SIZE AND SHAPE STASIS IN LATE PLEISTOCENE HORSES AND CAMELS FROM RANCHO LA BREA DURING THE LAST GLACIAL-INTERGLACIAL CYCLE

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Abstract—This study examines the fossil horses (*Equus "occidentalis"*) and camels (*Camelops hesternus*) from the Rancho La Brea tar pits at the Page Museum in Los Angeles, to see if climatic changes over the last glacial-interglacial cycle had any effect on the shape or size of their limb bones. Large samples from the pits with good radiocarbon dates were measured in order to see if there was a change in size or shape of the bones over the last 40,000 years. Even though pollen, plants, snails, and isotopic studies show that there were dramatic changes in climate and vegetation from the previous interglacial (40 ka-20 ka) to the peak glacial (20 ka-15 ka) to the glacial-interglacial transition (15 ka-10 ka) to the Holocene, camels and horses show size and shape stasis (as established by statistical tests) in their patellae, metapodials, astragali, calcanea, and cuboids. Living horses and camels exhibit larger body size in colder climates (Bergmann's rule), but there was no body size increase at Rancho La Brea when climate cooled dramatically at 20 ka. These results are consistent with the widespread stasis seen in most Pleistocene mammals during glacial-interglacial cycles, and call into question the models of evolution suggesting that organisms should respond to major changes in their environment by significant changes in size or shape.

INTRODUCTION

The classic neontological model of gradualistic evolution suggests that organisms are sensitive to small environmental changes, and readily adapt to such changes through transformations of body size or morphology. Such is the tradition of a century of research on the evolution of fruit flies, lab rats, and many other animals, as well as natural examples like the small-scale adaptations of Galapagos finches to drought and other local environmental stresses (Weiner, 1995; Grant and Weiner, 1999; Grant and Grant, 2007). Other studies have challenged this model of evolution. Eldredge and Gould (1972) and Gould (2002) suggested a different model, known as "punctuated equilibrium," which predicts that sexually reproducing species should undergo little net change in size or shape, and instead remain static over millions of years after a speciation event. Hundreds of studies undertaken since 1972 (Jackson and Cheetham, 1999; Jablonski, 2000, 2008; Gould, 2002; Geary, 2009; Hallam, 2009; Princehouse, 2009; Ruse and Sepkoski, 2009) conclude that most metazoan fossils show a preponderance of stasis rather than gradual change over time. More significant to our study are the many studies (e.g., Coope, 1979; Davis, 1983; Bennett, 1990; Prothero and Heaton, 1996; Prothero, 1999) demonstrating that most organisms remain static in size and shape even through dramatic climate changes. These results rule out the "stabilizing selection" explanation (Estes and Arnold, 2007) for stasis suggested by some neontologists because in these cases the environment is changing, not stabilizing (Lieberman and Dudgeon, 1996). Instead, the fossil record shows a pattern very different from the rapid change and climatic sensitivity of fruit flies and Galapagos finches.

Our study examines the effects of the changes in the climate on the large Rancho La Brea horse (*Equus occidentalis* Leidy, 1865 *sensu* Merriam, 1913; hereafter *E. "occidentalis"*) and the camel *Camelops hesternus* (Leidy, 1873) from the late Pleistocene until the Holocene, a period that spans the last glacial-interglacial cycle. The Rancho La Brea deposits have yielded many well-preserved fossils suitable for paleontological studies due to their unique geologic setting of sands, clays, and asphalt (Akersten et al.,1983; Stock and Harris, 1992; Friscia et al., 2008). The impeccable preservation of these fossils allows us to study the effects changing climate may have had on different species. In addi-

tion to being well preserved, these fossils are also well-dated using radiocarbon methods (Marcus and Berger, 1984; O'Keefe et al., 2009). These fossils also come from an area with a well-dated climatic record (Warter, 1976; Coltrain et al., 2004; Ward et al., 2005). A study by Heusser (1998) on pollen recovered from well-dated deep-sea cores just offshore showed that southern California went through intervals of extreme climatic and environmental changes over the past 59 ka. These transitions suggest a climate and landscape much different from the one today. Heusser (1998) found that over the past 59 ka, southern California has transformed from oak and chaparral vegetation to pine-juniper-cypress woodlands between 59 ka and 24 ka, snowy forests with juniper and closed-cone pines from 24 to 14 ka, then oak-chaparral and coastal sagebrush with occasional alder from 14 to 10 ka, and finally the modern landscape of oakchaparral-herbaceous vegetation in the Holocene.

