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Turnover Patterns and Species Longevity of Large Mammals from the Late Pliocene and Pleistocene of Southern Africa: A Comparison of Simulated and Empirical Data

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Two models of faunal turnover patterns were tested against observed frequencies of first and last appearances of large mammals from the late Pliocene and Pleistocene of southern Africa. Simulations based on a constant turnover model with subsequent sampling at fossil sites adequately explained the empirical data. Under a model with turnover pulses at the times of putative climatic events, i.e. at 2.5 and 0.9 Myr, simulated ranges of first and last appearance frequencies encompassed the fossil data with the exceptions of four time intervals in which observed frequencies of last appearances did not fit the model. Concordance between simulated and empirical data for apparent species longevity did not differentiate between the two models, but served to confirm the general validity of the assumptions of the simulations. Differential sampling of species at fossil sites is the simplest explanation for the observed "trends" in species appearances. The fossil record is then explicable by a model of constant turnover without the unnecessary conjecture of periodic abiotic forcing.

1. Introduction

It has been posited that abrupt climatic changes during the Pliocene and Pleistocene were largely responsible for evolutionary events among African mammals and, in particular, induced pulses of faunal turnover (Turner, 1983, 1990; Vrba, 1985*a*, *b*, 1988, 1993). One of these pulses, at the time of a putative global cooling event at 2.5 Myr (million years) (Shackelton *et al*., 1984; Van Zinderen Bakker & Mercer, 1986; Prentice & Denton, 1988), may have been associated with the origin of the genus *Homo* (Hill *et al*., 1992). Another climatic event has been hypothesized for 0.9 Myr (Prentice & Denton, 1988), near the time of origin of archaic *Homo sapiens*.

Trends among the fossil mammals from the southern Africa subcontinent have provided only moderate support for the turnover-pulse model. Vrba (1985*b*) based the model on bovids which showed more profound changes in East Africa than in the southern subcontinent. Turner (1990) was not able to distinguish a pulse among African carnivores, but suggested that a time-lag in turnover should be expected among large carnivores following climatic events. Both Vrba (1985*a*, 1988, 1993) and Turner (1990) suggested that climatically induced turnovers should affect a wide variety of lineages. Tobias (1991: 138) tallied such a spectrum of species, stating that "man, in the sense of *Homo*, was born as part of this wave of change, to a world of drier conditions, a rather rapidly changing biota and a generally more challenging and exacting environment".

In view of the need to look more closely at trends among multiple lineages, a complete data base of identified fossil mammal species from the Pliocene and Pleistocene of southern Africa was compiled and a chronological framework established (McKee, 1993; McKee *et al*., 1994). A cursory view of first and last

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appearances of large mammal species from these data, in the style presented by Vrba (1985*b*), is indeed suggestive of turnover-pulses (Fig. 1). There are sharp increases in apparent turnover at around 2.6 and 0.9 Myr. An additional apparent pulse occurred around 1.8–1.6 Myr, corresponding to the southern African origin of *Homo erectus* (*sensu* Clarke, 1985) and distinct changes in composition of biodiversity (Turner, 1990), but in response to no known climatic event.

Scrutiny of the fossil record in East Africa has led to challenges of the turnover-pulse hypothesis (Hill, 1987; Bishop, 1993). Likewise, despite the appearance of turnover-pulses among southern African lineages, some corresponding to global climatic changes, the lack of clarity in aspects of the fossil record leave sufficient room for doubt. Sampling certainly affects the first and last appearance of taxa, as opposed to the true time of origin and extinction (e.g. Hill, 1987; Marshall, 1990). Local environmental factors and taphonomic agencies further obscure the correlation between evolutionary events and the fossil record (Brain, 1981; Hill, 1987; McKee, 1991; McKee *et al.*, 1994).

Judgement on the tenability of the turnover-pulse hypothesis, as it applies to trends in the southern African data, thus requires more rigorous testing. In order to test the hypothesis, a general model was developed to simulate species turnover and subsequent sampling at fossil sites. Two specific models were tested against the fossil data, one with constant turnover and the other with two pronounced pulses. If the pulses were real, and indeed the dominant mode of turnover (Vrba, 1985*a*, 1993), then they should stand out beyond the expectations of the former model and fit those of the latter.

