

INFERRING BIOME ASSOCIATIONS OF RECENT MAMMALS FROM SAMPLES OF TEMPERATE AND TROPICAL FAUNAS: PALEOECOLOGICAL CONSIDERATIONS

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Reconstruction of past faunal assemblages is of primary concern to paleontologists because it yields important information concerning patterns of community structure, biogeography, and paleoclimatology. Unfortunately, the process of fossilization is serendipitous at best, resulting in fossil beds that only contain a sample of the extant fauna that existed at the time of fossilization. Herein, we examine the degree to which incomplete sampling of four well-known small mammal faunas gives rise to uncertainty concerning the biome association of each site using neontological data from two tropical (Brazilian Cerrado and Gallery Forest) and two temperate (Kansas Prairie and Kentucky Mixed Deciduous-coniferous Forest) areas. Two simulation approaches (variable and fixed sample sizes) were applied to each set of data to ascertain what proportion of the mammal fauna must be sampled before inferring the correct biome to which the fauna pertained. In the variable sample size approach, species were selected at random from the species pool until the sample correctly identified the biome from which the sample was obtained; this was repeated 200 times for each of the 4 sites. In the fixed sample size approach, a series of simulations were conducted in which each simulation had a fixed number of species, beginning at 2 and increasing at regular intervals until the entire fauna was included in the sample. The number of species required to correctly associate a site with the proper biome was highly variable for three of the four sites. As a result, the number of species required in a sample to be 95% certain of the biome association of Mixed Deciduous-coniferous Forest, Prairie, and Gallery Forest sites represented a large proportion of the fauna in each case (78%, 88%, and 89%, respectively). In contrast, only 23% of the fauna needed to be sampled from the Cerrado site to obtain the same level of confidence. Adjusting the Cerrado analysis for the effect of endemic species only resulted in an inflation of this value to 33%. The effects of endemics in reducing the certainty of biome associations are only pronounced when sample sizes are small compared to the total species pool. The accuracy of estimating the correct biome association of a fauna is predicated upon the proportion of the fauna in the sample as well as the particular distributional patterns of the species that compose the fauna. Caution should be exercised when inferring the biome association of fossil sites because neither of these features of the sample are usually known. Moreover, even when these features are known, as in the neontological analyses, a large proportion of the fauna frequently is required to be confident of the correct biome association of the fauna. Results indicate that the body size of species found in a fossil assemblage or their ordinal taxonomic affinities can affect the probability of accurately deducing paleoenvironments. Smaller species, and members of the orders Rodentia or Insectivora, are more stenotopic than larger species, or members of the orders Artiodactyla and Carnivora. Fossil assemblages containing only members of the latter groups will consist of

wide-ranging species of broad habitat tolerance. Thus the paleoenvironment of such a fossil assemblage will be difficult to discern.

KEY WORDS: Mammals, biomes, paleoecology, habitats.

INTRODUCTION

Paleontology offers a window through time that permits a view of ongoing biological processes and may allow us to examine how these might have originated, or how they operated in the past. Ecologists studying recent organisms must deal with communities that are the result of selective forces which occurred well before the earliest ecologist began making observations of nature. Indeed, like the light from distant stars that show tonight where the stars were millions of years ago, present-day communities are products of forces and interactions that occurred long ago. Thus Janzen and Martin (1982) described Neotropical forests in Central America as possibly being in a disclimax situation, where trees still produce seeds that have characteristics which apparently evolved to attract long extinct mammals (gomphotheres) as seed dispersers. Paleoecology is concerned with this "interaction between... the evolutionary consequences of ecological properties" (Kitchell, 1985, p. 92). Since its inception as a field of study, paleoecology has borrowed heavily from both theoretical and empirical ecology (e.g., Shotwell, 1955; Osman and Whitlatch, 1978; Grayson, 1978; Holtzman, 1979; Kitchell, 1985). Paleontologists are interested in deducing as much ecological insight as possible from a fossil assemblage, but especially have been concerned with describing paleoenvironments and the structure of fossil communities (Hoffman, 1979; Hopson and Radinsky, 1980). How community structure relates to possible competitive interactions or predator-prey relationships is an outgrowth of community organization described by patterns of co-occurrence in fossil beds (e.g., Dodson *et al.*, 1980; Prothero and Sereno, 1982). The data for such studies is composed of the fossils from one or more localities that are considered members of the same assemblage, i.e., are conterminous in both space and time.

Deciding which fossils are members of the same assemblage is no simple task. Fossil formation is in itself an unlikely occurrence, and many taphonomic processes influence which species will be buried together (e.g., Wolff, 1975; Holtzman, 1979; Koch, 1978; Lasker, 1978; Buzas *et al.*, 1982; Retallack, 1984; Kidwell, 1986). Despite the challenges of reconstructing a fossil assemblage, analysis of such communities can yield important information on paleoclimates and macrohabitat distributions (see Graham *et al.*, 1987, for an extended analysis), as well as information on biogeography (e.g., Marshall, 1979), habitat selection (e.g., Andrews and Evans, 1979), or community dynamics (e.g., Buzas *et al.*, 1982; Webb, 1976).

As mammal ecologists, we are aware of the paucity of good data on community structure for mammals from any particular site. Contrary to what one might think, few localities have been sampled adequately to yield a complete list of co-occurring mammal species, especially if flying and terrestrial forms are both included in the studies. No study has yielded reliable information on occurrence and abundance of each species included in an entire mammal assemblage. Not one. Knowing the limitations on such data, even for extant communities, we wondered if estimates of macrohabitat associations of fossil mammal assemblages were accurate given that fossil data are much more incomplete than are similar data on living mammals. Because fossilization is a serendipitous process at best, and because fossil beds contain only a sample of the fauna that actually occurred at the time of fossil deposition (Damuth,

1982), we decided to conduct a series of simulations on data from living mammal faunas to ascertain how ecological conclusions about macrohabitat associations might be influenced by samples containing different numbers and combinations of species.

