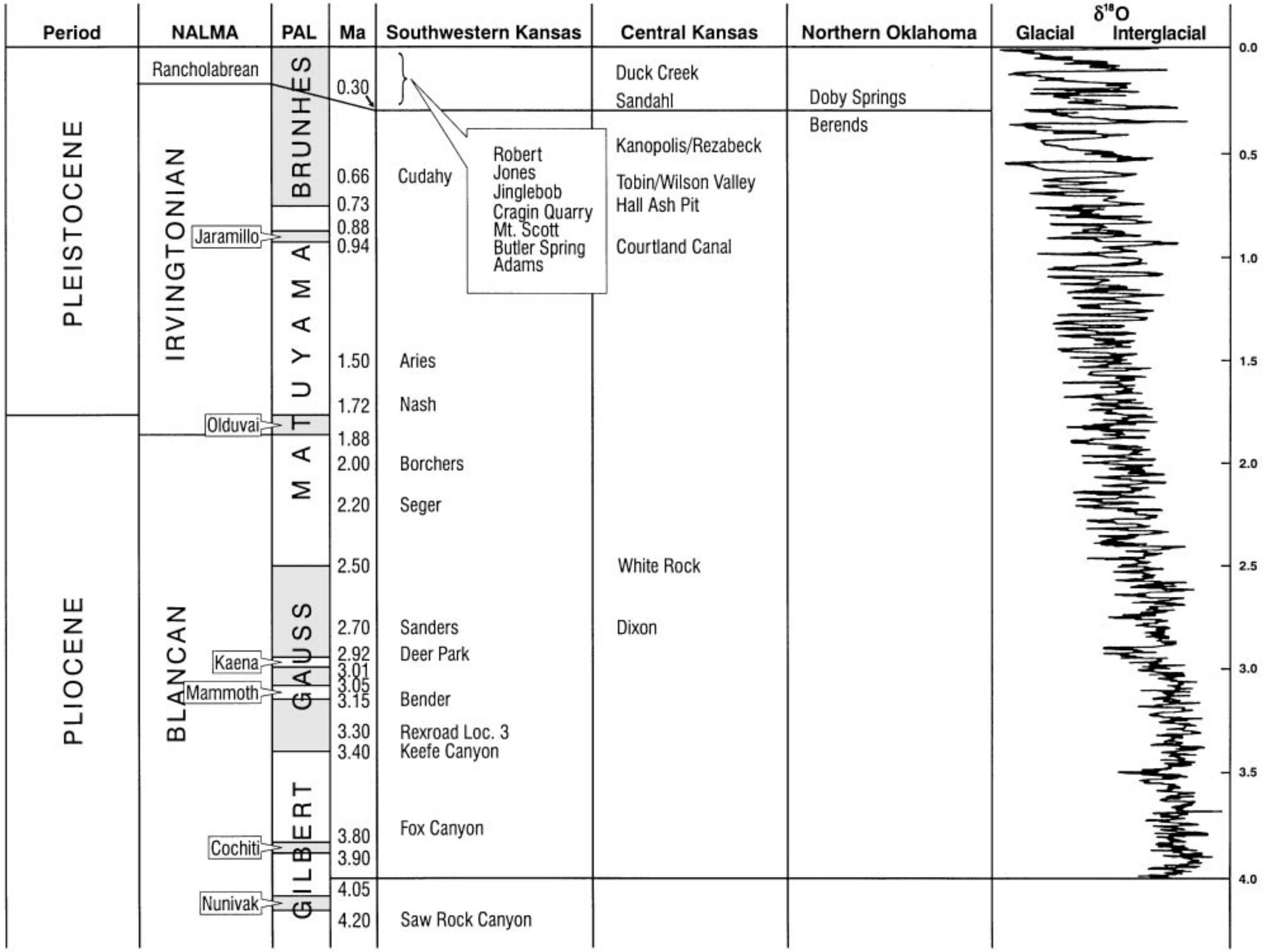

Fig. 2. Stratigraphic relationship of fossiliferous localities in the Meade Basin of southwestern Kansas and surrounding regions. Age of the localities and magnetostratigraphy follows Lundelius *et al.* (1987) and the oxygen isotopic stratigraphy is taken from deMenocal (1995).

biotic (e.g. competitive) forces on extinction patterns are necessary. Finally, we must identify an independent palaeoclimatic data set and pacemaker to support the component of stochastic environmental modification.

THE SYSTEM

Claude W. Hibbard's greatest contribution to science will undoubtedly be seen as the introduction of screenwashing for microvertebrates. With this method, he and his students discovered a sequence of late Pliocene and Pleistocene small mammal faunas from the Meade Basin of southwestern Kansas that remains one of the best documented stratigraphic successions from a single sedimentary basin of its age in the world. Twelve local faunas, spanning the time from about 4.2 million years ago (Ma) to the present, were considered in this analysis (Fig. 2). The sites from which the fossils were recovered are mostly fluvial, lacustrine aeolian sands, silts and gravels. Stratigraphic arrangement of the sites and their correlation with magnetic polarity chronology and the oxygen isotope record is illustrated in Fig. 2 following Zakrzewski (1975), Eshelman (1975), Bayne (1976), Davis (1975), Lindsay *et al.* (1975), Lundelius *et al.* (1987) and Morrison (1991). Two potassium–argon dates at 0.67 and 2.1 Ma securely place the Borchers and Cudahy local faunas, and radiocarbon dates at 0.027–0.029 and 0.011 Ma are available for the Jones and Robert local faunas, respectively. The remaining faunas are sequenced on the basis of the evolutionary stages of mammals in them and the magnetic polarity stratigraphy of the sediments from which they were derived (Lindsay *et al.*, 1975).

This study also includes small mammals from the White Rock local fauna, Republic County, and the Sandahl local fauna, McPherson County. These rich localities represent important segments of the late Pliocene and late Pleistocene either not currently represented or poorly represented in the Meade Basin sequence. Both sites lie today within the same general prairie ecosystem found in Meade County (the Needlegrass–Pronghorn–Grama Grass Biome of Shelford, 1963), and with certain notable exceptions that will be discussed below, the replacement sequence of rodent species from these localities is a reasonable proxy for what might have been expected for the same time periods in Meade County. New localities have been identified in the Meade Basin (J. Honey, personal communication), and the senior author is beginning a field programme to fill in critical temporal gaps. Based on the species represented in the Sandahl local fauna (e.g. *Microtus ochrogaster*, *M. pennsylvanicus*; Semken, 1966), we treat it as a Rancholabrean fauna and assign to it a date of 0.25 Ma.