2. Methods and Assumptions

Use of the data compiled on fossil mammals identified from key southern African fossils (McKee, 1993; McKee *et al.*, 1994) allowed for the establishment of dates of species' first and last appearances. Due to the total absence of identified microfauna (rodents, bats, shrews, etc) from many of the sites, only larger mammals were used for this analysis. Those species identified with the qualifiers "cf." or "aff." were included for analysis, following Turner & Wood (1993). Taxonomic inequities in delineating fossil species could affect the data, so it must be assumed that the effect would be negligible with respect to the turnover patterns tested here.

Site units chosen for this analysis were those for which a reasonable temporal context could be ascertained. Dates given for the site units (Table 1) were derived from a synthesis of paleomagnetic dates (Brock *et al.*, 1977; McFadden *et al.*, 1979), electron-spin-resonance dates (Grün *et al.*, 1990*a*, *b*; Schwarcz,

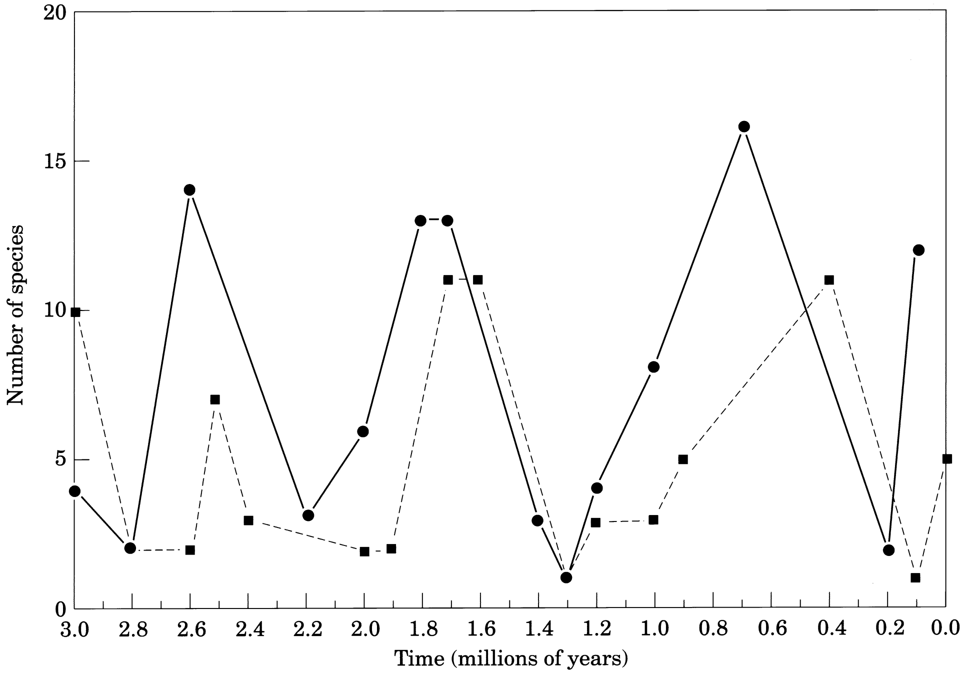

FIG. 1. Absolute frequencies of first and last appearances of species from the southern African site units listed in Table 1. (●) First appearances; (■) last appearences.

Table 1

Fossil site units, approximate ages, and number of species sampled, as used for parameters in the simulation. A total of 139 *species are represented at these sites, of which* 79 *are extinct in southern Africa*

Site unit	Age (Myr)	Sample size
Makapansgat Member 3	3.00–3.20	28
Makapansgat Member 4	2.80–3.00	13
Taung Dart Deposits	2.60–2.80	5
Sterkfontein Member 4	2.50–2.60	29
Taung Hrdlička Deposits	2.40–2.60	11
Sterkfontein Member 5	2.00–2.20	14
Kromdraai B	1.90–2.00	15
Kromdraai A	1.70–1.80	35
Swartkrans Member 1	1.60–1.70	39
Swartkrans Member 2	1.30–1.40	25
Swartkrans Member 3	1.20–1.30	32
Plovers Lake	1.00–1.20	15
Cornelia	0.90–1.00	18
Elandsfontein Main	0.40–0.70	37
Cave of Hearths (Acheulian)	0.60–0.70	18
Florisbad Springs	0.10–0.20	17
Klasies River Mouth	0.08–0.10	31
Equus Cave (MSA levels)	0.03–0.10	43

Myr = million years.