Paleontologists expend a great deal of effort in analyzing apparent adaptations of fossil species to particular environments, particularly as behavioral or ecological parameters influence morphology (e.g., Simpson, 1970). Thus, fossil species that are closely related to extant species that today inhabit a particular biome are assumed to have lived in a similar environment when the fossils were deposited (e.g., Graham, 1985). Similarly, dental adaptations for a specialized diet, such as grasses, or locomotor adaptations such as bipedality, that is commonly associated with drylands, will lead paleontologists to conclude that a particular paleoenvironment was a savanna or a semidesert (e.g., Simpson, 1970; Cooke, 1984).

In reality, species may be quite eurytopic or euryphagic. Even apparently specialized taxa, such as the genus *Dipodomys* (kangaroo rats), which typically occurs in deserts (e.g., Hall, 1981), may include species that are found in grasslands, riverine habitats, or even pine-juniper forests (e.g., Hoffmeister, 1986; Schmidly *et al.*, 1993). Similarly, food habits can be quite labile. Grasshopper mice (*Onychomys*), for example, are considered to be insectivorous, but their diet may consist of a significant proportion of plant matter during certain parts of the year, and may even be supplemented by vertebrates during periods when these carnivores consume lizards or mammals (Egoscue, 1960; Flake, 1973). Given the pronounced lability demonstrated for most ecological attributes of living species, we wondered how such variable factors affect conclusions based upon data from fossil assemblages. We herein examine how sampling of living faunas that have generally well-known habitat associations might affect conclusions about the characteristics of the surrounding environment and, by inference, apply these results to paleontological analyses.

METHOD AND MATERIALS

We utilized data from published sources for most species, as well as our own unpublished data for certain habitats in South America. We decided to limit our analyses to two major biomes: grasslands and forests. Additionally, we decided to compare temperate and tropical sites because it has been suggested that tropical organisms are more habitat specific than are temperate ones (e.g., Terborgh and Winter, 1983; Patterson, 1986, 1991). This would imply that it might be easier to determine macrohabitat associations in a tropical fauna than in a temperate one. Although we do not necessarily agree with the assumption of stenotopy in the tropics (Mares, 1986; Willig and Mares, 1990), it is a well-known hypothesis and merits examination utilizing the present methodology.

Four New World sites in which the terrestrial mammal fauna has been well documented were selected for analyses. The two temperate North American sites included Kansas grassland (Konza Prairie near Manhattan, Kansas, in east-central Kansas; Kaufman *et al.*, 1983; Finck *et al.*, 1986) and the mixed deciduous-coniferous forest of Kentucky (Big Black Mountain in the Appalachians in extreme southeastern Kentucky, Barbour, 1951), whereas the tropical South American sites comprised Brazilian Cerrado (a savanna grassland near Brasilia, Mares *et al.*, 1989) and adjacent gallery forest (Nitikman and Mares, 1987; Mares *et al.*, 1989). The general biome distribution of each mammal species (see Appendix) from each site was determined utilizing the biome descriptions and maps of Barbour and Billings (1988) for North America, and Hershkovitz (1972) for South America, as modified by Mares and Ojeda

(1982). The gallery forest is similar in many respects to both the Atlantic rain forest of Brazil and the Amazonian forest. Many mammal species are shared with both rain forests (Redford and Fonseca, 1986); thus we included the gallery forest in the Tropical Forest Biome, even though it is a narrow forest corridor that winds through the extensive Cerrado grasslands.

The Brazilian Cerrado was the only site found to contain a number of endemic species (4). In neontological studies, endemics immediately give unambiguous information about the biome from which a fauna is sampled, whereas in paleontological studies, such species, because of their restricted distribution and the nature of the fossil record, would not provide information about the kind of biome from which a fossil fauna was obtained, particularly since endemicity is difficult, if not impossible, to ascribe to a fossil species. As a result, the Cerrado site was analyzed in two separate fashions, once considering the presence of an endemic species in a sample as an unerring indicator of the biome association of the fauna, and once considering the presence of endemics in a sample as yielding no information concerning the identity of the source biome. We felt that the latter approach would more closely parallel the situation confronting paleontologists.

We compiled lists of all of the non-volant mammal taxa occurring in each of the four localities. Additionally, utilizing published information on the distribution and habitat selection of each species, as well as our own information on the species, we developed a species-biome matrix for each fauna (see Appendix). We also noted whether or not a species was endemic to a particular biome for the reasons previously mentioned.

An example of how we determined biome association of a fauna is given in Table 1. Five species are differentially distributed over 10 biomes, reflecting the broad range of habitat lability that characterizes most species. However, only biome 2 contains all five species. In the example, all five species must be represented in a sample in order to unambiguously assign that assemblage to biome 2. If only species 2 through 5 were present in a sample, one could not distinguish between biomes 1 or 2. Similarly, if the sample consisted of species 1 through 4, one could not distinguish between biomes 2 or 6. We randomly selected species from the fauna, and continued to increase sample size until the correct biome was identified. Because the species in any faunal assemblage include a combination of species varying from wide-ranging taxa whose ranges encompass many biomes, to more restricted species which might occur in only one or two biomes, the random selection process should have a highly variable success rate. Thus, if three species were randomly selected from a faunal

Table 1 Example of a simulation sample in which 5 species were randomly selected from a fauna before unequivocally identifying the source biome. The presence (1) or absence (0) of a species (row) in a particular biome (column) is indicated in the body of the matrix. A particular sample unambiguously identifies the correct source biome when the product of the entries in only a single column in the body of the matrix is 1. In the example, biome 2 is the only column that contains all ones; all other biomes contain at least one zero.

<i>Species</i>	<i>Biome</i>									
	1	2	3	4	5	6	7	8	9	10
1	0	1	0	1	1	1	0	0	0	1
2	1	1	1	0	0	1	1	0	1	0
3	1	1	1	1	1	1	1	1	1	1
4	1	1	1	0	0	1	0	1	1	1
5	1	1	0	1	1	0	1	0	0	0

pool, and if these three happened to be limited to a single biome (we use endemics merely to illustrate the point), the fauna could be assigned to the correct biome at that time. If wide-ranging eurytopic species were chosen, however, more species would have to be sampled to identify correctly the biome association of the fauna.

