Faunal turnover rates and mammalian biodiversity of the late Pliocene and Pleistocene of eastern Africa

Jeffrey K. McKee

Abstract.—Two models of faunal turnover patterns, one with constant turnover and another with climatically induced turnover pulses, were tested against the empirical fossil data of first and last appearances of large mammals from the late Pliocene and Pleistocene of East Africa. Computer simulations of each model were generated by first creating change in hypothetical faunal communities and then sampling the evolving communities in a manner scaled to the specific contingencies of the East African fossil record. Predictions of the two turnover models were compared with the empirical data. Neither model yielded predictions that deviated significantly from the observed patterns of first and last appearances of species, and both models produced extremely similar results. The implication is that the fossil data of East Africa are not refined enough to detect variations in the pace of turnover; the patterns of first- and last-appearance frequencies are determined more by the contingencies of the fossil record than by the underlying evolutionary and migrational patterns. Whereas these results undermine the primary basis of empirical support for the turnover-pulse hypothesis, they do not imply that other models are more likely. However, the simulation results were highly suggestive of significant reduction in species biodiversity of large mammals during the past 2 Myr.

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Introduction

There can be little doubt that ecological changes on the African continent played a role in shaping the evolutionary course of hominids and other mammals during the Pliocene and Pleistocene. Given the inadequacies of the fossil record, however, it is difficult to ascertain correlates of evolutionary and environmental changes, or to reconcile the fossil record with theories posited to explain patterns of species origins and extinctions. In this paper I explore the fossil evidence for changes in the pace of evolution among East African large mammals to test for correlations with climatic change.

Vrba (1985, 1988, 1992, 1993, 1995a) proposed the ''turnover-pulse'' hypothesis to explain apparent trends in the fossil record: that global shifts in climate precipitated an increase in the rate of mammalian turnover (species origins, extinctions, immigrations, emigrations) during the African Neogene. Variations in the first- and last-appearance frequencies of species in the fossil record were thought to reflect changes in underlying turnover rates. Global temperature declines, be-

ginning about 3.3 Ma and culminating about 2.5 Ma in 41-Kyr cycles (deMenocal and Bloemendal 1995; Shackleton 1995), have been correlated with an increased rate of turnover among bovids (Vrba 1995b) and with the origin of the genus *Homo* (Vrba 1985, 1995b; Hill et al. 1992; Stanley 1992; Schrenk et al. 1993). Vrba (1992, 1995a) employed a vicariance model to explain the evolutionary component of turnover, in which the environmentally induced fragmentation of mammalian species habitats encouraged divergent speciations among population isolates of climatically specialized mammals.

The turnover-pulse hypothesis has been criticized on a number of grounds. Hill (1987), Kimbel (1995), and White (1995) discuss the inadequacies of the African fossil record and potential biases in the record that could result in misconceived correlations of climatic and faunal change; such taphonomic and other biases of the fossil record are acknowledged by Vrba (1995a). McKee (1995, 1996, 1999) attributed perceived variations of turnover rates in the southern African fossil record to the uneven temporal distribution and sampling bi-

ases of faunal assemblages. Bishop (1994) found no evidence of turnover pulses among Plio-Pleistocene suids of East Africa. Reed (1996, 1997) demonstrated only gradual change in mammalian morphological adaptations with the shift to cooler and drier African climates. Behrensmeyer et al. (1997) studied the detailed fossil record of the East African Turkana Basin and found a correlation between variations in apparent turnover and the number of localities per time unit (used as a measure of ''fossil abundance''). Although they found the ecological signature of the fauna changed through time, the correlation between turnover and fossil abundance left the turnover-pulse hypothesis in question.

Observations from other fossil sequences have led to uncertainty about the causal relations between abiotic change and the synchronous turnover predicted by the turnover-pulse model (e.g., Alroy 1996; Prothero 1999). On the other hand, others have argued for relationship between climatic change and increases in extinction rates (Foley 1994; Jaeger 1994; Bennett 1997).

McKee (1995, 1996) tested the southern African fossil record against predictions of the turnover-pulse hypothesis by means of a computer modeling and simulation technique. The procedure was designed to couple theoretical rates of turnover in ancient mammalian communities with predictions for a fossil record of those communities. The advantage is that the predictions can be specifically scaled to the particular fossil record, rather than relying on a generalized logarithmic curve (e.g., Vrba 1995b), which does not take into account the unique characteristics of the African fossil record. Thus, simulated turnover rates can be used to predict frequencies of first-appearance dates (FADs) and last-appearance dates (LADs). It was found that the southern African fossil data were inadequate to support the turnover-pulse hypothesis, and that a model of constant turnover among Pliocene and Pleistocene mammals explained the fossil record equally well. However, the problem with the analyses is that the region's fossil sites were poorly dated, resulting in a large window of predictions generated by the computer simulations.