METHODS

We used dial and digital calipers to measure the most abundant postcranial bones (patellae, manus, and pes) with adequate sample sizes. Unfortunately, the longer limb bones (humerus, radius, ulna, femur, tibia) were not sufficiently abundant in enough pits to be statistically useful for this type of study. Our measurements encompassed maximum length, proximal width and depth, midshaft width and depth, distal width and depth for the metapodials, and proximal-distal length, lateral width and dorsal-plantar depth for the patellae, wrist and ankle elements. We entered the data in Microsoft Excel spreadsheets where they could be statistically analyzed, and plotted. We used the Shapiro-Wilk test to determine which samples were normally distributed. For those samples, we used ANOVA to see if there was a significant change in size between samples of different ages. For samples that were non-parametric, we used the Kruskal-Wallis test in order to find out if there was a significant change in size or shape between samples dating between 35 ka and 11 ka.

We studied samples only from pits with good radiocarbon dates and relatively small error estimates (O'Keefe et al., 2009), which excluded samples from Pits 4 and 16. We only measured adult bones that had no breakage or deformation, which eliminated many problems with questionable data. There is no associated or articulated material in these pits at Rancho La Brea, so we could not assume that one bone was connected to another. However, since we were looking at the total population this was not of great concern.

RESULTS Horses

A visual inspection of the data and their means plotted against time shows that there was almost no change in the mean size (Fig. 1) or shape (Fig. 2) throughout the samples. We found that most of the samples were parametric, but a few were not normally distributed (Tables 1-4). Therefore, we used ANOVA on those samples that were normally distributed, and the Kruskal-Wallis test on those that were non-parametric.

From ANOVA and the Kruskal-Wallis test, we found that the majority (about 70%) of the data showed no significant differences between samples of adjacent ages (Tables 5-6) As for the remaining data that showed some sort of significant change between temporally adjacent samples over the past 40,000 years, it was important to analyze the data further. Even though there were a few cases of significant change, the change was not following any expected trend. Size and shape were neither increasing nor decreasing over time, nor were there changes in size or shape at the glacial maximum at 20,000 years ago, which would be expected if the climatic changes during the peak glacial episode had an effect on the horses. Instead, these significant differences between samples showed a fluctuation around a mean, or a "random walk" pattern.

Camels

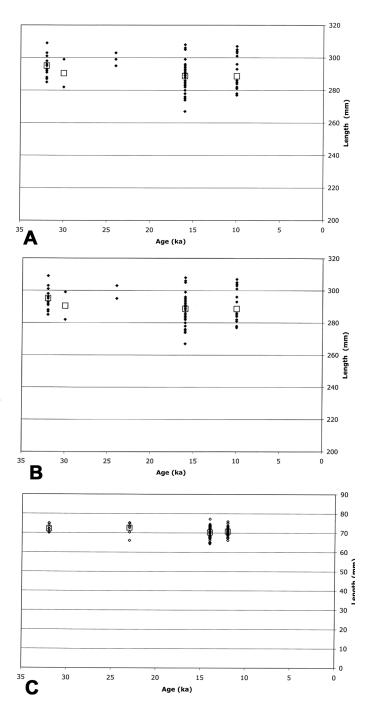
As with the horses, there were not enough long limb bones (humeri, radii, ulnae, femora, tibiae, patella), nor even the digit 3-4 metapodials ("cannon bones"), from enough different pits to use these elements in our study. However, there are large samples from multiple pits of astragali, calcanea, and cuboids (Webb, 1965). Representative plots of these elements are shown in Figure 3. As with the horses, there is almost complete stasis, with virtually identical means from one dated pit to the next. There is no apparent response in size change during the peak glacial at 20,000 years ago, as might be expected from Bergmann's rule.