MATERIALS AND METHODS

Classification

Table 1 presents a species list for all rodents considered in this study. Specimens of these taxa were examined in the Museum of Palaeontology collections at the University of Michigan in the summer of 1992. Presumed aquatic (*Pliopotamys* = *Ondatra*; *Neofiber*) and fossorial (*Geomys*, *Thomomys*) species were excluded. The list is arranged chronologically from left to right. Taxonomy of the fossil forms in Table 1 follows the literature, especially Kurtén and Anderson (1980) and numerous papers in which these species were described and examined in later taxonomic studies (e.g. Hibbard, 1941a,b, 1949a,b, 1950, 1952, 1953,

Table 1. The rodent fauna of southwestern Kansas over the past 4.2 million years

	SR	FC	RR3	WR	Bor	Cud	Sand	BS	MS	Jing	Jon	Rob	Mod
Sciuridae													
Spermophilus tridecemlineatus						cf	x	cf	cf		x	x	xM
Spermophilus boothi				x									
Spermophilus rexroadensis			x										
Spermophilus howelli		x	x										
Spermophilus meadensis				xx	x								
Spermophilus franklini						nr				xx	x		x
Spermophilus cragini					x								
Spermophilus spilosoma													xM
Spermophilus richardsoni						x	x	x			x	x	
Spermophilus sp.	x	x		x					x	x			
Tamias striatus													x
Cynomys ludovicianus							x	x					xM
Cynomys gunnisoni							cf						
Cynomys vetus				cf									
Cynomys hibbardi				x									
Cynomys sp.									x	xx	x	x	
Marmota monax													x
Marmota sawrockensis	x												
Heteromyidae													
Prodipodomys tiheni					x								
Prodipodomys centralis	cf	cf	x										
Prodipodomys sp.				x									
Dipodomys ordii								cf	xx	cf	xx	xx	xM

Dipodomys hibbardi					x								
Perognathus flavescens													xM
Perognathus flavus													xM
Perognathus pearlettensis		x		x	cf								
Perognathus rexroadensis		x											
Perognathus gidleyi			x										
Perognathus mclaughlini	x												
Perognathus hispidus							x	x	xx	x	xx	xx	xM
Perognathus sp.				x			x	x	xx	x	x	xx	
Cricetidae													
Calomys eliasi			x										
Calomys arizonae		x											
Calomys stirtoni	x												
Symmetrodontomys simplicidens		x	x										
Baiomys sawrockensis	x												
Baiomys kolbi		x											
Baiomys rexroadi			x										
Onychomys gidleyi	x	x	x							x			
Onychomys pedroensis				x	x								
Onychomys hollisteri				cf	x								
Onychomys leucogaster						xx		cf	xx		x	xx	xM
Onychomys sp.							x						
Reithrodontomys wetmorei		x											
Reithrodontomys montanus							cf			cf			xM
Reithrodontomys moorei						x							
Reithrodontomys pratincola				x	x								
Reithrodontomys fulvescens													x
Reithrodontomys megalotis								cf					xM

Table 1 (*continued*)

	SR	FC	RR3	WR	Bor	Cud	Sand	BS	MS	Jing	Jon	Rob	Mod
Reithrodontomys rexroadensis		x											
Reithrodontomys sp.			xx						x		xx	x	
Peromyscus berendsensis									x				
Peromyscus baumgartneri		x											
Peromyscus kansasensis			x										
Peromyscus sawrockensis	x	xx											
Peromyscus progressus							cf	x	x				
Peromyscus cragini				x	xx	x							
Peromyscus cochrani										x			
Peromyscus boylii													x
Peromyscus leucopus												x	xM
Peromyscus sp.	x						x		x	x	x		
Peromyscus maniculatus												x	xM
Oryzomys palustris									x	x			
Neotoma quadriplicatus		x	x										
Neotoma sawrockensis	x												
Neotoma taylori				x	x								
Neotoma micropus													xM
Neotoma floridana						xx			cf				x
Neotoma sp.							x	xx		x	xx	xx	
Sigmodon hispidus							x						xM
Sigmodon minor			x	x	x								
Zapodidae													
Zapus hudsonius							x	xx	x	x	xx	x	x
Zapus burti					x								
Zapus rinkeri		x											

Zapus sandersi			xx	x		cf							
Javazapus weeksi				cf									
Arvicolidae													
Ogmodontomys sawrockensis	x												
Ogmodontomys poaphagus		x	x										
Ogmodontomys sp.				x									
Pliophenacomys finneyi		x											
Pliophenacomys primaevus			xx	cf									
Pliophenacomys osborni				x									
Ophiomys meadensis				x									
Nebraskomys mcgrewi				x									
Nebraskomys rexroadensis			x										
Synaptomys rinkeri				cf									
Synaptomys landesi					x								
Synaptomys meltoni						x							
Synaptomys australis									x	x			
Synaptomys cooperi												x	xM
Microtus paroperarius						x							
Microtus meadensis						x							
Microtus llanensis						x	x						
Microtus pennsylvanicus							x	x	x	x	x	x	
Microtus ochrogaster								x	x	x	x	x	xM
Microtus xanthognathus									x	cf			
Species totals	11	17	16	22	13	12	15	13	18	17	14	15	16(23)

Abbreviations: SR, Saw Rock Canyon; FC, Fox Canyon; RR3, Rexroad Loc. 3; WR, White Rock; Bor, Borchers; Cud, Cudahy; Sand, Sandahl; BS, Butler Spring; MS, Mount Scott; Jing, Jinglebob; Jon, Jones; Rob, Robert; Mod, Modern. x = recorded from locality; xx = range-through taxon (presumed present); xM (Modern fauna) = extant today in Meade County; x (Modern fauna) = extant in Kansas, but not in Meade County; cf = compares favourably; nr = near.

1955, 1956, 1963; Hibbard and Taylor, 1960; Semken, 1966; Martin, 1979, 1987, 1993, 1996a; Zakrzewski, 1988, 1993). However, for calculation of similarity matrices, the taxa were treated differently. Some of the species represent intermediates in various phyletic series. For example, Carleton and Eshelman (1974) have shown there is continuity from one of the early grasshopper mice, *Onychomys gidleyi*, through *O. pedroensis* to *O. leucogaster*. For purposes of determining community similarity, these component species and others in Table 1 that are part of presumed phyletic sequences (representing 'pseudo-extinctions') were synonymized. In some cases the synonymy was not as clear as the grasshopper mouse series, because many of the taxa have not been reviewed recently. Nevertheless, certain patterns are obvious and have been discussed in the literature (e.g. Hibbard and Zakrzewski, 1967; Baskin, 1978; Martin, 1979; Koenigswald and Martin, 1984). We also occasionally took 'professional liberty' in assuming some synonymies, particularly if estimates indicated they were of approximately the same size. The following summary includes the exact synonymies used for community analyses and turnover patterns:

1. *Spermophilus howelli* = *S. meadensis.*
2. *Spermophilus rexroadensis* = *S. boothi.*
3. *Prodipodomys tiheni* = *P. centralis* = *Prodipodomys* sp.
4. *Perognathus maclaughlini* = *P. gidleyi* = *P. rexroadensis* = *P. pearlettensis* (although these may not all be synonymous, we assumed the presence of only one species in the approximate size range 20–40 g prior to Cudahy time).
5. *Calomys eliasi* = *C. arizonae*.
6. *Onychomys gidleyi* = *O. pedroensis* = *O. leucogaster*.
7. *Reithrodontomys*: we assumed continuity of one small species from *R. rexroadensis* = *R. wetmorei* = *R. pratincola* = *R. moorei* to either *R. megalotis* or *R. montanus.*
8. *Peromyscus cragini* = *P. progressus* = either *P. maniculatus* or *P. leucopus.*
9. *Peromyscus sawrockensis* = *P. kansasensis.*
10. *Ogmodontomys sawrockensis* = *O. poaphagus* = *Ogmodontomys* sp.
11. *Pliophenacomys finneyi* = *P. primaevus* or *P. osborni.*
12. *Nebraskomys mcgrewi* = *N. rexroadensis*.
13. *Synaptomys rinkeri* = *S. landesi* = *S. meltoni.*
14. *Microtus llanensis* = *M. ochrogaster.*
15. *Zapus rinkeri* = *Z. burti* = *Z. sandersi* = *Z. hudsonius* (morphological differences among these zapodid species are problematical, but since they have not been recorded from the same or contemporaneous faunas, for the purpose of community analysis and species turnover they are considered synonymous).
16. *Baiomys sawrockensis* = *B. kolbi* = *B. rexroadi.*