A stricter test of Vrba's hypothesis may be provided by East African data. Most East African fossil sites are dated by radiometric techniques, and the record is somewhat more complete than the southern African data for critical time periods. Moreover, the East African fossil record of bovids figures most prominently in Vrba's (1985, 1986, 1988, 1995b) support of the turnover-pulse hypothesis. My assumption is that if there were turnover-pulses in the mammalian communities of the eastern African Pliocene and Pleistocene that resulted from climatic change, then the fossil record should show unequivocal signals of increased turnover for multiple taxa. Here I employ a series of computer simulations to generate predictions for the East African fossil record over the past 4.4 Myr and compare these predictions with the empirical data for fossil species. The simulation results are used to test two competing hypotheses regarding the empirical patterns of FAD and LAD frequencies among East African large mammals:

Hypothesis 1: There is a significant difference between the empirical data (FAD and LAD frequencies) and a simulated fossil record generated from a model of constant turnover.

Hypothesis 2: There is a significant difference between the empirical data (FAD and LAD frequencies) and a simulated fossil record generated from a turnover-pulse model.

As the completeness of the fossil record is called into question, a further hypothesis is necessary to test whether the available data are complete enough to detect underlying patterns of turnover. With models scaled to the exigencies of the East African fossil record, the following hypothesis provides one such test.

Hypothesis 3: There is a significant difference between the simulated fossil record generated from a model of constant turnover (FAD and LAD frequencies) and a simulated fossil record generated from a turnover-pulse model.

Materials and Methods

The empirical data were collected primarily from published species lists and fossil descriptions of East African large-mammal assemblages (Table 1); these data cover a greater

TABLE 1. Fossil assemblage, minimum and maximum age (rounded to nearest Kyr), and number of identified large-mammal species. Sites in italics were excluded from the results reported here for reasons explained in the text. Data based on Turner et al. 1999, with updates and verifications from the following sources: Leakey 1971; Bishop et al. 1975; Isaac 1977; Cooke 1978; Harris 1978, 1983, 1991; Harris and White 1979; Szalay and Delson 1979; Kalb et al. 1982; Clark et al. 1984, 1994; Delson 1984; Harris et al. 1988; Fleagle et al. 1991; Harris and Leakey 1993; White et al. 1993; Leakey and Roe 1994; WoldeGabriel et al. 1994; Behrensmeyer et al. 1995, 1997; Bromage et al. 1995; Kimbel 1995; Vrba 1995b; Kappelman et al. 1996; Leakey et al. 1995, 1996, 1998; Suwa et al. 1996; Renne et al. 1999; de Ditchfield et al. 1999; Heinzelin et al. 1999. Unpublished fossil species identifications from the Hadar sequence were provided by K. E. Reed and G. G. Eck.

Assemblage	Min	Max	n	Assemblage	Min	Max	n
Tugen Hills / Lukeino	*5.0*	*5.5*	*7*	Hadar Makamitalu	2.3	2.4	6
Lothagam	*5.0*	*5.5*	*12*	*Chiwondo Beds Malawi*	*2.3*	*2.4*	*10*
Aramis	4.3	4.4	9	Shungura E	2.3	2.4	28
Lower Laetoli	*4.2*	*4.4*	*7*	Shungura F	2.3	2.4	27
Lonyumum Member (E. Turkana)	4.1	4.4	9	*Kanjera Fm. south*	*1.8*	*2.4*	*7*
Kanapoi	4.0	4.2	17	Shungura G	1.9	2.3	44
Fejej locality FJ4	4.0	4.2	1	Upper Burgi (E. Turkana)	1.9	2.0	43
Moiti Member (E. Turkana)	3.8	4.1	6	Shungura H	1.7	1.9	8
Kataboi (W. Turkana)	*3.3*	*4.1*	*8*	Kaitio Member (W. Turkana)	1.7	1.9	29
Mursi Fm. (Omo)	3.9	4.0	10	KBS Member (E. Turkana)	1.7	1.9	42
Upper Laetoli	3.6	3.8	25	Olduvai Bed I	1.7	1.8	41
Maka	3.4	3.5	6	Olduvai Bed II	1.5	1.7	48
Basal Hadar	3.3	3.4	13	Okote Member (E. Turkana)	1.5	1.6	47
Hadar Sidiha Koma	3.3	3.4	28	*Kanjera Fm. north*	*0.6*	*1.4*	*13*
Lower Lomekwi (W. Turkana)	3.2	3.3	26	Natoo (W. Turkana)	1.4	1.6	26
Hadar Denen Dora	3.1	3.2	22	Nariokotome (W. Turkana)	1.4	1.6	20
Kada Hadar	3.1	3.2	19	Chesowanja	1.4	1.5	8
Shungura B	2.9	3.0	29	Shungura L	1.1	1.3	8
Omo Usno Fm.	2.9	3.0	25	Olduvai Bed III	1.0	1.2	27
Middle Lomekwi (W. Turkana)	2.8	2.9	17	*Kanjera KN-3*	*1.0*	*1.1*	*3*
Shungura C	2.5	28	44	Kanam east/Kasibos Fm.	1.0	1.1	3
Upper Ndolanya Beds	2.5	2.6	16	Olduvai Bed IV	0.7	0.9	30
Upper Lomekwi (W. Turkana)	2.5	2.6	29	Olorgesailie	0.6	0.7	10
Awash Matabitu	2.4	2.5	18	Bodo (Awash)	0.5	0.6	12
Lokalalei (W. Turkana)	2.4	2.5	10	Kanjera/Apoko Fm.	0.1	0.4	3
Shungura D	2.4	2.5	27	Rawi/Apoko Fm.	0.1	0.4	1
Hata Member/Bouri Fm.	2.4	2.5	17	Kanam east/Apoko Fm.	0.1	0.4	1
Malema / RC11	*2.3*	*2.5*	*7*	*Kanam east / Abundu Fm.*	— *undated* —		*1*
Kalachoro (W. Turkana)	1.9	2.4	22				