These results are confirmed by statistical analysis. The fundamental statistics of each sample are summarized in Table 7. All of the samples that were large enough to analyze with a Shapiro-Wilk test proved to be normally distributed, so ANOVA was performed on each dated pit sample (Table 8). In every case, the differences between samples was not statistically significant ($F < F_{critical}$), so there is no statistically significant size change from one sample to the next.

DISCUSSION

The data revealed no statistically significant trends in the change of the size or shape of the Rancho La Brea horse or camel, suggesting morphological stasis over the last 40,000 years. Although the climate became considerably cooler during this time due to the last glacial-interglacial cycle at 20,000 years ago, with closed-cone coniferous forests and significant snow, the body size of Rancho La Brea horses and camels remained unchanged in the samples from Pit 3 (18,593 radiocarbon years), Pit 60 (21,383 radiocarbon years), and Pit 9 (26,427 radiocarbon years), according to the dates of O'Keefe et al. (2009).

This stasis in size and shape of the limb bones goes against the predictions of Bergmann's rule, which suggests that within a species the body mass tends to increases with latitude and colder climate. Among living horses (Groves, 1974; Nowak, 1991), there are some intraspecific size trends that suggest the influence of Bergmann's rule. For example, among the wild asses (Groves, 1974), the kiang (*E. kiang*) of the Tibetan Plateau weighs between 250-400 kg, while the desert-dwelling African wild ass (*E. asinus*) weighs about 250 kg. In other *Equus* species, the trend is less obvious. The cold steppe-dwelling Przewalski's horse (*Equus ferus przewalskii*) weighs about 200-300 kg, whereas the more tropical zebras tend to weigh 170-270 kg. However, Grevy's zebra, which weighs 350-400 kg, seems to go against this trend. Bergmann's rule is more apparent among living camelids (Franklin, 1983; Nowak, 1991). The steppe-dwelling Bactrian camel (*Camelus bactrianus*) weighs about 600-



FIGURES 1. A-C, Plots of dimensions of *Equus* bones against the age of the pit sample. Open squares indicate individual specimens; solid diamonds are the means for each time interval. A, Mc3 length. B, Mt3 length. C, Astragalus length.

1040 kg, while the desert-dwelling dromedary camel (*C. dromedarius*) weighs only 450-680 kg. In the wild New World lamine camelids, the guanaco (*Lama guanicoe*), which inhabits the cold mountains and steppes of Patagonia, weighs about 100-120 kg, whereas the more tropical mountain and grassland taxon, the vicuña (*Vicugna vicugna*) weighs only 35-65 kg.

Indeed, stasis during dramatic climate changes seems to be a prevalent occurrence among Pleistocene species despite the rapid changes of their environment and habitats (Barnosky, 1994, 2005). In addition to

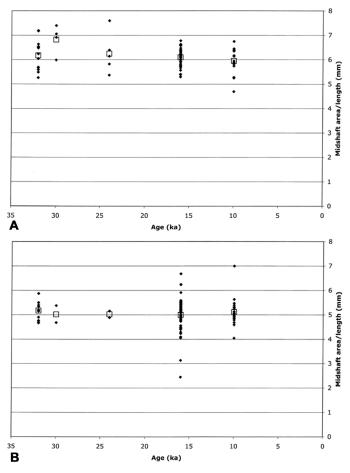


FIGURE 2. Plot of ratios of *Equus* metatarsal robustness (midshaft cross-sectional area divided by the length) against the age of the pit sample. Large open squares indicate mean of temporal sample; solid diamonds are individual data points. **A**, Mc3. **B**, Mt3.

our research, samples from well-dated pits of all the other common mammals and birds from Rancho La Brea have been measured and statistically analyzed. The preliminary results indicate that the common mammal species such as bison, ground sloths, saber-toothed cats, and American lions showed complete stasis from the late Pleistocene through the end of the Pleistocene (Prothero and Raymond, 2008; Prothero et al., 2009). A similar degree of stasis has been documented for all the most common birds at Rancho la Brea, including turkeys, condors, caracaras, golden eagles, and bald eagles (Syverson and Prothero, 2010; Fragomeni and Prothero, this volume; Molina and Prothero, this volume).