1993), and biochronologies (Vrba, 1982; Delson, 1984,1988; Harris & White, 1977; Klein, 1984; McKee *et al*., 1994). Due to the paucity of effective and accurate absolute geochronological techniques for most southern African caves, the chronology must be viewed as tentative.

Two specific models were tested against the fossil data, one of constant turnover and one in which turnover-pulses predominate over continuous origins and extinctions. Turnover-pulses were simulated within 100 Kyr (thousand year) periods, as defined by Vrba (1985*a*). Further parameters for these models were based on the fossil data. The initial number of evolving species was set at a constant of 66, the greatest number of contemporaneous large mammal species found in the fossil record.

The simulations began by assigning a date of origin of 3.2 Myr to a randomly chosen 66 species in an array of 300 possible species. Turnover was then modeled by assigning extinction dates to randomly selected extant species of the array, and dates of origin to new species, at 100 Kyr intervals.

Hypothetical numbers of origins and extinctions for each interval were based on the constant turnover rate plus the additional number of species from any turnover pulses. Although it is possible to calculate a turnover rate from the fossil data, such a rate differs from the actual evolutionary rate as some species (in both real and simulated worlds) never get sampled at any fossil site. Thus the rate of 3.3 species/100 Kyr for the constant turnover model was that which, after 1000 runs of the simulation, yielded average total first and last appearances closest to that found in the fossil record. (Fractional parts of the rate were covered by a stochastic rounding procedure which rounded to 3 in 70% of the intervals and to 4 in 30%, independently for origins and extinctions; thus the specific diversity could vary from the base size of 66.) Likewise, in the pulse model, two pulses of 22 species (at 2.5 and 0.9 Myr) with a background turnover rate of 1.8 species/100 Kyr, yielded the closest approximation of the total turnover expected after 3.2 Myr. A range of pulse sizes was simulated, but the size of the pulses in the simulations detailed here were the least number of species that would make turnover pulses the dominant mode of turnover over the background origins and extinctions.

At this stage the model then simulates evolution of a subcontinental community with a slightly variable level of specific biodiversity and evolutionary events among random, anonymous species. No differentiation is made among origins from phylogenetic splitting, lineal descent or migration into the area; likewise extinction could be either local, pseudo or terminal. These conditions also apply to the comparative data base. The output from the simulations, for each species of the array that "evolved", includes a date of origin and either a date of extinction or a date of zero if the species is still extant.

The first and last appearances in the fossil record were derived from a sample of the simulated evolved species. At each fossil site unit the number of species known was used as the sample size (Table 1). Sampling proceeded by randomly selecting species that were extant at any time during the period of deposition. Although taphonomic factors and agents of deposition may not have been totally random within an environmental context, the events leading to animal deposition, fossilization, recovery and identification are assumed to be random relative to the temporal context of species duration and thus modeled by a stochastic selection procedure.

The maximum age of the sites at which each species was selected constituted the age of first appearance. Likewise, the minimum date at which a species was found was assigned as the last appearance, with the exception of extant species. These dates remained coupled to the dates of origin and extinction of the animal for further analysis.

Hypothesis testing and verification of model proceeded in two steps. First, the frequencies of first and last appearances of fossil species at each time interval were compared with expectations based on the maximum, minimum and mean appearances after 1000 simulations. Mean expected frequencies were tested against the fossil-based data by a *chi*-square test. As a cross-check, the distribution of species longevity was compared between simulated and real data. Further information regarding the representativeness of the fossil data in relation to evolutionary trends was then gleaned from comparisons of simulated data before and after sampling.

3. Results of the Simulations

Incidences of first and last appearances from 1000 simulations under a model of constant turnover are displayed in Fig. 2 in comparison with the fossil-based data. The general pattern is remarkably similar, and there is no statistically significant difference between the mean simulated frequencies and the frequencies from the fossil record (*chi*-square, $p > 0.1$). In all cases the fossil-based frequencies fell within the simulated range of frequencies.