geographic and temporal range than those tested by Behrensmeyer et al. (1997). A number of assemblages were excluded on the basis of dubious data. Assemblages were excluded for any one of the following reasons: poor chronological control (i.e., unverified by reliable radiometric dates), mixed assemblages, or fauna not identified or published at species level. Two early East African sites (Lothagam, Lukeino), potentially the earliest of the sampled sites, were excluded because of poor dating. (Note: Should the dating of these sites prove their greater age, their exclusion accentuates first-appearance frequencies at the initial time periods of 4.4 and 4.2 Ma by a total of 13 species. It is assumed that the simulation model would mimic this possible effect.)

Initial tests were conducted on both the complete data set and a subset with some excluded assemblages. Exclusion of such assemblages (indicated in Table 1) altered the results in detail, but the same general results emerged regarding the hypotheses being tested. The results reported here are based on the subset of the most reliable assemblages. The time period covered was 4.4 Ma to present, using 182 identified fossil species from 48 fossil assemblages.

First- and last-appearance dates for each species, based on the faunal assemblage dates listed in Table 1, were determined at 100-Kyr intervals. Only taxa diagnosed to the species level were entered for analysis. Species published as ''aff'' or ''cf'' were treated as recognized species, following Turner and Wood (1993), Alroy (1994), Vrba (1995b), and McKee

(1995, 1996). From these dates, frequencies of first and last species appearances were determined for each 100-Kyr interval. FADs were determined on the basis of the older date of an assemblage age range, and LADs were given the latest date.

Assumptions and Design of the Computer Model

Overview—The computer model involved two basic steps. First, the model created a hypothetical community of species and then changed the composition of the community by one of several patterns of species turnover rates. Every 100 Kyr, a given number of new species would arise while an equal number of species would go extinct. The second bootstrapped step was to establish an empirically scaled fossil record out of this simulated community using random subsampling, yielding data on first- and last-appearance dates of the fossil species. The resulting data represent the expected fossil records of East Africa under different modeled patterns of turnover, thus coupling theoretical patterns of turnover with specific predictions for East African FADs and LADs.

The model is intended to be as simple as possible, employing the fewest assumptions and parameters to create specific simulations of the East African fossil record for hypothesis testing. More complex models may be more realistic, but analysis is compounded by the increased number of assumptions. The simpler models provide a baseline against which the fossil record can be compared. Where the empirical data then deviate from the model provides evidence or clues to underlying patterns that violate or complicate the initial assumptions.

The model included a mixture of stochastic and deterministic processes, so that each run of the simulation presented a different result. Thus, the simulations were run 1000 times to establish a range of predicted fossil records to be compared with the empirical data. The figure of 1000 was chosen because it was great enough to produce consistently replicable means and ranges of LAD and FAD frequencies.

Parameters of Population and Turnover.—The initial parameter established was the number of species in the simulated community. As this is unknown, the initial community was given 95 species, reflecting the greatest number of concurrent large-mammal species known from the East African fossil record. Each of the initial 95 simulated species was assigned by random to a computer array for the initial time period of 4.4 Ma. Species were represented in the array as being ''extant'' at that time period. No attempt was made to establish or track taxonomic identity. The species diversity parameter is robust, in that small deviations of the figure did not affect the patterns of FADs and LADs generated by the model.