We also calculated similar matrices for adaptational mode (e.g., fossorial, bipedal, arboreal, etc.) and for dietary preferences (e.g., omnivore, carnivore, etc.), but analysis of these data is beyond the scope of this paper. We limit our analyses to two major questions: 1) How large a sample of species must be drawn from the fauna in order to arrive at a correct decision as to the fauna's biome association?; and 2) What percentage of samples of a given number of species will yield a correct determination of the biome from which those species were drawn?

Simulation procedures – Two general simulation approaches (variable sample size and fixed sample size) were taken to ascertain what proportion of the mammalian fauna from a particular site must be identified before inferring the correct biome to which the fauna pertained. In the first approach (variable sample size), species were selected at random from a particular species pool (Kansas, Kentucky, Gallery Forest, Cerrado, modified Cerrado) until the set of selected species unequivocally and correctly identified the biome from which the sample was obtained. This procedure was repeated 200 times for each mammalian fauna. The mean number of species required to identify correctly the biome of the species pool, along with the standard deviation and 95% confidence interval of the mean, were estimated for each set of 200 simulations.

In the second approach (fixed sample size), a number of simulations of different sample size were conducted for each of the five mammalian faunas. Each simulation comprised 200 random selections of species from the species pool, but each simulation differed in the number of species selected (i.e., sample size). For each sample size ($N = 2, 3, 4...$ total faunal size), the proportion of the 200 simulations which unequivocally and correctly identified the source biome was determined and plotted to indicate the manner in which sample size affects the correct association of a particular mammalian fauna with the corresponding source biome.

Influence of size and systematic affiliation – Stenotopic species (those whose distributions include only a few biomes) provide considerable resolution when reconstructing paleoenvironments, whereas eurytopic species (those whose distributions include many biomes) provide equivocal information. We evaluated the degree to which systematic or size biases in the content of fossil assemblages could affect the ability of paleontologists to reconstruct paleoenvironments by assessing the association between size or systematic affiliation and the average number of biomes occurring within the geographic range of a species. We categorized all species regardless of site into four size categories (S) based upon weight ($S_1 \leq 100$ g; 100 g < $S_2 \leq 1000$ g; $1,000$ g < $S_3 \leq 10,000$ g; $10,000$ g < S_4) and calculated descriptive statistics (mean and standard deviation) on the number of biomes included within each species' distributional range for each size category. Homogeneity of variances among size categories was evaluated by an F-max test; a pure model I one-way analysis of variance (ANOVA) was conducted to evaluate whether the mean biome breadth differs among size categories (Sokal and Rohlf, 1981).

Systematic affiliation at the ordinal level may also influence the determination of paleoenvironments if different higher taxonomic categories contain species with markedly different biome breadths. We categorized all species regardless of site into nine orders and calculated descriptive statistics (mean and standard deviation) on the number of biomes included within each species' range for each mammalian order. Only a single species of *Perissodactyla* occurred in any of the four sites; it was

excluded from subsequent analyses. Homogeneity of variances among the remaining eight orders was evaluated by an F-max test; a pure model I one-way analysis of variance (ANOVA) was conducted to evaluate whether the mean biome breadth differs among orders (Sokal and Rohlf, 1981).

RESULTS

Variable sample size simulations – This procedure was one of incrementing sample size until the fauna's biome was correctly determined. Since the procedure was repeated 200 times for each of the faunas, it was possible to generate basic statistics on the results. Clearly, great variability characterizes the percentage of a fauna that must be sampled to identify that fauna unambiguously as to its biome association (Table 2). For the fauna of the Brazilian Cerrado, for example, a correct biome association could be obtained, on the average, after only four species had been selected at random (10.9% of the fauna). However, if one wished to be 95% certain that the fauna's environment was correctly identified, it was necessary to increase the number of species to eight (23% of the fauna). Considering the Brazilian Cerrado endemics as providing no information about biome association did little to change the results. The modified Cerrado analysis had a mean value of correct biome determination after only five species had been selected (15% of the fauna) and, for the 95% confidence interval, required 12 species (34% of the fauna) to be selected on the average.

In the grasslands of Kansas, only six species on the average had to be selected to identify correctly the biome association of the fauna, whereas about 29 species (88% of the fauna) had to be selected to have a 95% probability of being correct in the determination of the fauna's biome. The Kentucky forest fauna was correctly identified on the average after nine species had been selected (34% of the fauna), whereas 20 species (80% of the fauna) had to be selected to be within a 95% probability of correctly identifying the biome. In the gallery forest of Brazil, a habitat adjacent to the Cerrado grassland site, the situation was quite different. Here 13 species (43% of the fauna) had to be sampled randomly to arrive at the mean value that correctly identified the fauna as to biome. If one wished to be 95% certain of the results, 28 of the forest's 31 species would have to be sampled (90%). Either way, the pattern of correct faunal biome determination for both the tropical faunal analyses was the same: the grassland biomes could more easily be distinguished than could the forest biomes.

Table 2 Results of variable sample size simulations. Species were selected by incrementing sample size until the fauna's biome was determined correctly. N = faunal pool size; \bar{X} = mean number of species required to identify correctly the fauna's biome after 200 simulations; % fauna of \bar{X} = the mean percentage of the pool sampled to identify the biome; S.D. = standard deviation; 95% C.I. = 95% confidence interval; % fauna of C.I. = the percentage of the fauna that must be sampled to be 95% certain of having ascertained the correct faunal/biome association.