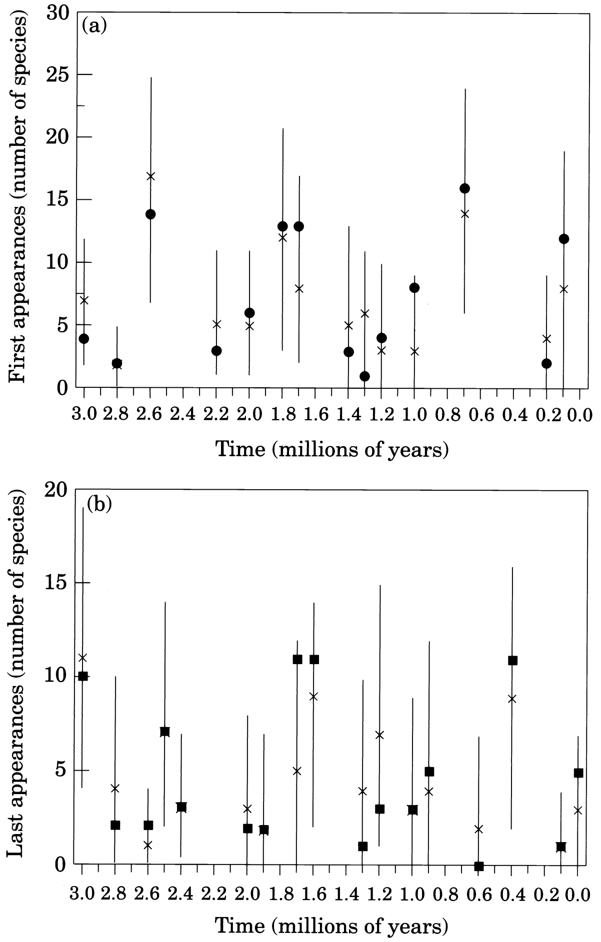

FIG. 2. Simulated frequencies of (a) first and (b) last appearances of species under a model of constant turnover, as compared to the empirical fossil data of Fig. 1. Vertical lines represent the ranges of simulated frequencies for each time interval and the crosses mark the mean simulated frequency from 1000 simulations.

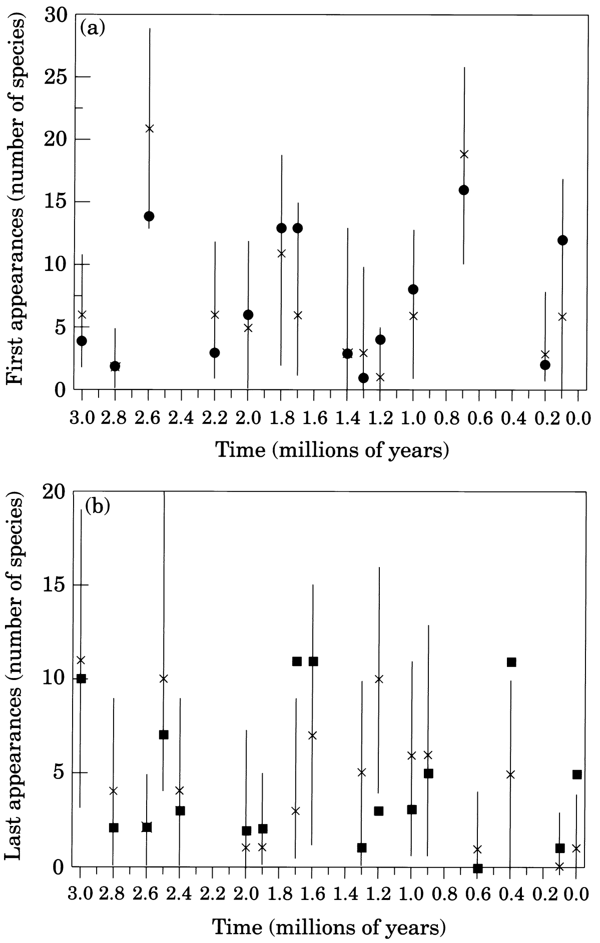

FIG. 3. Simulated frequencies of (a) first and (b) last appearances of species under a model with two turnover pulses at 2.5 and 0.9 Myr, as compared to the empirical fossil data of Fig. 1. Vertical lines represent the ranges of simulated frequencies for each time interval and crosses mark the mean simulated frequency from 1000 simulations.

Negligible differences in apparent turnover patterns appeared under a model with small turnover-pulses at 2.6 and 0.9 Myr, in comparison with the constant turnover model. With two pulses of 26 species, comprising nearly 40% of the large mammal species available for the fossil record and making pulses the dominant mode of turnover, all of the first appearances of fossil species fell within the simulated expected range (Fig. 3). Last appearances, however, showed a discordance between the empirical data and simulated expectations, as four of the fossil-based interval frequencies fell outside the expected ranges. In this light it should be noted that mean expected frequencies around the times of the pulses were consistently higher than the observed frequencies, in contrast to expectations based on the constant turnover model. On the other hand, there was no statistically significant difference between the observed and mean expected frequencies under a model with turnover pulses.