The simulated turnover proceeded through 100-Kyr intervals. For each successive time period, randomly chosen ''extant'' species were terminated by the assignation of an extinction date (corresponding to the time period), and new species were assigned a concurrent date of origin. Each species was treated equally in terms of turnover probability. The number of species randomly chosen for origins or extinctions depended upon the ''turnover rate.''

The species turnover rate could not be established a priori, as origin and extinction rates cannot be gleaned directly from the fossil record of first and last appearances. Thus the rate was determined by an iterative process of experimental runs of the simulations meant to scale the process to the empirical data. In particular, it was scaled to 182 total first appearances over the full 4.4-Myr time period—the total number of species first appearances known from the East African fossil record. A series of initial runs were completed with different turnover rates to find the rate that resulted in an average of 182 first appearances from 1000 simulations. The resulting rate was used for both species origins and species extinctions. The fractional parts of the turnover rates were covered by a stochastic rounding procedure (McKee 1995) such that whole species would originate or go extinct in each 100-Kyr time interval.

The turnover rate was held constant throughout the simulated time period to simulate constant turnover. In a second model, the rates were varied to represent ''pulses'' of or-

igins and extinctions. In all simulations the numbers of origins and extinctions were held equal to each other within each time period; this was necessary to avoid either random pulses in the constant turnover model or the masking of pulses in the pulsed model.

The turnover-pulse model was run with a number of rate variants, ranging from two to five times the normal background turnover rate. The time periods for the pulses of origins and extinctions were 2.8 to 2.5 Ma and 0.9 to 0.7 Ma based on the hypothesis of Vrba (1995b). The iterative method described above was used to determine the respective background and pulsed rates on the basis of 182 species appearances.

Parameters for Establishing FAD and LAD Frequencies.—FADs and LADs of species were derived from the simulated evolving community on the basis of parameters gleaned from the East African fossil record. This is where empirical scaling was introduced to yield more specific predictions about the fossil record than those available from logarithmic predictions used by Vrba (1995b) or other generalized procedures (e.g., Foote and Raup 1996). For each fossil assemblage, ''extant'' species for the assemblage's time period were sampled for simulated fossilization at random, on the basis of the total number of identified species in known fossil assemblages (Table 1). For example, there are 41 identified species from Olduvai Gorge Bed I, so the computer model randomly chose 41 simulated species that were extant in the time period 1.7 to 1.8 Ma. An independent sample was taken from each site, such that species could appear across many sites. Sites with dates spanning longer time periods (e.g., Shungura G) sampled any species extant within the full time range (see McKee 1994 for a discussion of the effect of this sampling procedure).

For purposes of this modeling technique, the number of identified species per assemblage is deemed to be a more precise means of determining ''fossil abundance'' than the number of fossil localities per assemblage used by Behrensmeyer et al. (1997). Different localities can yield vastly different quantities of identifiable fossils, owing to taphonomic differences or varying degrees of sampling and excavation. Thus the number of localities does not give an adequate measure of how many species should be sampled in this type of simulation. The number of identified species provides a more direct means of scaling the simulated sampling procedure to the East African fossil assemblages.

The stochastic nature of the sampling procedure for each assemblage was employed to mimic the complex effects of different taphonomic processes, local environmental differences, and varied paleontological procedures of recovery and classification—all of which play a part in determining the recognized composition of an assemblage. It could be argued that some species, such as very large mammals, are more likely to be fossilized than others. Thus, in order to test the verity of the random-sampling procedure, each species was checked for the number of assemblages in which it appeared. The distribution of frequencies of simulated site appearances was compared with the empirical data.

Following each run of the simulation, the first- and last-appearance dates yielded data on the frequencies of first and last appearances for each time period. This was repeated 1000 times for each model (constant turnover and pulsed turnover).

To test the hypotheses, the average and range of simulated appearance frequencies for each time period was then charted for comparison with the empirical fossil data. The empirical and average frequencies were tested for statistically significant differences by means of a two-sided chi-square test, with an a priori rejection of no significant difference set at a value of $p = 0.05$.

In a chi-square test of FAD and LAD frequencies for each 100-Kyr interval, a number of cells in the contingency table had expected values below 5, violating the assumptions of the statistical test. This problem was overcome in two ways. In the initial test, these cells were eliminated from the calculations, thus only well-sampled intervals were tested. To accommodate all of the data, a subsequent test of FAD and LAD frequencies was conducted on grouped time periods of half-million-year intervals (4.4 to 4.0, 3.9 to 3.5, etc.). This second test also has the further advantages of testing

TABLE 2. Average total of 1000 simulated FAD and LAD frequencies under different turnover models as compared with the empirical observations of the East African fossil record. n/a = not applicable.