<i>Fauna</i>	<i>N</i>	\bar{X}	% Fauna of \bar{X}	<i>S.D.</i>	95% % Fauna C.I. of C.I.	
Kentucky	25	8.9	33.5	5.4	19.5	78
Kansas	33	5.6	17.0	11.4	28.5	86
Brazilian Gallery Forest	31	13.4	43.1	7.1	27.6	89
Brazilian Cerrado	35	3.8	10.9	2.1	8.1	23
Modified Cerrado	35	5.4	15.3	2.6	11.5	33

Fixed sample size simulations – In these simulations, the sample size was fixed at a particular value (beginning with a sample of two species selected randomly from the known pool) and the sample size was increased until the entire fauna was included in the sample. In the Cerrado grassland (Figure 1), a sample size of only two species correctly identified the biome in 39.5% of the cases. Increasing the sample by a single species improved the rate of correct determination to almost 60%. At four species (10.9% of the fauna), the biome of the fauna was correctly identified approximately 70% of the time. This percentage began to attain an asymptotic value between six and eight species, and did not improve appreciably if sample size were increased beyond eight (23% of the fauna). As expected, in the modified Cerrado (Figure 2), where endemics were considered to provide no resolution as to biome association, it required a larger sample size to identify correctly the biome, and these results were most pronounced when a small proportion of the fauna was included in a sample. Selection of only two species yielded a rate of correct identification of approximately 13%; selection of four species resulted in a rate of about 30%; and the rate reached an asymptote at a sample size of 12 species. Thus even if endemic species cannot be recognized, biome determination will be correct in more than 90% of the cases after about one-third of the fauna has been examined.

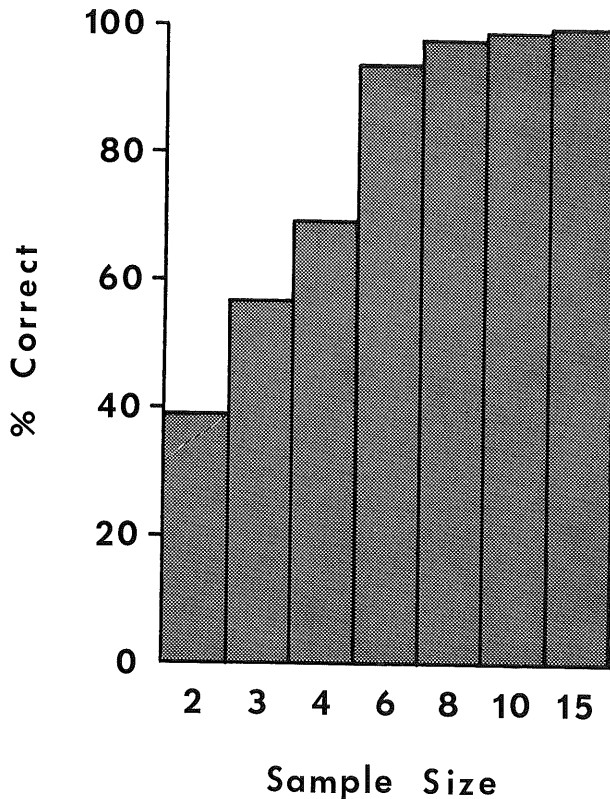


Figure 1 Results of fixed sample size analyses for the Brazilian Cerrado tropical grassland site. Number of species utilized in each sample (sample size) is shown versus the percentage of 200 simulations at that sample size that correctly identified the biome of the fauna.

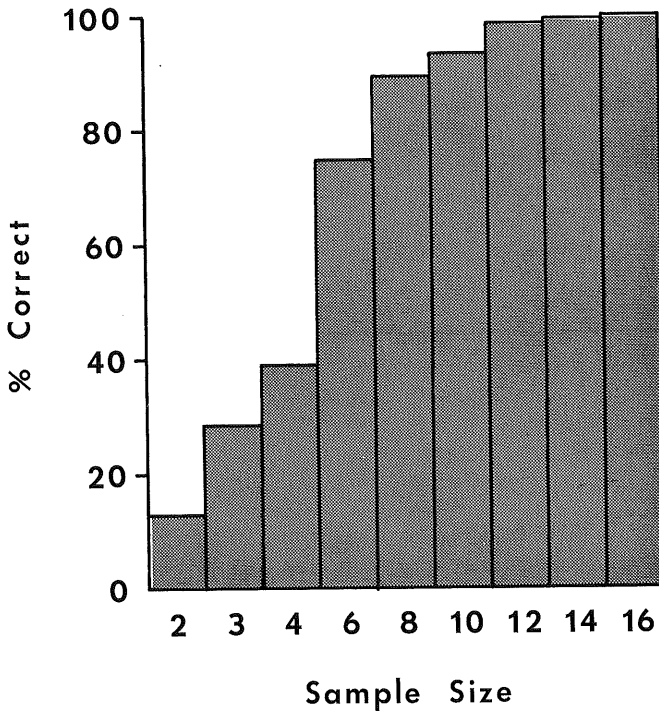


Figure 2 Results of fixed sample size analyses for the modified Brazilian Cerrado tropical grassland site. Endemic species were considered to provide no information as to biome identification. Simulation methodology and graph design as in Figure 1.

In the tropical gallery forest the results were quite different (Figure 3). Selecting two species randomly from the species pool resulted in a correct biome determination only 2% of the time. When eight species (26% of the fauna) were selected, a correct biome determination was made only about 28% of the time. Indeed, an asymptote in the percent accuracy of biome determination with increasing sample size did not occur in the tropical forest biome. Each increase in sample size resulted in a more accurate determination, but biome determinations were not accurate more than 90% of the time until 28 species (90% of the fauna) had been sampled.

In the North American grassland site (Figure 4), a pattern very similar to the Cerrado of Brazil was evident. Sampling only three species (9% of the fauna) yielded a correct biome determination about one-third of the time. The percentage of correct biome determination reached an asymptote between 10 and 12 species (30–36% of the fauna). Increasing the sample size beyond this point did not result in an appreciable increase in the ability to discern the correct biome association of the fauna.

Analysis of the data for the Kentucky fauna of the mixed deciduous-coniferous forest resulted in a pattern similar to that of the gallery forest of Brazil (Figure 5). Sampling a small percentage of the fauna, for example three species (12% of the fauna), resulted in a correct biome determination only about 10% of the time. Increasing sample size to eight species (one-third of the fauna) yielded a correct biome determination less than 60% of the time. No pronounced asymptote occurred as sample size was increased and correct determinations at the 90% level or above did not result until 80% of the fauna was sampled.