General distribution of species longevity predicted by both models were comparable to that found in the fossil record. Average frequencies based on 100 simulations are presented in Fig. 4, but the range was of course much greater, encompassing frequencies derived from the fossil data.

Simulated distributions of species longevities may not distinguish between the two models to any great degree, but they do point out the importance of sampling in the fossil record. For example, a peak frequency at 0.7 Myr (Fig. 4) is greater in either model *after* sampling than in the simulated real species duration. This is largely due to a substantial number of species ranging from 0.7 Myr to the present in association with a large sample covering a long time period at Elandsfontein; species of shorter duration were lumped in with those from the beginning of the time period.

Hypothetical effects of sampling discordance can be assessed by a look at the differences between simulated species longevity before and after sampling at the fossil sites (Fig. 5). Of the species sampled at any fossil site, up to 2.5 Myr of duration can be missed. Some species can appear to have existed longer than they did by up to 3 Kyr due to appearing at the tail end of a site unit with long depositional timespan covering multiple 100 Kyr intervals. As expected, short-lived species are more likely to be missed by sampling than those with greater longevity, but even a species that survived 1.5 Myr (out of those simulated as available for the fossil record) can be totally missed.

4. Implications for Interpretation of the Fossil Record

Analysis of the simulated results make it clear that sampling at the fossil sites is the primary determinant of the turnover patterns observed in the fossil record. A model of constant origins and extinctions and subsequent sampling is sufficient to explain the apparent peaks and troughs in fossil species turnover. Although evolution with turnover-pulses may have occurred, a model in which pulses are the dominant mode of turnover fit the data less well than one in which constant turnover predominates.

Putative climatically induced turnover-pulses at 2.5 and 0.9 Myr are clearly explicable on the basis of sampling without the necessity of invoking abiotic forces as a causal mechanism. Indeed, if pulses were the dominant mode of turnover—and only two occurred—one would expect (on average) greater numbers of simultaneous first and last appearances at the

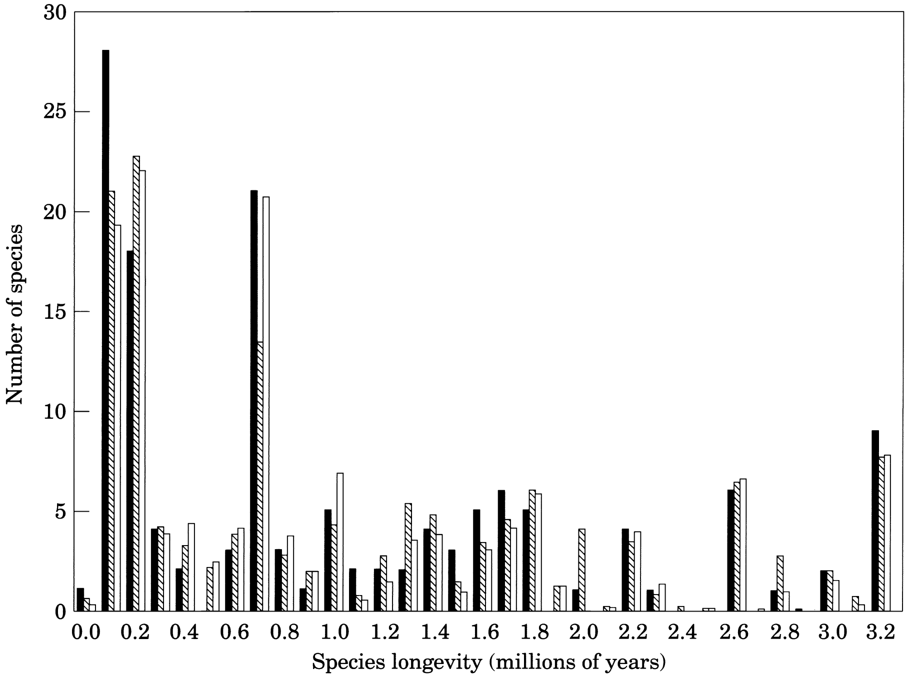

FIG. 4. Distribution of species longevity based on first and last appearances in the fossil record as compared to simulated longevities under models with constant turnover and turnover-pulses (mean of 100 simulations). (■) Fossil data; (▨) simulated constant; (□) simulated pulse.