	Total FADs	Total LADs	Normal-turnover rate (no. of species)	Pulsed-turnover rate (no. of species)
Empirical	182	146	n/a	n/a
Constant turnover	181.62	110.73	3.25	n/a
Turnover with 3× pulse model	181.56	109.15	2.77	8.31
Turnover with 5× pulse model	181.95	109.42	2.44	12.20

potential broader trends in the data that might not be picked up in short 100-Kyr intervals and buffering errors that may arise from incorrectly dated assemblages.

Results

Effects of Parameters and Assumptions

The initial phase of establishing rates through an iterative process yielded the rates in Table 2. It is important to note that, unlike simulations of the South African fossil record (McKee 1995, 1996), the total expected first and last appearances did not balance with the East African fossil record; the empirical data always had *more* last appearances than the simulated data (which was scaled to 182 first appearances) in both constant and pulsed models. This implies an excess of species extinctions over origins during the time period examined. Further possible implications of these results are examined in the Discussion section.

FIGURE 1. Range of frequencies of site appearances for individual species (bars) compared with the empirical frequencies (circles).

To ensure that the random sampling procedure adequately represented possible taphonomic biases in the fossil record, the empirical and simulated data were compared for the frequency at which individual species appear in different site assemblages (Fig. 1). For this test, as a matter of computational pragmatics, a random sample of 100 simulations of constant turnover was used. For both simulated and empirical data, individual species appeared in a minimum of one and a maximum of nine site assemblages. The most common type of species appeared at only one site; the empirical data were on the high end of the simulated range. This could be due to a number of reasons, including the possibility that the empirical data have relatively more extinctions than modeled by the simulation technique, thus shortening the life expectancy of the species (see Discussion). Otherwise the empirical data followed a pattern similar to that of the simulated data, suggesting that taphonomic biases in frequencies of species appearances were not a significant deterrent to the efficacy of the model.

Tests of Hypotheses

The simulated and empirical FAD frequencies for the constant-turnover model are displayed in Figure 2A. All of the empirical frequencies were encompassed within the range of simulated values. One can see from the graphic illustrations that the pattern of mean expectations generally follows that of the fossil record. This observation is borne out by the statistical test, in which the average and empirical frequencies do not show a statistically significant difference in a chi-square test (Table 3).

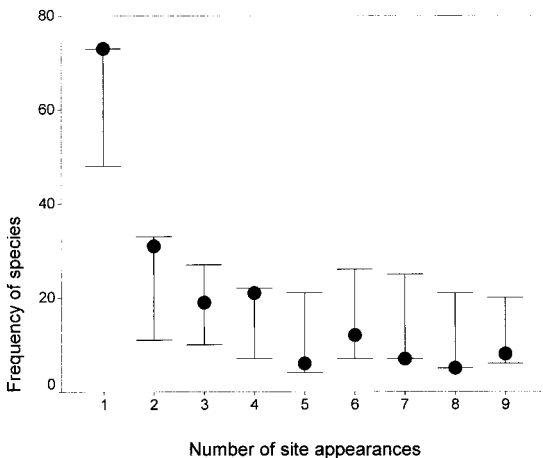Simulations of pulsed first-appearance dates are displayed in Figure 2B. Only the tri-