With an analysis of this type, sampling error must always be considered a powerful bias. The local faunas represented by this study came from stream and spring deposits with varying efficiencies of trapping small mammals. The Butler Spring site was apparently relatively poor, whereas the Fox Canyon and White Rock 'energy sinks' were exemplary. Unfortunately, other Pleistocene faunas from southwestern Kansas (Aries, Nash, Cragin Quarry) were rejected from this study either because the small mammal contingent was too limited or because the material could not be located in museum collections. Only faunas with nine or more documented rodent species were included. Corrections for sampling error were made in one manner. When a fauna lacked a species that was found in faunas bracketing it in time, the species was added to the intermediate fauna (the 'range-through' taxa of Barry *et al.*, 1995 and Maas *et al.*, 1995; first used in ecology by Hilborn *et al.*, 1976). Such corrections are noted in Table 1 by 'xx'. In rare instances, although bracketed in time by congeneric species, the absence of a species was considered ecologically valid. An example is Cudahy time, approximately 0.67 Ma, when southwestern Kansas was populated by an array of advanced arvicoline rodents such as *Microtus llanensis* (= *M. ochrogaster*), *M. meadensis* and *M. paroperarius* plus two species of *Onychomys*. Species of cotton rats are recorded both before (*S. minor*; primitive and small) and after (*S. hispidus*; advanced and large) this interval, but their absence from the Cudahy local fauna is considered quite likely in the face of potential competition with arvicolines and possible habitat differences. Prairie dogs apparently did not arrive in Meade County until approximately 0.15 Ma, as the large *Cynomys ludovicianus*. Earlier (and smaller) members of this genus are recorded from the White Rock and Sandahl local faunas (Table 1), but these faunas lie to the east and north of Meade County and this distributional segregation was probably maintained until the late Pleistocene.

The Completeness Index (CI_1) of Barry *et al.* (1995) was used as a quantitative means to assess sampling bias:

$$\mathrm{CI}_1 = N_{\mathrm{a}}/(N_{\mathrm{a}} + N_{\mathrm{rt}}) \tag{1}$$

where N_{a} is the total number of species recorded from an interval and N_{rt} is the number of range-through species. This index, as with others noted by Maas *et al.* (1995) and Barry *et al.* (1995), is a helpful indicator of sampling error, but is severely limited in one regard; the index offers no way to assess the lower species boundary. For example, if one had recovered five rodent faunas in temporal succession, each of which contained only five species and none of which were range-through taxa, the Completeness Index for the middle three would be 1.00. Yet it may be that all five were poorly represented for a variety of taphonomic reasons. There is at present no method that adequately quantifies sampling bias, and the best we can do now is use methods such as the Completeness Index, coupled with professional judgement of taphonomic influences. We chose to use fossil faunas in which there were at least nine species records, but there was no specific mathematical reasoning involved other than the obvious; to be certain there were enough faunas and species present to provide biologically meaningful results.

The range-through, or 'minimum census', correction can overestimate diversity of a given local fauna if any of the absences are not the result of sampling bias. This would tend to prejudice subsequent mathematical analyses towards identifying community cohesion (see Rosenzweig and Duek, 1979). The results of this study demonstrate rapid turnover of small mammal communities in Kansas, and our confidence in this conclusion is actually bolstered by the conservative census procedure used here.

Each of the localities from which fossil rodents were collected represents an accumulation from surrounding plant communities. The agents of accumulation have not been securely determined, but in no case is there evidence of substantial transport by water. However, fossils are so concentrated at the Borchers locality that it could at least partly represent an owl roost, and owls can forage over rather large areas. These taphonomic influences all bear on the manner in which we interpret the fossil aggregations to represent 'communities'. Undoubtedly, some fine-grained community structure information has been lost. Slight changes in plant diversity that might have ecologically segregated one or more rodent species from some of the others will probably not be discernible. However, we suspect that the monotonous topography of southwestern Kansas would not have supported many distinct plant community types in the past, and that only one or two species, such as the bog lemmings, would be severely restricted in their distribution. In a sense, the topography is working in our favour to limit taphonomic bias. Thus, in representing the modern rodent community, we have made no attempt to isolate rodents from distinct microhabitats, in part because we suspect they actually did function mostly as a single community, but also precisely because this is the level of precision we can expect from the fossil record, at least at this time.

Community similarity

Numerous indices have been developed to test for similarity of species composition. Some of these were reviewed by Krebs (1989), who also provided the rationale for such tests, based primarily on the review by Wolda (1981). In practice, as Krebs (1989) demonstrates, there is little difference in the resulting pattern of many index matrices, and each is probably satisfactory as long as one does not assume that all can range freely between 0 and 1.0. Basically, one must be able to determine the degree of relatedness between the sites, regardless of the absolute value of the numbers. Similarity matrices for the Meade Basin sequence were based on the Jaccard Index:

$$\frac{a}{a+b+c} \tag{2}$$

where a = the number of species in common, b = the number of species in sample A but not in sample B and c = the number of species in sample B but not in sample A (see Krebs, 1989, p. 294). This ratio cannot equal 1.0 if sample sizes are unequal. The value

$$J' = J/J_{\max} \tag{3}$$

represents a transformed index that can range from 0 to 1.0, where $J_{\max}$ is the maximum possible value for a given comparison and is calculated as the ratio of the lowest species number divided by the highest species number.

Survivorship and turnover

These are difficult concepts to examine, because taxonomic practices and statistical methods can so easily influence the outcome. In this study, we controlled for ‘pseudo-extinction’ by collapsing all known or suspected phyletic series, following the guidelines noted above. Therefore, with the possible exception of interpretive errors, the influence of phyletic speciation is considered minimal.

Because the number of extinction events is correlated with interval length (Fig. 3), observed values of extinction could be compared with those expected over a given period of time. A power function offered the best fit in plots of both immigration and extinction numbers versus interval length, and expected values of these parameters were generated by the resulting equations. One thousand bootstrap samples were generated from both the log-transformed immigration and extinction data using a program written with SAS and its random number generator. Confidence intervals were computed from the bootstrap distributions following Plotnick (1989) and are presented in Table 2, converted to original units by an exponential transformation.