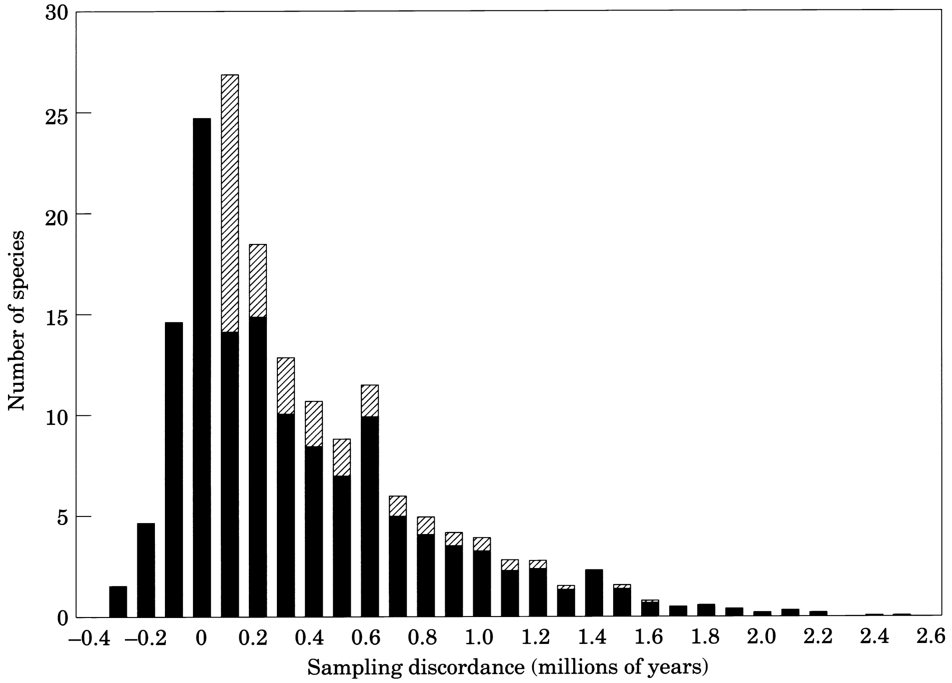

FIG. 5. Time differences between simulated species longevity (difference between date of origin and date of extinction) and simulated observed longevity (difference between dates of first and last appearances). Longevity of species not sampled in the fossil record are included in the frequency bars. Frequencies are based on a mean of 100 simulations. (■) Longevity difference; (▨) unsampled species.

times of the pulses. On the other hand, again using average expectations, both constant and pulsed models tend to underestimate the turnovers between 1.8 and 1.6 Myr, a time at which the composition of biodiversity changes with the loss of many large carnivores and increased diversity of bovids (Turner, 1990). Nevertheless, the range of possibilities after sampling under the constant turnover model can still accommodate such data.

Possibilities illustrated by the simulated data lead to further important caveats for interpretation of the fossil record. It is certainly not a new revelation to note that the longevity of a species would not be fully represented in the fossil record, but it may be of use to consider the distribution presented in Fig. 5. Prolonged delays in appearances or premature last appearances of species, common in the 1–3 Kyr range and running up to 2.5 Myr, could either increase or decrease the number of apparent simultaneous species turnovers.

Evaluation of negative side of the sampling discordance distribution, in which apparent species duration is longer than the real duration (Fig. 5), is of particular relevance to the turnover-pulse hypothesis. The situation arises because of either the long duration of site unit deposition or the prolonged length of time assigned to a site due to uncertainties in dating, with the former increasing the number of apparent first or last simultaneous appearances. Simultaneous first and last appearances, and thus apparent pulses, can also be increased by an inadvertent mixing of fauna from adjacent site units, a prospect that is not altogether unlikely at a number of the fossil sites (McKee *et al*., 1994). This may be particularly apropos to the apparent pulse in the 1.8–1.6 Myr time range.

Nature is undoubtedly very complex, so the general model presented here was designed as a mere simulacrum of reality, with evolutionary events and taphonomic processes happening randomly among species. Yet in terms of observed patterns in faunal turnover and species longevity, the model is tenable and yields a reasonable facsimile of trends in the fossil record. This retrodiction of nature's tendencies is especially remarkable in light of the model's simplifying assumptions. Either the evolutionary events were so complex as to be explicable by a stochastic model, or perhaps paleontologists have underestimated the substantial component of chance and randomness in evolution.

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