Tracking mammal body size distributions in the fossil record: a preliminary test of the 'rule of limiting similarity'

Robert A. MARTIN

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Abstract. Ecologists have puzzled for years over the distributions of body sizes in organismal communities. G. E. HUTCHINSON (1959) suggested the spacing of body sizes among guild members might serve to reduce competition for resources. He proposed that a ratio of at least 1.3 between average linear dimensions of trophic parts or some other measure in potential competitors would indicate appropriate distance. This ratio would translate to 2.0, or a doubling, when body mass is used as a proxy. These "Hutchinsonian ratios" have been explained by other investigators as statistical anomalies. This study proposes methods, based on the accurate estimation of body mass in extinct species, to track the evolution of body size distributions in mammalian communities. Preliminary data and resulting size ratios from the Fox Canyon local fauna of the Meade Basin in Kansas do not conform to expectations under the rule of limiting similarity.

Key words: Hutchinsonian ratios, body mass, competition, Quaternary mammals, guild, community evolution, biodiversity.

Robert A. MARTIN, Department of Biological Sciences, Murray State University, Murray, KY 42071, USA.

I. INTRODUCTION

In one form or another, evolutionary biologists work to answer the question "How do we explain the diversity of life on Earth?" The ecologist G. E. HUTCHINSON provided a framework for approaching this question by setting up a series of potential explanatory factors, including trophic dynamics, natural selection, plant diversity, and body size relations among species based on a mosaic environment (HUTCHINSON 1959). Fundamental to his model was the premise that competition helped shape organismal communities, and he proposed that body size relations among what were later called "guild" members (ROOT 1967), would illustrate this principle. His expectation, supported by some preliminary data among birds, mammals and insects, was that those guild associates most closely related in size would nonetheless be separated in size by a factor that would serve to minimize competition between them. This would be most obvious if the associates exhibited both sympatric and allopatric distributions, and if the size displacement were observable primarily when they were sympatric. BROWN & WILSON (1956) had earlier termed this sort of response *character displacement*. HUTCHINSON (1959) reasoned that the size displacement would be most likely reflected in feeding, or trophic, structures, such as the culmen in birds. But proxy structures, such as skull length in mammals, were also used in HUTCHINSON's study, and through the years various linear measurements have been used by other authors. HUTCHINSON (1959) concluded that a ratio of at least 1.3 between average measurements of trophic apparati would serve to separate guild members. Following standard physical laws, this extent of linear change would translate to a doubling of body mass. These relationships are often referred to as the "rule of limiting similarity."

Since the publication of the papers by BROWN & WILSON and HUTCHINSON, many studies have been dedicated to testing these hypotheses, with varying results. For example, GRANT (1972) concluded that most studies purporting to prove character displacement were flawed in one way or another. Nevertheless, his own studies support this model at least to a limited extent in birds (GRANT 1986). MAIORANA (1978) pointed out that the same approximate degree of divergence among species could also be seen among developmental stages (larval instars) in arthropods ("Dyar's constant"). After challenging the literature on character displacement and Hutchinsonian ratios on a statistical basis (e.g., SIMBERLOFF & BOECKLEN 1981) Daniel SIMBERLOFF and colleagues proposed recently not only that character displacement was a real phenomenon, but that it could be identified in the fossil record (see review in DAYAN et al. 1993). DAYAN et al. (1993) de-emphasized the exact approximation to 1.3, and instead focused on the *equality* of size ratios among guild members, forming a nonrandom series. In their studies, ratios among guild associates generally averaged between 1.2-1.3. These authors also emphasized that the choice of a variable can influence the results. Body size may not always reflect competitive interactions.

But the most intriguing investigations have come from ecologists who have also looked at aggregations of inanimate objects. For instance, HORN & MAY (1977) reported that HUTCHINSON's rule can also be approximated in aggregations of children's bicycles, sets of kitchen skillets, and groups of musical instruments. MAIORANA (1978) determined that the rule of limiting similarity holds for sets of plates, glasses, small pewter cans and animal figurines. These findings call into question the biological basis of HUTCHINSON's rule and suggest instead that HUTCHINSON may have discovered, not an underlying ecological principle, but a general mathematical relationship among any objects in assemblages; that is, a statistical artifact. EADIE et al. (1987) provided an elegant mathematical argument to support this alternative.