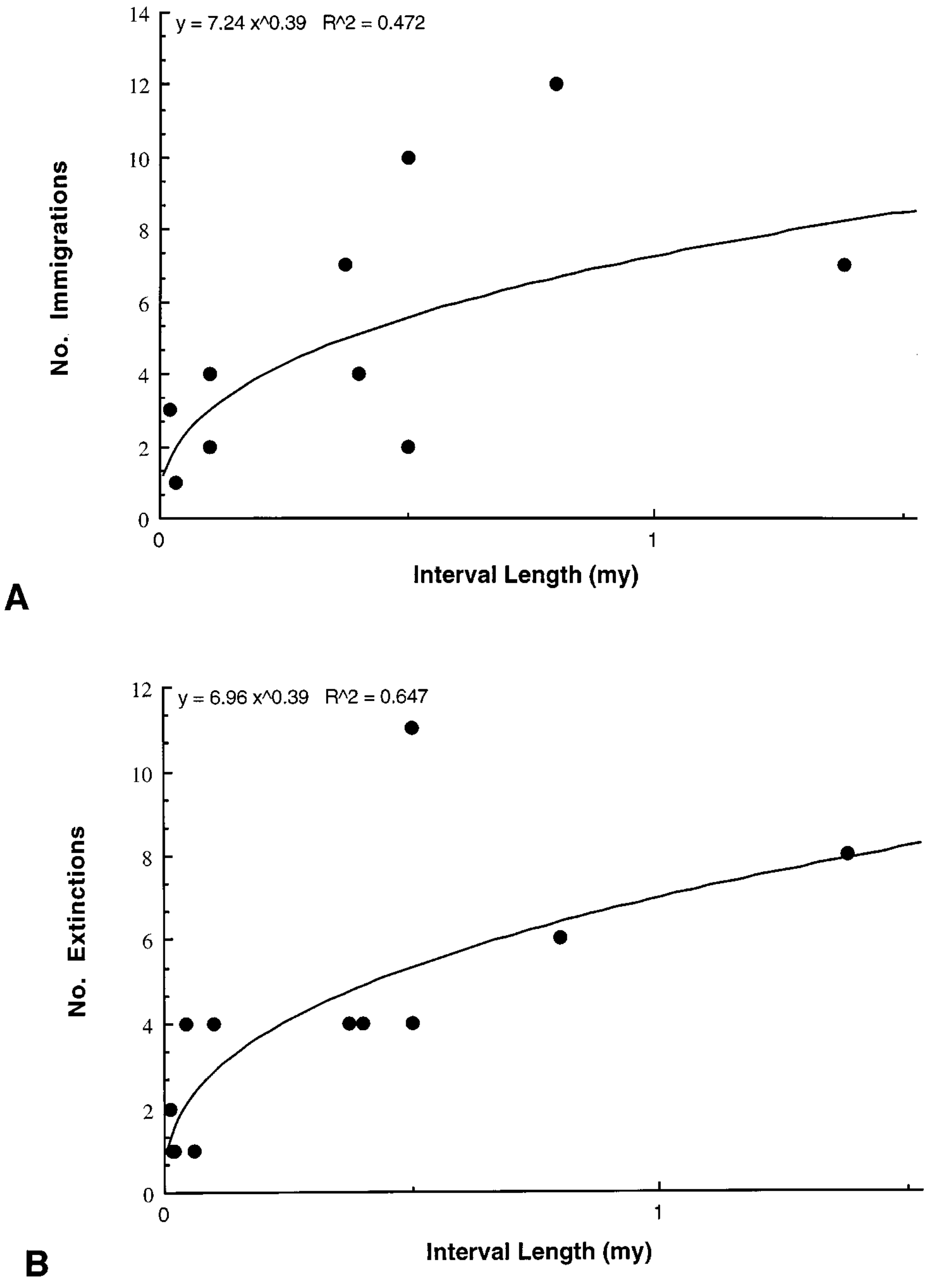

Fig. 3. Bivariate plots and equations relating the number of immigrations and extinctions to the interval lengths in millions of years (my) over which they occurred. These equations generated expected values of immigrations and extinctions provided in Fig. 4.

Table 2. Ninety-five percent confidence intervals for least-squares regression parameters of bootstrap distributions (1000 iterations) of log-transformed immigration and extinction numbers as a function of interval length

	Percentile method	Bias-adjusted method
Number of extinctions		
Intercept = 1.946	1.648–2.319	1.660–2.338
Slope = 0.398	0.246–0.579	0.245–0.579
Number of immigrations		
Intercept = 2.001	1.392–2.579	1.306–2.487
Slope = 0.394	0.125–0.722	0.105–0.691

Survivorship was examined in the classic fashion of population biology by following the history of each rodent fauna considered as a species cohort. Logs of the percentages of species numbers were plotted on the ordinate against geological time on the abscissa. This approach avoids many of the pitfalls of other survivorship methods (see Raup, 1978; McCune, 1982). Following this analysis, extinction was partitioned over brief periods of late Pliocene and Pleistocene time to determine extinction patterns on a finer temporal scale.

Using the extinction and immigration functions noted above, we also compared expected and observed immigration and extinction data for each faunal sampling interval, represented as a mirror diagram, in which extinction and immigration values are plotted opposite each other in histogram form (Fig. 4). Ninety-five percent confidence levels of particular immigration or extinction estimates were computed from 1000 generated bootstrap values. In this manner, we were able to determine if observed values for individual sampling regimes were significantly higher than expected.

RESULTS AND DISCUSSION OF THE DATA

Sampling bias

The Completeness Indices (CI_1) for the Meade Basin faunas are as follows: Saw Rock Canyon (not applicable), Fox Canyon (1.00), Rexroad Loc. 3 (0.81), White Rock (0.90), Borchers (0.92), Cudahy (0.91), Sandahl (1.00), Butler Spring (0.85), Mount Scott (0.78), Jinglebob (0.88), Jones (0.64), Robert (0.67). Although there are no theoretical limits beyond which one can say that species numbers are represented at a satisfactory level, these values indicate that the proportion of range-through species is not high for most localities. It is interesting that N_{rt} is highest in the most modern faunas, which runs counter to intuitive expectations. The high number of range-through species and lower Completeness Index in these faunas appears to be the result of a few species that immigrated into Kansas during the late Pleistocene but became regionally extinct before modern time.

Community cohesion

The Jaccard Index values in Table 3 demonstrate that a rodent fauna on the Great Plains is, at any given time, a loosely knit association. If we examine the J' values for faunas from