Many attempts have been made to explain the stasis of species during such dramatic climate and ecological changes. Eldredge and Gould (1972) suggested that the stasis might be due to developmental constraints and canalization, although Gould (2002) rejected that notion. Bennett (1990, 1997) proposed that the climatic changes during the glacial-interglacial cycle were too rapid and did not allow time for adaptation. However, the Galapagos finches changed in a matter of years in response to a small-scale climatic change. A more popular idea is that no matter how severe an environment changes, most large animals have the ability to adapt to a wide range of environments, and, therefore, are not responsive to local changes in climate (Lieberman et al.1995; Lieberman and Dudgeon, 1996; Eldredge et al., 2005). This may be appropriate for the large mammals at Rancho La Brea, but not for the many cases where small mammals show stasis across climate change (e.g., Barnosky, 1994, 2005; Prothero and Heaton, 1996).

TABLE 1. Equus MC3: basic statistics and Shapiro-Wilk normality test.

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	Age (Ka)	Sample Size	Minimum	Maximum	Mean	Standard deviation	p-value	Normal?
Max Length:	10	15	240.000	267.000	250.000	8.089	0.301	Yes
	16	34	236.000	265.000	248.765	5.955	0.812	Yes
	24	5	247.000	254.000	250.800	3.114	0.332	Yes
	30	4	244.000	260.000	253.750	6.850	0.362	Yes
	32	15	247.000	267.000	254.867	5.540	0.529	Yes
Proximal Width:	10	15	55.000	65.000	58.467	2.748	0.177	Yes
	16	34	46.000	62.000	58.235	2.872	< 0.0001	No
	24	5	51.000	65.000	58.600	5.177	0.955	Yes
	30	4	61.000	63.000	61.750	0.957	0.272	Yes
	32	15	57.000	64.000	60.000	2.070	0.302	Yes
Proximal Depth:	10	15	36.000	42.000	38.333	1.496	0.137	Yes
	16	34	35.000	43.000	38.382	1.724	0.063	Yes
	24	5	34.000	44.000	38.800	3.701	0.984	Yes
	30	4	38.000	42.000	40.750	1.893	0.086	Yes
	32	15	37.000	42.000	39.333	1.345	0.264	Yes
Midshaft Width:	10	15	33.000	42.000	38.800	2.569	0.029	No
	16	34	35.000	43.000	39.529	1.727	0.088	Yes
	24	5	39.000	43.000	40.400	1.673	0.314	Yes
	30	4	41.000	43.000	42.500	1.000	0.001	No
	32	15	34.000	45.000	40.000	2.928	0.811	Yes
Midshaft Depth:	10	15	27.000	32.000	29.867	1.552	0.074	Yes
	16	34	28.000	34.000	31.059	1.632	0.084	Yes
	24	5	30.000	32.000	31.200	0.837	0.314	Yes
	30	4	30.000	32.000	31.250	0.957	0.272	Yes
	32	15	29.000	34.000	31.400	1.352	0.189	Yes
Distal Width:	10	15	50.000	54.000	52.267	1.387	0.040	No
	16	34	48.000	56.000	52.794	1.737	0.077	Yes
	24	5	51.000	58.000	54.000	2.739	0.833	Yes
	30	4	53.000	56.000	54.750	1.500	0.224	Yes
	32	15	50.000	57,000	53.267	2.017	0.605	Yes
Distal Depth:	10	15	37.000	42,000	39,467	1.246	0.386	Yes
	16	34	35.000	42.000	39.676	1.718	0.037	No
	24	5	39,000	42,000	40,600	1.140	0.814	Yes
	30	4	40.000	42.000	41.000	0.816	0.683	Yes
	32	15	38.000	44,000	40.800	1.612	0.842	Yes
Robustness:	10	15	3.427	5.230	4.652	0.527	0.042	No
	16	34	4.126	5.593	4.942	0.407	0.387	Yes
	24	5	4.737	5.526	5.028	0.304	0.344	Yes
	30	4	4.731	5.639	5.243	0.382	0.801	Yes
	32	15	3.913	5.953	4.942	0.549	0.974	Yes