The reality of competition and coevolution are rarely debated any longer; rather, we need to know the extent of these processes in shaping entire animal and plant communities. The ongoing controversy on the meaning of size ratios in animal communities has been interesting and sometimes ingenious, but there has been only minimal movement towards resolution of this issue. This is primarily because there has been no way to examine the evolution of such communities; that is, community arrangement at the species level in evolutionary rather than ecological time. It is my contention that with increased density of the Quaternary mammal fossil record and the development of methods to estimate body size and other parameters in mammals, the evolution of community structure may become accessible (also see LEGENDRE 1986). In this brief essay I will attempt to show how this may be accomplished, and I will also provide some preliminary data from a mammalian fossil fauna in the Meade Basin of Kansas as an example.

When I first considered this project, I had intended to restrict my focus to the seed-eating guild of midwestern rodents, if for no other reason than to have a direct comparison with investigations of this guild in desert communities (e.g., BROWN et al. 1986). However, I decided to expand the study to include all of the small mammalian herbivores that might have interacted with one another in any fashion, and then to compare results from a variety of subsets of this small mammal community defined on different premises. For example, a number of different arvicolines have inhabited the Meade Basin over the past 3.7 million years, beginning with *Ogmodontomys poaphagus* and *Pliophenacomys primaevus* at Fox Canyon, and I felt it would be instructive to follow the progression of changes in this generally aggressive, grazing contingent along with modifications in species composition of the granivores.

II. MATERIALS AND METHODS

The principles upon which body size estimation in extinct mammals are based have been discussed at length in a number of papers and at least one book (MARTIN 1986, 1993; GINGERICH 1990; DAMUTH & MACFADDEN 1990), and will not be repeated here. Suffice it to say that accurate estimation of average values for body mass of extinct mammal species is possible based on tight correlations between mass and various dental and skeletal measures among extant species. Regression analyses can lead to predictive equations with high correlation coefficients (although one cannot always infer extreme accuracy from such high *r* values; SMITH 1990). A compendium of predictive equations was published by DAMUTH & MACFADDEN (1990) and other equations have since been reported for a variety of mammalian taxa (e.g., LEGENDRE & ROTH 1988; MARTIN 1993).

The data for this study include body mass estimates for five groups of rodents: sciurids, cricetines, arvicolines, heteromyids and zapodines. The equations published by MARTIN (1986, 1993) were used for cricetines and arvicolines, but new equations were developed here for heteromyids and sciurids. Because there are not enough living zapodids upon which to base a predictive equation limited to that group, and because there is general agreement between the shape of advanced zapodine first lower molars and those of cricetines, the cricetine equation was used to estimate jumping mouse body mass. The full set of equations for this study are as follows (y in g; x in mm):

Sciurids	$y = 35.5x^{2.81}$	$r^2 = 0.96$
Heteromyids	$y = 44.7 x^{3.19}$	$r^2 = 0.70$
Cricetines	$y = 4.05 x^{3.33}$	$r^2 = 0.96$
Arvicolines	$y = 0.71 x^{3.59}$	$r^2 = 0.88$

Length of the lower fourth premolar was used for sciurids and heteromyids; length of the lower first molar was used for cricetines and arvicolines.

I measured lengths of the P4 and M1 in small mammal fossils from all of the late Pliocene and Pleistocene mammalian faunas from the Meade Basin of Kansas housed at the Museum of Paleontology, University of Michigan, and calculated average values for these teeth for all taxa. I made similar measurements on as many modern species as I could find from the Meade County area in collections of the Museum of Zoology, also at Michigan. In some cases a modern population from another county or state had to be substituted. Body mass information from specimen tags was recorded when available. Only results for the Fox Canyon l.f. (local fauna) at 3.7 Ma (million years ago) and the modern mammal fauna from Kansas are reported here. I followed the identifications of C.W. HIBBARD and his students for fossil specimens, but I cannot comment on the validity of their taxonomic assignments outside of the zapodines and arvicolines, which I have studied in detail. I do feel fairly secure that the species in Table I from the Fox Canyon l.f. are valid for the time of deposition. Because of space limitations, original data from the samples cannot be presented here and are available on request. I followed ZAKRZEWSKI (1975) and LUNDELIUS et al. (1987) for stratigraphic arrangement and ages of the Meade County faunas.