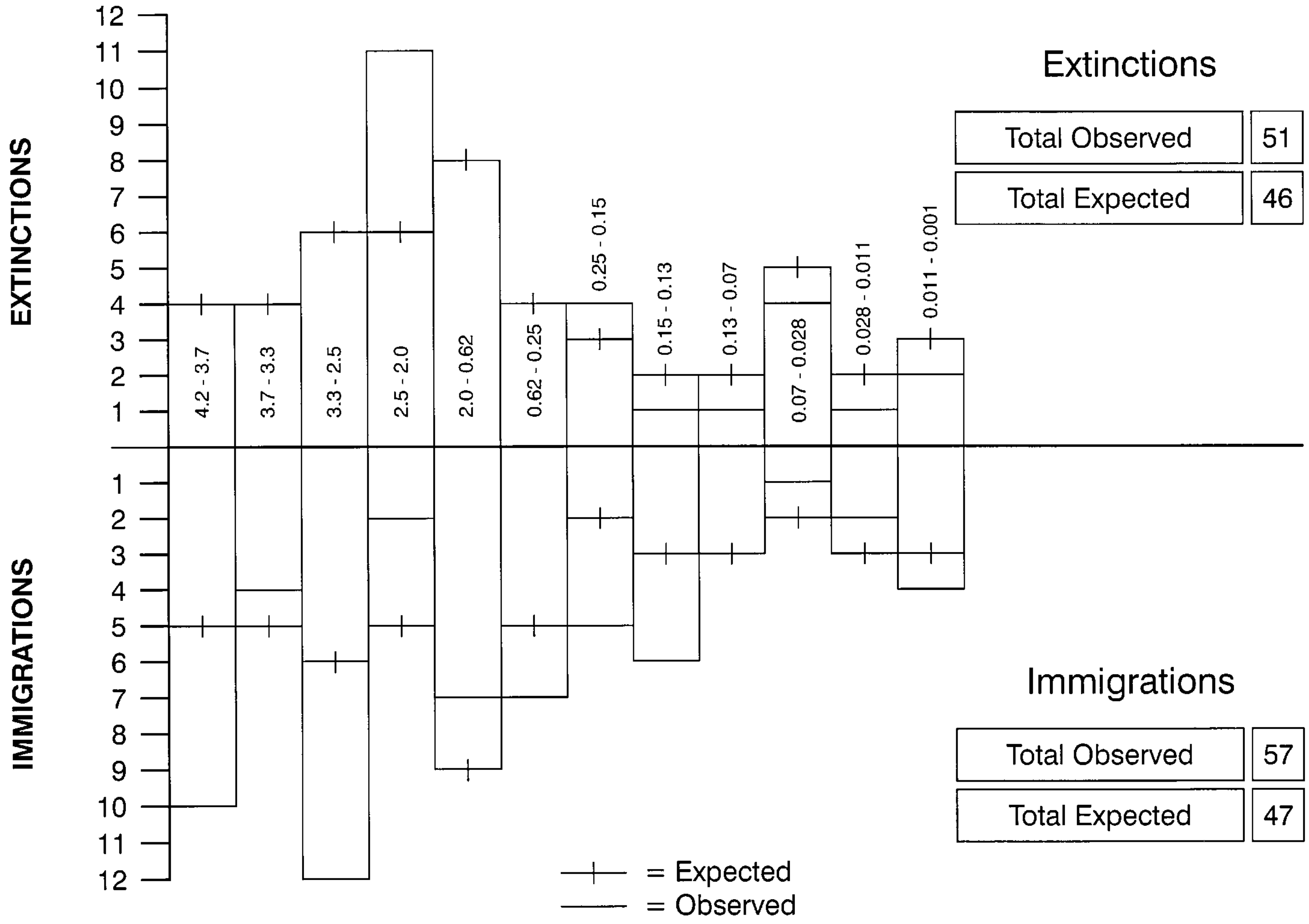

Fig. 4. Turnover of terrestrial rodent faunas in southwestern Kansas over the past 4.2 million years. Intervals are noted in millions of years (my).

Table 3. Calculated Jaccard Index values

	J												
J′	SR	FC	RR3	WR	Bor	Cud	Sand	BS	MS	Jing	Jon	Rob	Mod
SR		0.33	0.29	0.18	0.14	0.05	0.04	0.04	0.04	0.04	0.04	0.04	0.04
FC	0.51		0.65	0.3	0.25	0.12	0.1	0.11	0.09	0.1	0.1	0.1	0.07
RR3	0.42	0.69		0.36	0.26	0.12	0.11	0.12	0.1	0.1	0.11	0.11	0.07
WR	0.36	0.39	0.49		0.46	0.21	0.09	0.09	0.08	0.08	0.09	0.09	0.09
Bor	0.17	0.33	0.32	0.78		0.25	0.17	0.18	0.15	0.15	0.17	0.17	0.12
Cud	0.05	0.17	0.16	0.38	0.27		0.42	0.39	0.3	0.32	0.37	0.35	0.27
Sand	0.06	0.11	0.11	0.13	0.2	0.53		0.65	0.43	0.46	0.71	0.58	0.41
BS	0.05	0.14	0.15	0.15	0.18	0.42	0.75		0.63	0.67	0.8	0.75	0.61
MS	0.07	0.1	0.11	0.1	0.21	0.45	0.52	0.88		0.94	0.68	0.6	0.48
Jing	0.06	0.11	0.11	0.1	0.2	0.45	0.68	0.87	1		0.72	0.68	0.48
Jon	0.05	0.16	0.13	0.14	0.18	0.43	0.76	0.86	0.87	0.88		0.87	0.59
Rob	0.06	0.11	0.12	0.13	0.2	0.44	0.58	0.86	0.72	0.77	0.93		0.8
Mod	0.06	0.08	0.07	0.12	0.15	0.36	0.44	0.75	0.54	0.51	0.67	0.85	

Abbreviations: SR, Saw Rock Canyon; FC, Fox Canyon; RR3, Rexroad Loc. 3; WR, White Rock; Bor, Borchers; Cud, Cudahy; Sand, Sandahl; BS, Butler Spring; MS, Mount Scott; Jing, Jinglebob; Jon, Jones; Rob, Robert; Mod, Modern.

contiguous temporal intervals (i.e. Saw Rock Canyon–Fox Canyon or Borchers–Cudahy), we see that these values range from 0.27 to 1.00, with an average of 0.71. That is, any two sequential faunas average about 70% faunal similarity. However, when we follow each fauna as a distinct cohort of species through time, we see that its similarity to succeeding faunas diminishes rapidly, and that there is little relationship of late Pliocene faunas with those of today. Even the Sandahl local fauna, about 0.25 Ma, has only about 44% species in common with the modern fauna from Meade County. Only one species (*Onychomys leucogaster*) appears throughout the 4 million year interval, and only two extant species in Meade County extend to 3.7 Ma (*O. leucogaster*, *Reithrodontomys montanus* or *R. megalotis*). It is curious that the Butler Spring rodent fauna, supposedly deposited around 0.15 Ma, has a greater mathematical similarity to the modern Kansas fauna than three succeeding faunas. Examination of Table 1 shows that a few species immigrated into Kansas following Butler Spring time and then became locally extinct prior to Recent time (e.g. *Synaptomys australis*, *Microtus xanthognathus*, *Oryzomys palustris*). Another explanation would be that the Butler Spring Site is incorrectly sequenced, but there is at this point no physical evidence to support this possibility.

For the ‘open’ community concept to become widely accepted, there has to be a preponderance of historical data demonstrating that species respond over time more in an individual than in a collective manner. The Jaccard data presented here for rodent turnover in Kansas clearly support this model; species aggregates do not remain together for long periods. Graham (1986) similarly concluded that small mammal distributional shifts during the late Pleistocene in North America were expressed on an individual rather than collective basis. Rather than disperse as a community when glacial and Holocene climates prevailed, species formed new and unique associations that are not encountered today. Palaeovegetational data, more directly representing habitat integrity, demonstrate similar patterns over the same time period. Davis (1986) documented a number of cases where individual tree species dispersed at different rates during the Pleistocene. For example, following the beginning melt-off of the Wisconsinan continental glaciation about 16,000 years ago, both *Quercus* and *Acer* expanded their ranges northeastwards from the Mississippi Valley quickly, but hickory (*Carya*) lagged behind. The chestnut did not reach its current distributional limits until 2000 years ago, and both hemlock and white pine moved northwestwards instead of to the northeast. Davis concluded that the movement of these species was not determined solely by displacement of temperature regimes, but by a complex combination of ecological factors acting on each species individually. Other investigators have commented on the unique vegetational types that characterized Pleistocene biotas in North America until less than 10,000 years ago at the beginning of the Holocene (West, 1970; Wright, 1981; Thompson and Mead, 1982; Delcourt and Delcourt, 1984; Peteet *et al.*, 1990; Latham and Ricklefs, 1993; Withers and Mead, 1993), and Gear and Huntley (1991) also documented changes in the range limits of Scots Pine in Europe within the last 4000 years.

Unfortunately, the botanical record for western Kansas is sparse. The meagre data do suggest that, during the late Quaternary, northern Oklahoma and western Kansas were encroached by western needle-leaf forests, particularly during the glacial periods (Kapp, 1965, 1970; Fredlund and Jaumann, 1987; Wells and Stewart, 1987). Spruce and pine pollen have been recorded in substantial amounts from the Doby Springs and Berends localities in Oklahoma, considered to be of Illinoian glacial age and located just across the Kansas border from Meade County. Fredlund and Jaumann (1987) interpret the Mt. Scott Illinoian pollen record to indicate a grassland steppe, with considerable pine forests nearby. Fossil pollen from the Jinglebob locality is represented by 50% *Pinus*, with various deciduous trees in trace amounts. Throughout the Great Plains in other states, the oscillation between forested glacial advances and drier prairie or steppe interglacials and interstadials seems to be well documented. The modern prairie ecosystems of Kansas and other Great Plains states appear to be only about 9000 years old (Fredlund and Jaumann, 1987).