A - FADs, Constant Turnover Model
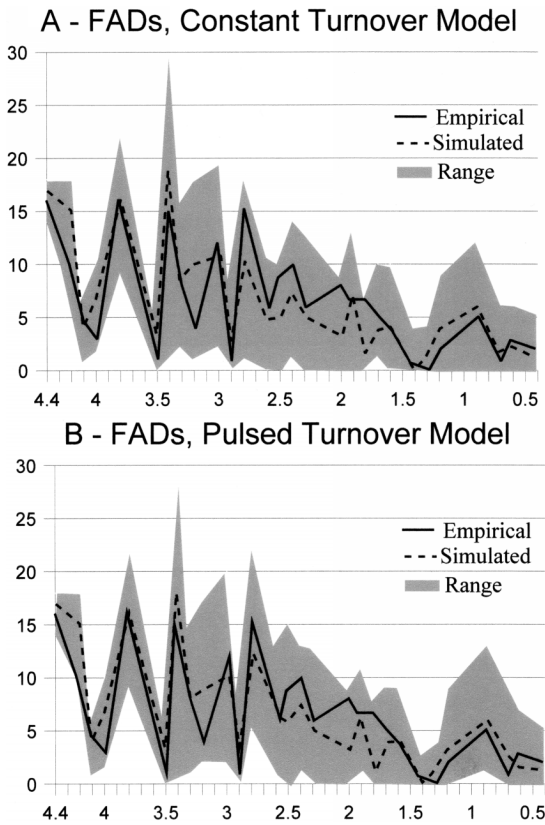

B - FADs, Pulsed Turnover Model

FIGURE 2. The simulated range and mean of species FAD frequencies over the past 4.4 Myr under a constant-turnover model (A) and a pulsed-turnover model (B), as compared with the empirical frequencies from the East African fossil record. (Note: the lines adjoining the data points are visual aids and are not meant to imply species turnover during intervening time periods.)

pled-pulse model is displayed, as the simulated patterns of other pulse magnitudes are remarkably similar to—and not significantly different from—the results obtained with a model of constant turnover (Table 3), and pulses of greater magnitude deviated further from the empirical data. Again, all empirical FAD frequencies were encompassed in the range of simulated values. The average and empirical frequencies do not show a statistically significant difference in a chi-square test (Table 3).

Close examination of the patterns in Figure 2A reveals that empirical FAD frequencies tend to be lower than the average expectation in the period preceding the climatic ''event'' at 2.8–2.5 Ma and higher than expected at 2.8–2.5 Ma, perhaps suggesting a pulse. However, this trend appears in both constant and pulsed models. Indeed the tripled-pulse model increased the total number of first appearances between 2.9 and 2.5 Ma by only five species, still shy of the empirical value (Fig. 2B). No notable differences between expected and empirical FAD frequencies are evident around the other proposed pulse at 0.9–0.7 Ma in either model. Furthermore, the differences between the average expectations of the constant and pulsed models were not significantly different (Table 3), contrary to hypothesis 3 (that the two models would produce significantly different results).

TABLE 3. Results of chi-square tests comparing empirical FAD and LAD frequencies with mean simulated frequencies of a constant-turnover model and of pulsed models in which the background turnover rate was increased by three times and five times during two turnover pulses.

	Empirical FAD frequency	Constant	Empirical LAD frequency	Constant
		100-Ky intervals		
Constant	$\chi^2 = 10.98$, df = 15 $p = 0.754$		$\chi^2 = 3.887$, df = 7 $p = 0.793$	
3× pulse	$\chi^2 = 8.999$, df = 15 $p = 0.878$	$\chi^2 = 0.623$, df = 14 $p = 1.00$	$\chi^2 = 3.787$, df = 7 $p = 0.804$	$\chi^2 = 1.095$, df = 7 $p = 0.993$
5× pulse	$\chi^2 = 9.697$, df = 15 $p = 0.838$	$\chi^2 = 2.460$, df = 13 $p = 0.999$	$\chi^2 = 4.250$, df = 7 $p = 0.751$	$\chi^2 = 2.589$, df = 6 $p = 0.858$
		500-Kyr intervals		
Constant	$\chi^2 = 6.753$, df = 7 $p = 0.455$		$\chi^2 = 5.781$, df = 7 $p = 0.566$	
3× pulse	$\chi^2 = 6.760$, df = 7 $p = 0.454$	$\chi^2 = 0.742$, df = 7 $p = 0.998$	$\chi^2 = 7.428$, df = 7 $p = 0.386$	$\chi^2 = 1.33$, df = 7 $p = 0.988$
5× pulse	$\chi^2 = 8.0327$, df = 7 $p = 0.330$	$\chi^2 = 3.529$, df = 7 $p = 0.832$	$\chi^2 = 10.346$, df = 7 $p = 0.170$	$\chi^2 = 2.987$, df = 7 $p = 0.886$