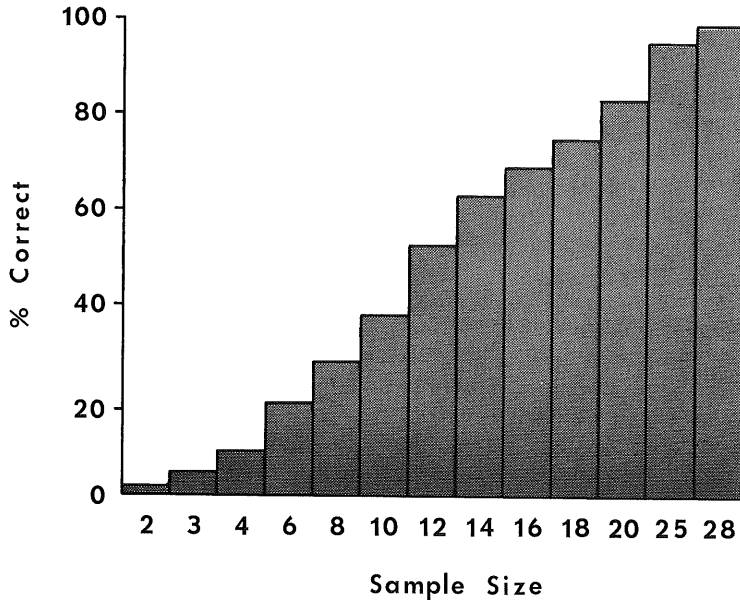


Figure 3 Results of fixed sample size analyses for the Brazilian tropical gallery forest site. Simulation methodology and graph design as in Figure 1.

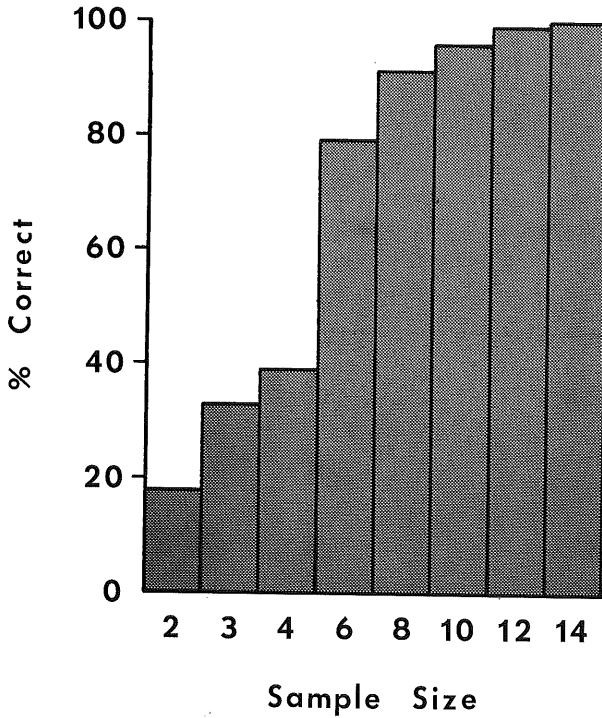


Figure 4 Results of fixed sample size analyses for the Kansas temperate grassland site. Simulation methodology and graph design as in Figure 1.

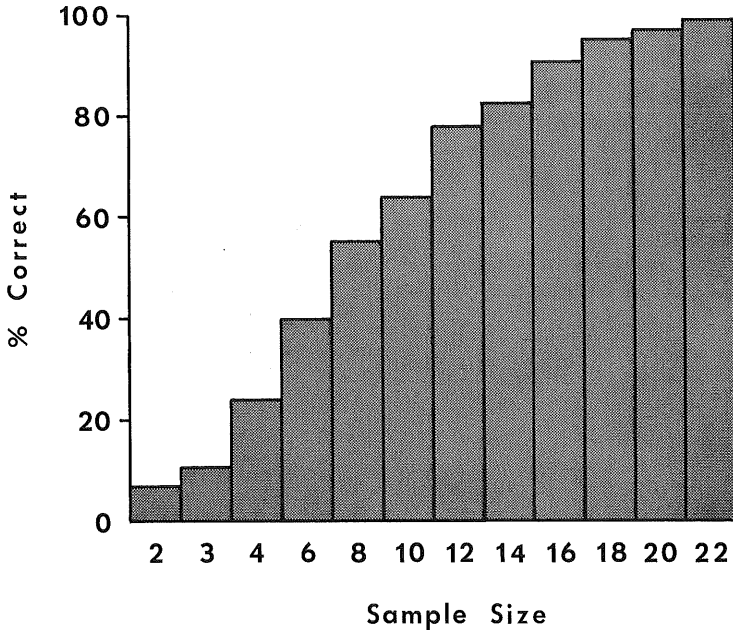


Figure 5 Results of fixed sample size analyses for the Kentucky temperate forest site. Simulation methodology and graph design as in Figure 1.

Influence of size and systematic affiliation – Size-related factors may play an important role in the estimation of paleoenvironments based upon species lists from fossil sites. We detected a very highly significant difference among size categories in the mean number of biomes (mean biome breadth followed by standard deviation – $S_1 = 3.9, 1.43$; $S_2 = 3.8, 2.02$; $S_3 = 5.2, 2.00$; $S_4 = 5.9, 2.53$) across which species were distributed (ANOVA: d.f. = 3, 100; $F = 6.18$; $P = 0.001$). Similarly, systematic affiliation at the ordinal level may influence the estimation of paleoenvironments based upon specimens from fossil digs. We detected a very highly significant difference among the eight mammalian orders in the mean number of biomes (mean biome breadth followed by standard deviation – Marsupialia = 5.0, 2.14; Edentata = 4.5, 1.77; Insectivora = 3.4, 1.72; Primates = 4.3, 0.57; Carnivora = 6.4, 2.29; Artiodactyla = 5.8, 1.50; Rodentia = 3.88, 1.65; Lagomorpha = 4.3, 2.08) across which species were distributed (ANOVA: d.f. = 7, 95; $F = 4.52$; $P < 0.001$).