If turnover, as seen in the Meade Basin rodent community, is typical for small mammals everywhere, it suggests that at least some predator–prey systems are fortuitous associations, where the carnivores function predominantly as opportunists. Carnivore fossils are insufficiently known from the Pliocene and Pleistocene of Kansas to analyse in the same manner as the rodents, but there is one distinct difference from the rodents that can be seen even with the meagre material at hand: modern carnivore species (or phyletic relatives of modern species) extend back farther in time than rodents. For instance, probable ancestors to *Mustela frenata* (= *M. rexroadensis*), *Spilogale putorius* (= *S. rexroadi*), *Canis latrans* (= *C. lepophagus*), *Urocyon cinereoargenteus* (= *U. progressus*) and *Procyon lotor* (= *P. rexroadensis*) were present in the Rexroad Loc. 3 fauna about 3.3 Ma. The absence of other modern carnivores from early Pliocene deposits in Kansas may be a taphonomic bias, and it is possible that, with the exception of some species that probably immigrated later from Beringia (e.g. grey wolf, red fox, cave bear, lion), most other modern species (or their immediate phyletic ancestors) were also present throughout much of the Pliocene and Pleistocene. This consideration supports the proposition that larger mammals have longer species lifespans than small ones (Martin, 1992), and it also suggests it might be profitable to examine the evolution of predator–prey systems, and thus the potential for co-evolution, as a function of body size. Perhaps small- to medium-sized carnivores are more opportunistic than large ones because their prey tend to have shorter species lifespans.

Table 4. Ninety-five percent bootstrap confidence intervals of extinction and immigration estimates (1000 iterations)

Interval length (my)	Observed	Estimated	95% CI
Percentile method			
0.50	10 (I)	5.54	3.55–8.39
0.50	11 (E)	5.31	4.13–7.19
0.80	12 (I)	6.64	3.90–11.31
Bias-corrected method			
0.50	10 (I)	5.54	3.41–8.11
0.50	11 (E)	5.31	4.19–7.46
0.80	12 (I)	6.64	3.56–10.52

Abbreviations: CI = confidence interval; my = millions of years; I = number of immigrations; E = number of extinctions.

We end this section with a candid quote from Brown (1995). In response to his own review of the literature, especially Graham's (1986) essay documenting changes in late Pleistocene mammalian communities, Brown (1995, p. 45) reflects:

> It is hard to imagine how fine-tuned species-specific coevolutionary relationships could develop and persist in the face of such spatial and temporal variation. If such examples are the rule, then during the last few decades many evolutionary ecologists – myself included – probably overestimated the degree to which communities were structured by coevolutionary adaptations.

Now, as Van Valen (1973) suggested, did the rodent species which became extinct do so at a constant rate, or were there dramatic episodes of extinction and origination, perhaps coupled with catastrophic climatic events of some magnitude? Does immigration balance extinction? We can approach this question by examining classic turnover and survivorship patterns of the faunas represented.

Turnover patterns

Because time intervals between successively sampled horizons were unequal, it was essential that we have some measure of expected extinction and immigration numbers over the various periods to compare with the observed values. This was provided by the generally high correlation between extinction and immigration numbers as a function of interval length (Fig. 3). A mirror diagram of expected versus observed extinction/immigration scenarios is provided in Fig. 4. Three peaks stand out in this figure. Two are immigration events that occurred between 4.2–3.7 and 3.3–2.5 Ma, and another is an extinction pulse between 2.5–2.0 Ma. The 95% bootstrap confidence intervals for estimates of immigration and extinction numbers within periods of these durations are given in Table 4. All observed values exceed 95% confidence interval limits. Nevertheless, the first immigration event is probably a mathematical artifact, as species diversity of the Saw Rock Canyon local fauna cannot be corrected for sampling bias and may therefore be under-represented. The first immigration pulse was characterized by a series of small cricetines and two archaic arvicolines; the second almost exclusively by archaic arvicolines. The extinction event, between White Rock and Borchers time, saw the demise of all archaic arvicolines. No new grazing competitors were introduced during this period, and one must conclude that either climatic conditions or predation pressure must have increased tremendously. It is unlikely that a group of geographically widespread rodent species could have been eliminated by predators, and so the most likely explanation is that there was a significant habitat reconstruction from White Rock to Borchers time. Because of the absence of terrestrial arvicolines and the presence of *Sigmodon*, the time represented by the Borchers local fauna has been interpreted as a warmer, moister interval as compared to White Rock. Further environmental information is not currently available for these localities, but it is noteworthy that 2.5 Ma marks the first evidence of ice-rafting in the North Atlantic, and generally depressed oceanic temperatures worldwide (see review in Vrba, 1988). Repenning (1987) identified this as a significant immigration period for arvicolines (event 6 to event 7).

Then there are patterns that, while not statistically significant when compared to other intervals, nevertheless can offer clues to the fate of a given aggregation. For instance, the earliest faunas, Saw Rock, Fox Canyon and Rexroad Loc. 3, include some species with relatives now currently limited to South America. These are the ‘akodont-like’ cricetines, such as *Calomys* and (probably) *Symmetrodontomys*. About the size of modern *Peromyscus*, they became extinct in Kansas between 3.3 and 2.5 Ma, precisely during the time that saw an influx of archaic arvicolines such as *Ogmodontomys*, *Ophiomys*, *Nebraskomys* and *Pliophenacomys*. One cannot at this point identify the specific agents for this replacement, but lowered sea levels at 2.5 Ma may have introduced a set of arvicoline ancestors from Beringia, or sponsored by habitat modification the explosion of these species throughout the Plains from points westward. As noted above, ice-rafting is first recorded in the North Atlantic about 2.5 Ma, and this specific time period is also considered a major global influence on evolutionary patterns, possibly even in humans (Vrba, 1988).

During the next 1.38 million years (from Borchers to Cudahy time), there was a change from warm to cooler conditions, which saw the introduction on the Great Plains of a new group of advanced arvicolines with rootless molars. One, *Microtus ochrogaster/llanensis*, was the direct ancestor of the modern prairie vole, *M. ochrogaster/ochrogaster* (Martin, 1995). The Aries and Nash local faunas of Meade County and the Kentuck local fauna of McPherson County, not quantitatively examined for this study, represent transition faunas between Borchers and Cudahy time, and include the probable ancestor of *M. ochrogaster* as well as an extinct, large cotton rat (e.g. Kentuck local fauna with *Microtus pliocaenicus* and *Sigmodon* cf. *S. curtisi*) (Hibbard, 1972; Martin, 1975; Eshelman and Hibbard, 1981). During this period, the small grazing cricetine *Sigmodon minor* became extinct. Martin (1986, 1993) suggested that this was a direct competitive outcome, with either the larger *S. curtisi* or species of the genus *Microtus*.

Overall, there is a net increase of six species during the 4 million year study period, but it is unclear if this number has any statistical meaning. The observed number of extinctions ($n = 51$) basically balances the number of immigrations ($n = 57$). It is an amazing testimony to the idea that ecosystems have a limited number of available adaptive zones, at least over limited geographic areas and temporal intervals (see Rosenzweig, 1995). These results also suggest that Van Valen’s (1973) Red Queen hypothesis deserves serious consideration.