A - LADs, Constant Turnover Model

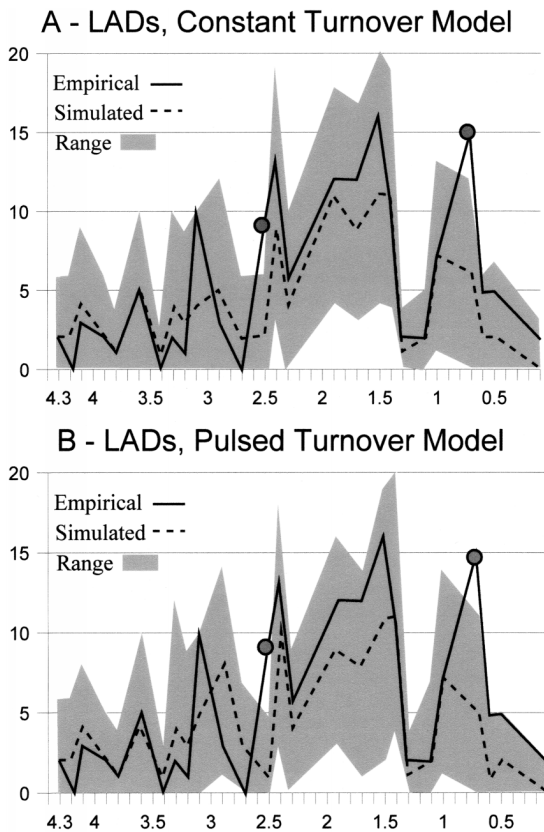## B - LADs, Pulsed Turnover Model

FIGURE 3. The simulated range and mean of species LAD frequencies over the past 4.3 Myr under a constant-turnover model (A) and a pulsed-turnover model (B), as compared with the empirical frequencies from the East African fossil record. The circles denote points where the empirical data fall outside the range of simulated expectations.

The results for LAD frequencies were similar in some respects, but both constant and pulsed models revealed some interesting discrepancies with the empirical fossil data (Fig. 3). Under a model of constant turnover, the empirical data fell outside the simulated range of possibilities at two time periods (2.5 Ma and 0.7 Ma). However, overall for the constant-turnover model, the chi-square test showed no statistically significant difference between the empirical and average expected frequencies (Table 3).

LADs in the pulsed model (tripled-pulse) followed a similar pattern, again deviating from the simulated range at 2.5 and 0.7 Ma, but with no statistically significant difference between the patterns of empirical and average expected frequencies (Table 3).

Finally, the differences between the average expectations for LAD frequencies of the constant- and pulsed-turnover models were not significantly different (Table 3), contrary to hypothesis 3.

Discussion

A simulation technique was used to create expected patterns of FAD and LAD frequencies from the East African fossil record of large mammals under models of constant and pulsed turnover. Neither model produced results that were significantly different from the empirical fossil record. Thus neither hypothesis of turnover patterns can be rejected. It was also found that the predictions of the models did not differ significantly from each other, suggesting that one can reject a third hypothesis—that the fossil record is good enough to be tested by this technique.

One can conclude that the data are not good enough to detect true pulses of turnover, even if such pulses had occurred in the Pliocene or Pleistocene of East Africa. Thus, whereas the effects of climatic change on the pace of turnover cannot be eliminated, there is no supportive evidence from the East African fossil data. The apparent correlation of events in the fossil record with evidence of climatic change cannot be said to be more than a coincidental artifact of the data.

Much of the apparent pattern of variation in LAD and FAD frequencies can be attributed to exigencies of the fossil record, i.e., unequal recovery across different sites and different time periods. This conclusion comes despite the use of chance to model taphonomic, ecological, and taxonomic biases. More detailed attention to such biases, in a more complicated model, may explain some of the anomalies that exist between the empirical and simulated data. For example, the empirical data show a rise in FAD frequencies at 1.8 Ma, whereas the simulated data show an expected decline. However, this datum marks the first inclusion of data from Olduvai Gorge, the most southerly of the sampled sites and one with a different environment (which may or may not be caused by temporal factors). The same is true of LAD frequencies at 1.7 Ma.