DISCUSSION

One of the major points that emerges from our analyses is the pronounced differences in the ability to identify correctly faunas that had a grassland biome origin versus those that derived from a forested biome. Our data provide a 4-way comparison of grasslands and forests, as well as a similar comparison of temperate biomes and tropical ones. Recent suggestions (e.g., Patterson, 1986; Diamond, 1980; Terborgh and Winter, 1983) that tropical organisms are stenotopic, whereas temperate species are more wide-ranging are not borne out in our analyses. We found that species of forest

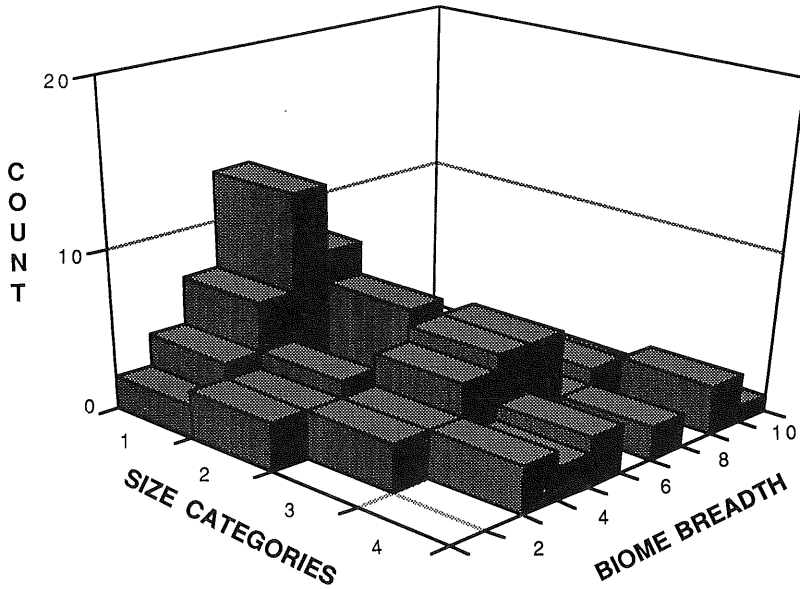


Figure 6 Three-dimensional bar diagram representing the frequency distribution of biome breadths for species occurring within each of four size categories. The distribution of biome breadths for the smaller size categories (S_1 and S_2) is skewed to the left, whereas the distribution of biome breadths for larger size categories (S_3 and S_4) is skewed more to the right. This suggests that smaller taxa, which are more stenotopic, provide more accurate indications of paleoenvironments than do the more eurytopic larger species.

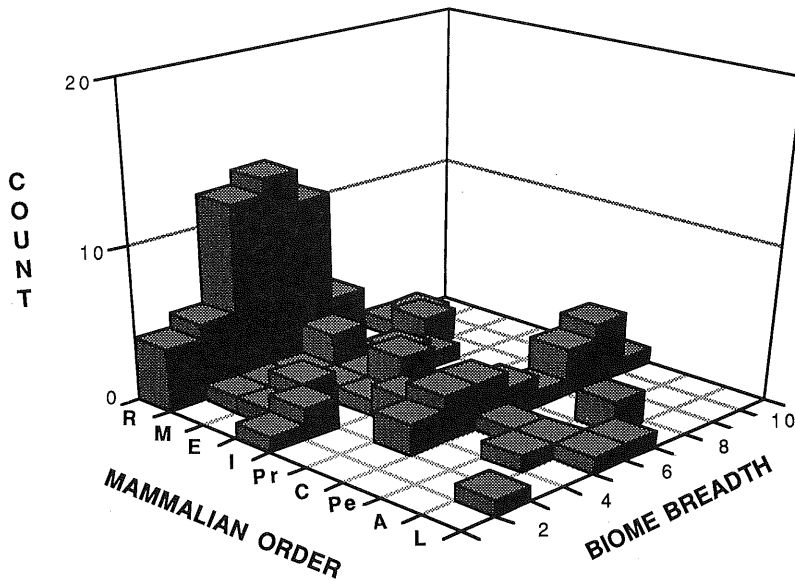


Figure 7 Three-dimensional bar diagram representing the frequency distribution of biome breadths for species contained within each of nine mammalian orders (R = Rodentia, M = Marsupialia, E = Edentata, I = Insectivora, Pr = Primates, C = Carnivora, Pe = Perissodactyla, A = Artiodactyla, L = Lagomorpha). Rodents numerically dominate the mammalian fauna and have a biome breadth distribution skewed to the left, whereas carnivores have a distribution skewed to the right. This suggests that rodents, which are more stenotopic, provide more accurate indications of paleoenvironments than do the more eurytopic carnivores.

mammals, whether inhabitants of temperate mixed deciduous-coniferous forests of North America, or of the tropical gallery forest of Brazil, occur across a broader spectrum of biomes than do grassland mammals. Within the tropics, the patterns of stenotopy and eurytopy are similar to what we determined for temperate faunas. Grassland mammals are less catholic in their biome associations than are forest mammals. Both variable sample size and fixed sample size analyses yielded similar results.

If tropical forest species were more specialized as to biome association, it would have been possible to ascertain correctly the biome of the fauna after a relatively small sample of species had been examined. This pattern was observed in the Cerrado grassland analyses. Both of the Brazilian faunas are tropical. Indeed, they occur within a few meters of one another in markedly different biomes. But the trenchant differences we observed are not related in some mystical manner to latitude, rather they are the result of the type of biome with which the respective faunas are associated.

Forest mammals are suggested to be generalists (= primitive) in many of their morphoecological characteristics (e.g., Hershkovitz, 1962), including dental traits and limb proportions, among others. Grassland species, on the other hand, like the biome with which they are associated, are thought to be more derived (Mares, 1980). Grasslands are plant communities that evolved from forest biomes in response to increasing aridity (e.g., Axelrod, 1950; Webb, 1978), and it is likely that they demanded special adaptations from forest-dwelling mammal species that colonized the newly developed dryland habitats. Certainly our data suggest that grassland mammals are less generalized than forest species, whether in temperate zones or in the tropics.