Survivorship

It may be useful to begin with some simple theory. With regard to the rodent faunas considered here, four survivorship models can be proposed for testing.

1. *Steeply convex*: most rodent species in a cohort survive through the study period, only to become extinct quickly, towards modern time, and the probability of extinction remains low throughout most of the study period.
2. *Steeply concave*: most species become extinct early in time, and the probability of extinction decreases dramatically with time.
3. *Linear*: the probability of extinction with respect to time is constant.
4. *Slightly convex*: corresponding to a uniform extinction rate, where the same number of species become extinct in each interval of equal duration.

It is important to note that the only statistical distribution resulting in a straight line on a semi-log survivorship plot is the exponential distribution. This distribution is labelled the distribution 'without memory' by statisticians, because the amount of time that has elapsed prior to a termination event has no bearing on the probability of survival for those remaining over the next posited interval. It is an unusual distribution, because in applied systems (such as the lifetime of light bulbs or the decay of a radioisotope), 'survival' is controlled by internally generated processes that result in the system wearing out. The implication of an exponential distribution for any biological system would be that extinction is predominantly, if not exclusively, controlled by external forces (this can include biotic forces such as competition as well as environmental change; external is not meant here to read solely 'abiotic'); the system does not 'senesce' in any conventional sense. If data on a survivorship graph take the form of a straight line, it also follows that extinction has a random, or stochastically unpredictable, tempo except to the extent that one can say that over time extinction is roughly correlated with interval length. Constant extinction, in this usage, is not to be confused with *uniform* extinction, which would in any case generate a slightly convex pattern on a semi-log plot. A uniform extinction rate is of theoretical interest, as it would provide an extinction clock that ticked regularly like the purported mutation clock of the biochemists, but it would not be intuitively expected for a complex ecosystem over geological time.

Figure 5 compares the survivorship of seven species cohorts, spanning times of 4.2 to 0.25 Ma. A highly correlated, systematic decay pattern is obvious for these systems and the data are best fit by a linear model (Table 5). Additionally, extinction rates appear to increase towards modern time. The average slope for Blancan time is 0.228, which translates to about 16% loss per million years. The average for late Irvingtonian and early Rancholabrean time is 0.614, or about 56% per million years. Similar patterns were observed by Jaeger (1994) for Neogene rodents in Europe.

These data can be examined at a more refined level by partitioning cohort survivorship patterns into briefer intervals (= correcting for interval length). When this is accomplished (Table 6), we once again observe a real trend of increasing extinction rates towards modern time, but elevated rates were not restricted to that period. For example, of the 22 original species from the White Rock fauna, 50% were lost during the 0.5 million year period from 2.5 to 2.0 Ma (White Rock to Borchers time). Extinction rates greater than 50% per million years are seen during a variety of the more ancient intervals. In short, there is a pattern of extinctions that appears stochastic with regard to time but comprehensible when reviewed

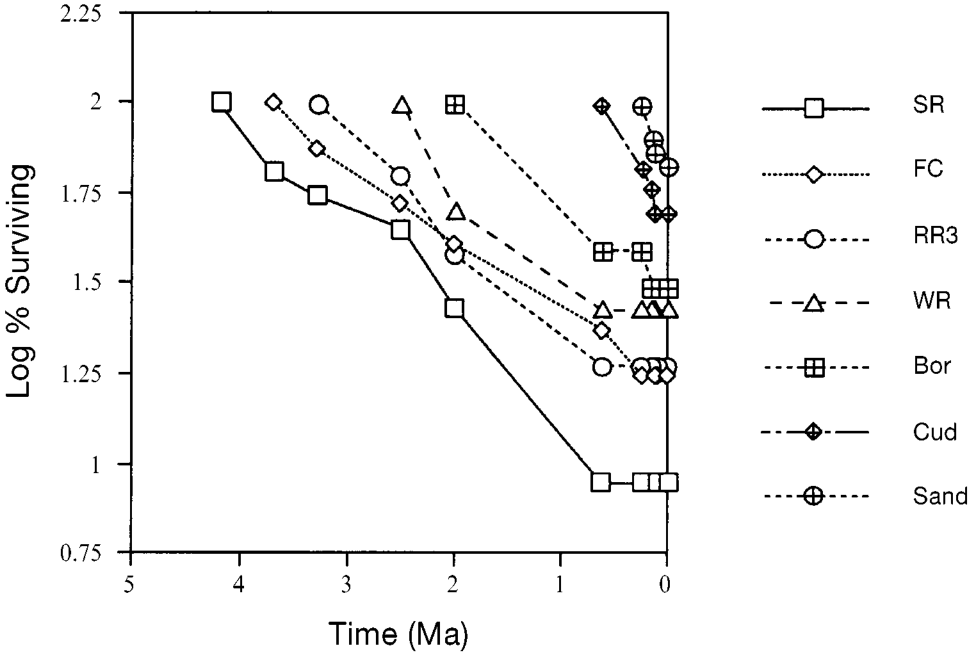

Fig. 5. Survivorship data for the rodent fauna from southwestern Kansas. SR, Saw Rock Canyon; FC, Fox Canyon; RR3, Rexroad Loc. 3; WR, White Rock; Bor, Borchers; Cud, Cudahy; Sand, Sandahl.

Table 5. Descriptive equations for survivorship data

Fauna	*d*	*N*	N_e	*b*	*a*	*r*
SR	4.20	11	10	0.257	0.910	0.992
FC	3.70	17	14	0.200	1.232	0.998
RR3	3.30	16	13	0.218	1.231	0.982
WR	2.50	22	16	0.205	1.389	0.951
Bor	2.00	13	9	0.260	1.472	0.986
Cud	0.62	12	6	0.532	1.670	0.973
Sand	0.25	15	5	0.695	1.840	0.940

Abbreviations: SR, Saw Rock Canyon; FC, Fox Canyon; RR3, Rexroad Loc. 3; WR, White Rock; Bor, Borchers; Cud, Cudahy; Sand, Sandahl. d = duration of study period; N = number of total rodent species recorded from the study period; N_e = number of species becoming extinct during the study period; r = correlation coefficient based on a linear regression model; b = slope; a = y-intercept.

in the biological and geological context of the times in which they occurred (e.g. immigration waves of potential competitors, eustatic changes in sea level, global climate changes, differential speciation rates, the individualistic response of plant distributions, etc.). It is important to note that these episodes of extinction, with one possible exception (the period of 2.5 to 2.0 million years, from White Rock to Borchers time), are not in excess of expected values given the intervals over which they were measured. This result correlates with the

Table 6. Survivorship examined over brief intervals between Saw Rock Canyon and Sandahl time

	SR		FC		RR3		WR		Cud		Sand	
I	%E	%/my	%E	%/my	%E	%/my	%E	%/my	%E	%/my	%E	%/my
0.80	10	13	22	28	37	46						
0.62									50	81		
0.50	36	72										
0.50	18	36	12	24	25	50	50	100				
0.40	9	23	25	63								
0.37									33	89		
0.25											33	132

Abbreviations: SR, Saw Rock Canyon; FC, Fox Canyon; RR3, Rexroad Loc. 3; WR, White Rock; Cud, Cudahy; Sand, Sandahl. *I* = interval length in millions of years; %E = percent of fauna becoming extinct during interval; %/my = %E transformed to percent per million years.

linearity of extinction seen in the survivorship analyses. That is, the positive correlation between absolute extinction numbers and interval length is a function of a generally constant extinction rate over the study period.