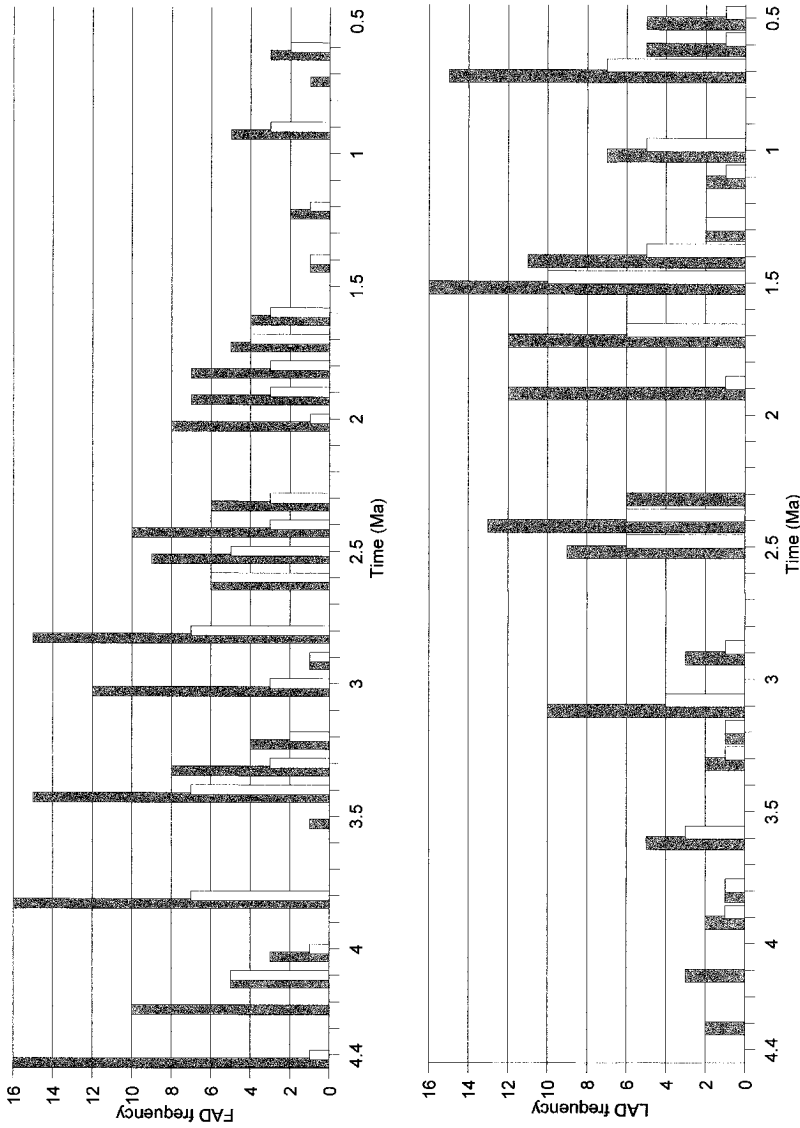It is worth asking why Vrba observed ap-

FIGURE 4.   Observed FAD and LAD frequencies of bovid species (gray bars) shown as a proportion of total FAD and LAD frequencies of East African large mammals (dark bars).

parent pulses of bovids, whereas this analysis and others (Bishop 1993; Reed 1996, 1997; Behrensmeyer et al. 1997) focusing on different taxa cannot confirm the pulses. In part, it may be that Vrba's logarithmic curve of expected FADs does not take into account important scaled details of the fossil record or alterations in fossil abundance. Furthermore, the bovids play an increasingly important role through time in the fossil record, as shown in Figure 4. At certain times, bovids account for a disproportionate component of first appearances and last appearances. For example, 24% of the bovids first appear between 2.8 and 2.5 Ma, as compared with 11% of non-bovid fauna. This could be due to any combination of taphonomic effects, local ecological effects, or an adaptive radiation of bovids. Given the strong effect of the fossil record upon observed patterns, as evidenced by this analysis, there can be no confident correlation of increased bovid FAD and LAD frequencies with climatic events. Thus the turnover-pulse hypothesis loses its primary source of empirical support; other long-term paleontological databases weaken the hypothesis further (Foote 1994; Alroy 1996; Prothero 1999).

Of overriding interest is the apparent disparity between FAD and LAD frequencies. When the model is scaled to total first appearances with a constant level of species biodiversity, there is a paucity of LADs relative to FADs in the simulated data, as compared with empirical data (Table 2). The high rate of LADs manifests itself in disparities at 2.5 and 0.7 Ma (Fig. 3 circles), but the underlying extinctions cannot be securely placed around those time intervals owing to the nature of the fossil record. Nevertheless, what is evident is a relative loss of species biodiversity through time (i.e., a deviation from the assumption of constant levels of biodiversity). Behrensmeyer et al. (1997) found a similar pattern: an apparent rise in biodiversity from 3 Ma to 2 Ma (which I suspect is a product of increased fossil representation due to better sampling within the time period) followed by a decline, which is consistent with this analysis. Thus the climatic changes that characterized Africa during the late Pliocene and Pleistocene either appear to have no effect on turnover rates

(e.g., Prothero 1999) or may prove to correlate more to species extinctions than to species origins, as suggested by Foley (1994) and McKee (1999). The apparent decline of biodiversity is more complex than that modeled here and is worthy of further modeling and characterization in relation to climate, paleoecology, and perhaps the diversification and spread of the genus *Homo.*

The lack of evidence for a climatic effect on the *pace* of species origins, as postulated by Vrba, should not imply a rejection of climatic influence on the direction of evolutionary adaptations among hominids, bovids, or other taxa. Clearly climatic conditions set adaptive parameters for many species. Climatic influences on adaptive evolution may also be mediated through changes in floral and faunal community structure. However, the apparent decline in biodiversity of large-mammal species is an important part of that structure and may prove to be a key consideration in assessing the nature of the evolutionary origin of our human genus and species.

Acknowledgments

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