Our results indicate a number of interesting points for both paleontologists and neontologists, some of which were unexpected. However, we emphasize that this type of analysis would have been impossible had we not been able to describe the habitat associations of all species considered in the analyses with some degree of confidence. We could only do these analyses because literally thousands of papers have been published on the entire set of species considered in this study. Such a plethora of information is, of course, a luxury not available to the paleontologist, who must infer biome associations from only a few fossil localities or from comparisons with recent material. We would surmise, however, that paleontologists usually select the most common habitat of a genus or a species and not one that apparently lies towards the extremes of its range of habitat tolerance. This would be a potential source of error.

Clearly paleontologists would seldom, if ever, have as much information available on faunal composition and biome association as we had for living mammals. Nevertheless, our results have application to paleontology. In grasslands, it is possible to have some degree of confidence in inferences of the biome association of a fauna. This would hold, presumably, for other habitats (e.g., deserts) that demand a degree of specialization from the ancestral forest type of species. However, if a high degree of statistical confidence is desired in biome determination, it may be necessary to sample up to 90% of the fauna. The exception to this pattern was the tropical grassland fauna. Apparently species of the tropical grassland are less likely to occur among diverse biomes than are tropical forest mammals, or temperate grassland and forest faunas.

If endemic species are included in a sample, their effect is only pronounced when sample size is small. Thus in the modified Cerrado analysis, the rate of correct biome determination increases more slowly than in the analysis where endemics are used to identify unambiguously the source biome. However, as sample sizes approach one-third of the fauna, correct biome identification is equally likely whether or not endemism is discernible.

Unlike our simulations, where species were included in a fauna based upon their

being randomly selected from a faunal pool, many processes that contribute to the composition of a fossil fauna are distinctly nonrandom. In addition to taphonomic considerations that can give rise to selective fossilization, other factors influence this phenomenon. For example, some sites may contain principally rodents or insectivores – small mammals that may be quite abundant in certain localities or at particular times of the year and may appear with great frequency in fluvial beds. Similarly, cave faunas that are reconstructed primarily from mammal remains in owl pellets (which themselves result from selective choice of prey by a predator) may be nonrandom assemblages. The manner in which nonrandom sampling affects inferences about paleoenvironments is unclear without knowing in advance whether more eurytopic species have been differentially included or excluded by the nonrandom processes of fossilization and fossil collecting. Our study permits us to comment on the degree to which the determination of a paleoenvironment could be biased as a result of possible differences in body size or taxonomic affinity of species comprising a fossil fauna.

Based upon our analyses of body size categories of all species included in the four faunas utilized in this study, we were able to detect a very highly significant difference among size categories and the variety of biomes in which species occurred. Basically, species of rather small body size (100 grams or less) were found in fewer biomes, on the average, than species of larger size (greater than 100 grams). Small species occurred, on the average, in fewer than four biomes (i.e., were more stenotopic), and larger species were found, on the average, in more than five biomes (i.e., were more eurytopic). Hence, all other things being equal, the recovery of small mammals from fossil sites is more likely to provide an accurate determination of the paleoenvironment at that site than would an equivalent number of fossils of larger mammals.

The ordinal affiliation of mammals comprising a fossil fauna may also exert a significant influence on the estimation of the type of paleoenvironment in which that fauna was found. We categorized all species, regardless of site, into eight orders and detected a very highly significant difference among them in the number of biomes over which they were found. For example, species of Carnivora were found to occur, on the average, over more than six biomes, whereas species in the orders Rodentia and Insectivora occurred in fewer than four biomes on the average. Other things being equal, this means that a selection of specimens taken from a fossil site dominated by rodents and insectivores would be more likely to lead to an unambiguous determination of the correct paleoenvironment of that fossil fauna than would a selection of fossils that included primarily carnivores or artiodactyls.

Our results suggest that biome determinations made from fossil species assemblages can be affected by factors beyond the merely taphonomic, including the type of source biome that gave rise to the fauna, the habitat lability of the constituent species, and the degree of specialized adaptations required of species inhabiting a particular biome.

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APPENDIX

Listing of mammal species by locality and their biome associations (in parentheses). North American biomes are: 1 (Tundra), 2 (Taiga), 3 (Pacific Coastal/Cascade), 4 (Deserts), 5 (Chaparral), 6 (Montane Forests), 7 (Grasslands), 8 (Mixed Deciduous Forest), 9 (Piedmont Oak/Pine), 10 (Marshes, Bogs, Coastal Plain Forest). South American biomes are: 1 (Lowland Rain Forest), 2 (Cerrado), 3 (Caatinga), 4 (Páramo), 5 (Upland Semideciduous Forest), 6 (Upland Rain Forest), 7 (Puna), 8 (Deserts), 9 (Thorn Scrub), 10 (*Araucaria* Forests), 11 (Pampas).

Kansas Grassland

1. *Didelphis virginiana* (3–10)
2. *Blarina hylophaga* (7)
3. *Cryptotis parva* (6–10)
4. *Scalopus aquaticus* (6–10)
5. *Sylvilagus floridanus* (4, 6–10)
6. *Marmota monax* (2, 6, 8)
7. *Spermophilus tridecemlineatus* (7, 9)
8. *Sciurus niger* (6–10)
9. *Geomys bursarius* (7, 9)
10. *Perognathus hispidus* (4, 7, 9)
11. *Castor canadensis* (1–4, 6–10)
12. *Reithrodontomys megalotis* (4, 5, 7)
13. *R. montanus* (4, 7)
14. *Peromyscus leucopus* (4, 6–9)
15. *P. maniculatus* (1–4, 6–9)
16. *Sigmodon hispidus* (4, 7–10)
17. *Neotoma floridana* (6–10)
18. *Microtus ochrogaster* (7,10)
19. *M. pinetorum* (6–10)
20. *Synaptomys cooperi* (2, 6–8)
21. *Zapus hudsonius* (2, 6–8)
22. *Canis latrans* (1–9)
23. *Urocyon cinereoargenteus* (3–10)
24. *Vulpes vulpes* (1, 2, 6–10)
25. *Procyon lotor* (2, 3, 5–10)
26. *Mustela nivalis* (1, 2, 7, 8)
27. *M. frenata* (2, 3, 5–10)
28. *M. vison* (1–3, 6–10)
29. *Taxidea taxus* (2, 4, 5, 7)
30. *Mephitis mephitis* (2–10)
31. *Felis rufus* (2–10)
32. *Odocoileus hemionus* (2–4, 6, 7)
33. *O. virginianus* (2, 3, 6–10)