TESTING FOR THE RED QUEEN

As originally conceived by Van Valen (1973), the Red Queen model proposes that species are involved in a complex, dynamic competitive dance choreographed by the environment. The fitness of one competing species is directly affected by the fitness gains and losses of others in its adaptive zone, and natural selection operates continuously to drive each species towards an optimum condition which is never reached because the adaptive landscape changes continually. Van Valen (1973) proposed this hypothesis to explain his observation that most animal groups go extinct at a constant rate. In this model, on the scale of millions of years, the Red Queen is driven by stochastically constant environmental change. Briefly then, the Red Queen *competitive dynamic* on the scale of ecological time results in the *observed pattern and process* of constant extinction on a scale of millions of years. It is driven by the *mechanism* of stochastically constant environmental change. Translated into simple mathematical terms, this implies an exponential distribution of extinction and environmental change. Once again, this does *not* equal uniform change; changes in both are inherently unpredictable, and are expected to occur episodically on the time scales where selection operates. With regard to extinction, the unusual and fascinating aspect of this hypothesis is that there is no long-term benefit to specific adaptations; sooner or later the grim reaper catches all species, and there is no way to predict when extinction will occur. Living long does not imply prosperity. Now for the difficult part; how to recognize the influence of the Queen and her arsenal in the fossil record.

Raup (1978) and Ridley (1993) suggested that a log-linear plot of cohort survivorship in real time would provide strong evidence for the Red Queen's influence. Certainly, a log-linear plot is necessary for the Red Queen to be operating, but it is not sufficient for her identification. The reason for this is that log-linear plots of extinction can result from either biotic (e.g. competitive) or abiotic (e.g. climatic) influences. Stenseth and Maynard Smith

(1984), Rosenzweig *et al.* (1987) and Kauffman (1995) have all demonstrated that an aggregate of species may opt for a strategy in which evolution, and therefore fitness competition, ceases. This is referred to as an evolutionarily stable strategy (ESS). In the ESS model, extinctions still occur, but competitive co-evolution is not involved. The group fitness landscape stabilizes, and species terminations are due entirely to abiotic causes.

The polycohort plots in this study display an average *r* of 0.975, thus fulfilling the first requirement for identification of the Red Queen's influence. However, Table 6 shows that, within this linear pattern, at a finer scale, there were embedded various pulses of enhanced extinction. To repeat, this is *expected* of the Red Queen's domain, but to prove her presence we must have evidence that many of these extinction events were the result of failed competitive co-evolution; we need some way to discriminate biotic from abiotic causation. A wholly abiotic cause to extinction favours the ESS equilibrium, where stasis of character traits would be expected. It is for this reason that Rosenzweig *et al.* (1987) allied the ESS with the concept of punctuated equilibrium popularized by Eldredge and Gould (1972). Therefore, if we had a dense enough fossil record to compare the morphological traits of guild associates through time, and if we could see those traits changing in ways that are consistent with competitive interaction, this would be helpful in identifying the influence of the Red Queen. But what would we need to perceive? The answer is not simple, for observed patterns of change may have many causes, including a random walk.

Evidence of character displacement (e.g. Dayan *et al.*, 1993), changes that minimize competition and allow guild associates to co-exist, would be of consequence. Almost any stepwise, balanced changes in predators and presumed prey, or in guild associates, would also be circumstantial evidence in favour of the Red Queen's influence. Certainly, it would logically refute the predicted stasis of the ESS equilibrium. Evidence from rodent evolution in the Meade Basin is currently equivocal. We think it likely that environmental change powered the community restructuring from White Rock to Borchers time. On the other hand, the invasion of pastoral habitats by both large species of *Sigmodon* and the ubiquitous *Microtus* probably extinguished the diminutive *Sigmodon minor* and restricted extant arvicolines with rooted molars (the plesiomorphic condition) to sylvan and aquatic habitats. Few morphological studies exist for the Meade Basin rodents, and those that have been done [e.g. *Onychomys*: Carleton and Eshelman, 1974; *Sigmodon*: Martin, 1979; *Microtus* (*Pedomys*) *llanensis*: Martin, 1995] have focused on one genus or species and have not been interpreted in an ecological context. One notable exception is the muskrat, *Ondatra zibethicus*. This species, with a 3.75 million year record on the Great Plains, increased in size from about 100 g to approximately 1 kg. Martin (1996b) discussed the profound changes this implies in many natural history and physiological parameters. Most Pliocene and Pleistocene rodents, on a global scale, do not characteristically demonstrate stasis in size or dental morphology. The most dominant theme is a pattern of complex episodic phyletic change (Martin, 1993).

Even with extant species of the genus *Microtus*, competition seems to have limited the more underived species morphologically (e.g. *M. pinetorum*) to sylvan and marginal habitats. And the dance continues. Martin (1986) summarized a current competitive dynamic that co-occurs at the northern border of the range of *Sigmodon hispidus* and the southern limit of the geographic range of *Microtus ochrogaster* in Kansas, where the diminutive *M. ochrogaster* dominates and expands its range after harsh winters. *Sigmodon hispidus* cannot put on relatively as much fat stores as *M. ochrogaster* and it cannot breed under the snow as does *M. ochrogaster*. However, during warmer years, the larger

S. hispidus expands its range northward at the expense of *M. ochrogaster* because it is much larger and more aggressive. It would be interesting to see if there have been any shifts in dental morphology or size in these taxa through modern time.

Central to the Red Queen hypothesis – indeed, the driving mechanism – is the idea of a constantly and stochastically changing environment. Log-linear species survivorship plots in real time are not, in themselves, direct evidence for this condition. For the Red Queen to be identified as a likely prime player in the assembly of organismal communities, an independent, dynamic climatic record and a pacemaker must be identified. As shown by the deep-sea benthic foraminiferan record of stable oxygen isotopes in Fig. 2, on the 4 million year scale there has been a gradual march from humid, warmer conditions to the temperate seasonality we see today. No significant environmental stasis has occurred. On a finer scale, also shown in Fig. 2, there has been extreme climatic flux. At least 17 interglacial–glacial cycles have occurred in the last 1.65 million years alone (Morrison, 1991). There is considerable evidence that these cycles are driven by variations in Earth–Sun orbital geometry, the Milankovitch mechanism (Morrison, 1991). So the third requirement for activity of the Red Queen is satisfied.

In conclusion, rodent species aggregates (cohorts) in southwestern Kansas changed in composition continuously throughout the 4.2 million year study period, although species diversity, represented by richness, remained fairly stable. Turnover patterns identify one significant pulse of immigration and one of extinction. Survivorship analysis reveals that extinction rates among cohorts were constant with regard to time, but increased between cohorts towards the present. Although we cannot be certain at this time of the operative mechanisms in all of the rodent extinctions during the past 4 million years in southwestern Kansas, the preliminary evidence suggests a combination of biotic and abiotic influences, supporting what Ridley (1993) labels a 'weak' version of the Red Queen hypothesis. Regardless, for rodents of the Meade Basin, life over the past 4.2 million years seems aptly described by the sentiment from Lewis Carroll's novel *Through the Looking Glass*, which both Felsenstein (1971) and Van Valen (1973) used as a metaphor for organisms as players in the evolutionary game: 'Now here you see, it takes all the running you can do, to keep in the same place'.

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