III. RESULTS

Table I presents body mass estimates and size ratios for small mammals from the Fox Canyon I.f. Seventeen species of rodents ranging in size from 7.4 g (*Baiomys kolbi*) to 435 g (*Spermophilus* sp.) are represented. In Table II we see that the modern small mammal fauna of Meade County includes 14 species with a 7.0 g (*Perognathus flavescens*) to 158 g (*Spermophilus tridecemline-atus*) range. At Fox Canyon there are nine cricetines (53 %), three heteromyids (18%), one zapodid (6%), two sciurids(12%), and two arvicolines (12%). The modern fauna includes six cricetines

Table I

Body size relations of the small mammal fauna from Fox Canyon, Kansas (3.7 Ma). Est. = estimated, W = mass, R_{hw} = Hutchinsonian ratio calculated from body mass estimates, R_{hl} = Hutchinsonian ratio calculated from P4 or M1 length averages; only those species in the same families can be compared directly

Species	Est.W(g)	R _{hw}	R _{hl}
Baiomys kolbi	7.4	alat C <u>u</u> ngslad	101.000-00000
Reithrodontomys rexroadensis	9.2	1.24	1.07
Reithrodontomys wetmorei	10.2	1.11	1.03
Perognathus pearlettensis	11.3	1.11	10000-00-000
Peromyscus baumgartneri	14.6	1.29	-
Zapus rinkeri	16.3	1.12	1.03
Bensonomys arizonae	20.2	1.24	
Symmetrodontomys simplicidens	23.7	1.17	1.05
Peromyscus sawrockensis	26.6	1.12	1.04
Perognathus rexroadensis	27.6	1.04	
Onychomys gidleyi	29.2	1.06	—
Pliophenacomys primaevus	35.8	1.23	
Ogmodontomys poaphagus	39.8	1.11	1.03
Prodipodomys centralis	75.9	1.91	-
Neotoma quadriplicatus	172	2.27	-
Spermophilus howelli	242	1.41	-
Spermophilus sp.	435	1.80	1.23
	Mean $R_h = 1.33$		

Table II

Body size relations of the modern small mammal fauna from Meade County, Kansas. Est. = estimated, W = mass, R_{hw} = Hutchinsonian ratio calculated from actual (not estimated) body mass, R_{hl} = Hutchinsonian ratio calculated from P₄ or M₁ length averages; only those contiguous species species in the same families can be compared directly

Species	W (g)	Est.W(g)	% Error	R _{hw}	R _{hl}
Perognathus flavus	6.8	8.3	22	-	_
Perognathus flavescens	7.0	5.9	5.9	1.03	1.11
Reithrodontomys montanus	10.0	9.5	5	1.35	-
Reithrodontomys megalotis	13.0	11.3	13	1.30	1.05
Peromyscus maniculatus	19.0	12.7	33	1.46	1.04
Peromyscus leucopus	22.0	19.4	12	1.16	1.14
Synaptomys cooperi	36.0	38.9	8	1.64	-
Onychomys leucogaster	37.0	36.8	0.05	1.03	-
Perognathus hispidus	40.0	21.0	48	1.08	-
Microtus ochrogaster	51.0	36.7	27	1.28	-
Dipodomys ordii	60.0	84.5	41	1.18	-
Sigmodon hispidus	100.0	91.5	8.5	1.67	-
Spermophilus spilosoma	113.0	105	7	1.13	-
Spermophilus tridecemlineatus	158	105	34	1.40	1.00
Mean $R_h = 1.29$					1.09

(43%), four heteromyids (29%), two sciurids (14%), and two arvicolines (14%). There are no zapodids.

Size ratios derived from both linear dental measurements and body mass estimates are provided in Tables I and II. Obviously, only those species for which the same dental dimension was measured can be directly compared with regard to a linear measure. The average size ratios based on linear dental dimensions in both the Fox Canyon and modern mammalian faunas are slightly above 1.0, whereas those based on mass estimates average around 1.3.

In Table II, body mass averages taken directly from specimen tags or from the literature (when tag data were unavailable) were compared to those generated from predictive equations. Most estimates are reasonably accurate, but in a few cases the error appears to be pronounced. This is especially true for the heteromyids and sciurids, where the prediction error is in excess of 30 percent in three cases. This seems to be reflected in the lower correlation coefficients for the predictive equations in these two groups, and larger sample sizes of modern species may help to correct this problem in the future.

Fig. 1 presents a direct comparison of rodent herbivores under 100 g from the Fox Canyon l.f. with those of the modern fauna from Meade County. Some observations of interest include which species fill which mass categories, the absence or presence of certain species, the relative proportion of different taxa and especially the *gaps*, or absences of species in certain mass ranges. For instance, the range from about 22-35 g was well populated at 3.7 Ma, but is empty today. The range from 40-50 g is empty in both faunas.