Kentucky Forest

1. *D. virginiana* (3–10)
2. *Parascalops breweri* (6, 8)
3. *Sorex cinereus* (1, 2, 6–8)
4. *S. fumeus* (6, 8)

5. *Blarina brevicaudata* (2, 6–8)
6. *S. floridanus* (4, 6–10)
7. *S. transitionalis* (6, 8)
8. *M. monax* (2, 6, 8)
9. *Tamias striatus* (2, 6, 8)
10. *Sciurus carolinensis* (6, 8–10)
11. *Glaucomys volans* (6, 8–10)
12. *Reithrodontomys humulis* (6, 8, 10)
13. *P. maniculatus* (4, 7–10)
14. *P. leucopus* (4, 6–9)
15. *Ochrotomys nuttalli* (8–10)
16. *N. floridana* (6–10)
17. *S. cooperi* (2, 6–8)
18. *Clethrionomys gapperi* (1, 2, 6, 8)
19. *M. pinetorum* (6–10)
20. *Ondatra zibethica* (1–3, 8–10)
21. *Napeozapus insignis* (2, 6, 8)
22. *P. lotor* (2, 3, 5–10)
23. *M. frenata* (2, 3, 5–10)
24. *M. vison* (1–3, 6–10)
25. *U. cinereoargenteus* (3–10)

Brazilian Cerrado

1. *Didelphis albiventris* (1–3, 5, 6, 9–11)
2. *Monodelphis domestica* (2, 3, 5, 6, 9)
3. *M. kunsii* (2, 5, 6)
4. *Cabassous unicinctus* (1, 2, 5, 6, 9)
5. *Dasybus novemcinctus* (1–3, 5, 6, 9, 11)
6. *D. septemcinctus* (1–3, 5, 6, 9)
7. *Euphractus sexcinctus* (2, 3, 9)
8. *Priodontes maximus* (1, 2, 9)
9. *Tolypeutes tricinctus* (2, 3)
10. *Myrmecophaga tridactyla* (1–3, 9)
11. *Tamandua tetradactyla* (1–3, 5, 6, 9)
12. *Akodon reinhardti* (2, 5, 6)
13. *Bolomys lasiurus* (1–3, 5, 6, 9)
14. *Calomys callosus* (2, 3, 5, 6, 9, 11)
15. *C. tener* (2, 5, 6, 9)
16. *Juscelinomys candango* (2)
17. *Kunsia fronto* (2, 9)
18. *Oryzomys fornesi* (2, 5, 6, 9)
19. *O. subflavus* (1–3, 5, 6)
20. *Oxymycterus roberti* (2, 5, 6)
21. *Plectomys paludicola* (2)
22. *Cavia aperea* (1–3, 9, 11)
23. *Galea spixii* (1–3)
24. *Hydrochaeris hydrochaerus* (1, 2, 9)
25. *Carterodon sulcidens* (2)
26. *Clyomys laticeps* (2)
27. *Thrichomys apereoides* (2, 3, 9)

28. *Cerdocyon thous* (1-3, 5, 6, 9)
29. *Chrysocyon brachyurus* (2, 3, 9)
30. *Speothos venaticus* (1, 2, 6)
31. *Nasua nasua* (1, 2, 5, 6, 9)
32. *Eira barbara* (1, 2, 5, 6)
33. *Felis concolor* (1-3, 5-11)
34. *Tayassu tajacu* (1-3, 5, 6, 8, 9)
35. *Mazama americana* (1, 2, 5, 6)

Brazilian Gallery Forest

1. *Chironectes minimus* (1, 2)
2. *D. albiventris* (1-3, 5, 6, 9-11)
3. *Marmosa agilis* (2, 3, 5, 6, 9)
4. *Monodelphis americana* (2, 5, 6, 10)
5. *Philander opossum* (1, 2, 5, 6, 9)
6. *Cebus apella* (1, 2, 5, 6, 9)
7. *Alouatta caraya* (2, 5, 6, 9)
8. *Callithrix jacchus* (2, 3, 5, 6)
9. *D. novemcinctus* (1-3, 5, 6, 9, 11)
10. *Sylvilagus brasiliensis* (1-3, 5, 6)
11. *Akodon cursor* (2, 3, 5, 6)
12. *B. lasiurus* (1-3, 5, 6, 9)
13. *Holochilus brasiliensis* (1, 2, 6, 9, 11)
14. *Nectomys squamipes* (1, 2, 6)
15. *Oryzomys bicolor* (1, 2, 5, 6)
16. *O. capito* (1, 2, 5, 6, 9)
17. *O. concolor* (1, 2, 5, 6, 9)
18. *O. nigripes* (2, 5, 6, 9)
19. *Rhipidomys mastacalis* (1, 2, 5, 6)
20. *Coendou prehensilis* (1, 2, 5, 6)
21. *H. hydrochaerus* (1, 2, 9)
22. *Dasyprocta azarae* (2, 5, 6, 9)
23. *Proechimys longicaudatus* (1, 2, 5, 6, 9)
24. *Procyon cancrivorus* (1-3, 5, 6, 9)
25. *Eira barbara* (1, 2, 5, 6)
26. *Felis pardalis* (1, 2, 5, 6, 9)
27. *F. yagouaroundi* (1, 2, 5, 6, 9)
28. *Tapirus terrestris* (1, 2, 5, 6, 9)
29. *Speothos venaticus* (1, 2, 6)
30. *Tamandua tetradactyla* (1-3, 5, 6, 9)
31. *Nasua nasua* (1, 2, 5, 6, 9)