Fig. 1. Body size distribution of rodents under 100 g from the Fox Canyon l.f. and modern Kansas fauna.

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IV. DISCUSSION

The complexity of herbivore associations and their abiotic environment assures that an analysis of this sort will not reveal all of the intricacies of mammalian community evolution, if for no other reason than that birds and ants are also important potential competitors (BROWN et al. 1986). However, we can generate some insights that are unavailable to investigators working in "ecological time" that should provide a welcome addition to their data base. For instance, in this preliminary data set we do not gain confirmation for the principle of limiting similarity. The size ratios for linear dimensions from the Fox Canyon and modern Meade Basin data sets (Tables I-II), which should average about 1.3, instead average less than 1.1. The associated mass ratios, instead of averaging close to 2.0 as predicted by HUTCHINSON's model, average about 1.3, the expectation for linear dimensions. A quick scan of the tables also shows that the ratios are not equal, regardless of their value. Thus, neither the small mammal fauna 3.7 Ma or the modern Kansas fauna from the same area demonstrate a size organization that would suggest a diminution of competition. Rather, there seems to be abundant competitive potential in most size categories. However, one could argue that Table I includes a number of species that are not members of the same guild. For instance, Onychomys gidleyi was mostly carnivorous, Pliophenacomys primaevus and Ogmodontomys poaphagus were likely grazers, and the spermophiles were likely diurnal and are very large. Consequently, I constructed Table III with a more limited data set from Fox Canyon, the granivorous cricetines. Here, too, the average Hutchinsonian ratio for body mass, not including the large Neotoma quadriplicatus, is around 1.2.

Table III

Body size relations of the cricetine rodent fauna from Fox Canyon, Kansas (3.7 Ma). Est. = estimated, W = mass, $R_{hw} =$ Hutchinsonian ratio calculated from body mass estimates

Species	Est.W(g)	R _{hw}	
Baiomys kolbi	7.4		
Reithrodontomys rexroadensis	9.2	1.24	
Reithrodontomys wetmorei	10.2	1.11	
Peromyscus baumgartneri	14.6	1.43	
Bensonomys arizonae	20.2	1.38	
Symmetrodontomys simplicidens	23.7	1.17	
Peromyscus sawrockensis	26.6	1.12	
Neotoma quadriplicatus	172	_	
Mean $R_h = 1.24$			

Gap analysis, or the comparison of empty size categories between faunas, may prove instructive in a number of ways. Why is the region between 22-35g empty in the modern fauna but filled in the fauna at 3.7 million years? A number of hypotheses come to mind. These differences might be due to estimation error, and therefore the gaps would be artificial. Abiotic influences may have led to local extirpations. Competition may have eliminated some species. These questions may be testable, but careful consideration will be necessary to determine how to go about it. For instance, we need to identify the proper statistical procedures to evaluate the progression of species replacements in different local faunas. Also, the data may be transformed, evaluated and interpreted in ways that may prove equally or even more instructive (e.g., MAIORANA 1990). The influence of body size on speciation rate should also be considered. SCHOENER (1974) suggested that contiguous size ratios should increase as one goes up the size scale. He provided an ecological/adaptive explanation for this phenomenon, but an equally likely proposition is that increased ratios (if such a trend actually exists) are created by gaps at the higher end of the size continuum because larger animals speciate less frequently than small ones (MARTIN 1992).

My purpose in this exercise has been to acquaint the reader with relatively new methods for examining the evolution of mammalian guilds and communities. Studies on this subject can range from testing ecological concepts such as the rule of limiting similarity to the more ambitious question of determining if mammalian communities are random associations or tightly coevolved, nonrandom entities. Preliminary data from the late Pliocene Fox Canyon 1.f. of the Meade Basin of Kansas are intriguing, and do not seem to conform to expectations under HUTCHINSON's model of niche segregation. However, the question remains open. It may be that plant communities in southwestern Kansas 3.7 Ma were more patchy than today, and that the species represented in the Fox Canyon 1.f. were actually separated during the time of deposition. Another variable, such as incisor width, might better express competitive spacing than molar size or body mass. Much remains to be done, but the recent wave of interest by investigators throughout the world in using the fossil record to test important ecological as well as evolutionary models is exciting, and I look forward to the time when ecologists will regularly cite paleobiological research to substantiate the historical perspective of community structure.

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