TABLE 2. Equus MC3: basic statistics and Shapiro-Wilk normality test.

	Age (Ka)	Sample Size	Minimum	Maximum	Mean	Standard deviation	p-value	Normal?
Max Length:	10	21	277.000	307.000	288.619	9.861	0.004	No
	16	50	267.000	308.000	288.720	8.278	0.311	Yes
	24	2	295.000	303.000	299.000	5.657	1.000	Yes
	30	2	282.000	299.000	290.500	12.021	1.000	Yes
	32	13	285.000	309.000	295.077	6.813	0.965	Yes
Proximal Width:	10	21	54.000	63.000	57.905	3.145	0.024	No
	16	50	47.000	62.000	57.080	3.043	0.014	No
	24	2	57.000	61.000	59.000	2.828	1.000	Yes
	30	2	58.000	59.000	58.500	0.707	1.000	Yes
	32	13	50.000	64.000	58.615	3.618	0.467	Yes
Proximal Depth:	10	21	37.000	53.000	49.048	3.892	0.000	No
	16	50	40.000	65.000	49.160	3.738	< 0.0001	No
	24	2	50.000	54.000	52.000	2.828	1.000	Yes
	30	2	49.000	52.000	50.500	2.121	1.000	Yes
	32	13	48.000	54.000	50.385	1.805	0.425	Yes
Midshaft Width:	10	21	32.000	53.000	39.333	3.812	0.000	No
	16	50	26.000	46.000	38.600	3.017	< 0.0001	No
	24	2	39.000	39.000	39.000	0.000	0	No
	30	2	40.000	41.000	40.500	0.707	0	No
	32	13	37.000	42.000	39.692	1.750	0.209	Yes
Midshaft Depth:	10	21	34.000	40.000	37.524	1.861	0.079	Yes
	16	50	26.000	46.000	37.380	3.380	0.002	No
	24	2	38.000	39.000	38.500	0.707	1.000	Yes
	30	2	35.000	37.000	36.000	1.414	1.000	Yes
	32	13	36.000	41.000	38.462	1.266	0.464	Yes
Distal Width:	10	21	50.000	55.000	52.667	1.623	0.055	Yes
	16	50	45.000	59.000	53.720	2.339	0.007	No
	24	2	50.000	56.000	53.000	4.243	1.000	Yes
	30	2	50.000	55.000	52.500	3.536	1.000	Yes
	32	13	51.000	58.000	53.923	1.801	0.397	Yes
Distal Depth:	10	21	38.000	55.000	42.429	3.249	< 0.0001	No
Distai Deptii.	16	50	32.000	45.000	41.580	2.148	< 0.0001	No
	24	2	40.000	46.000	43.000	4.243	1.000	Yes
	30	2	43.000	43.000	43.000	0.000	0.000	No
	32	13	40,000	56,000	43.615	4.011	1.000	Yes
Robustness:	10	21	4.042	6.997	5.116	0.550	0.002	No
Robustiless.	16	50	2.449	6.685	5.020	0.550	0.002	No
	24	2	4.891	5.156	5.024	0.187	1.000	Yes
	30	2	4.682	5.379	5.024	0.187	1.000	Yes
	32	13	4.682	5.877	5.179	0.493	0.660	Yes
	34	13	4.071	3.6//	5.179	0.334	0.000	1 08

TABLE 3. Equus patellae basic statistics and Shapiro-Wilk normality test.

	Age (Ka)	Sample Size	Minimum	Maximum	Mean	Standard deviation	p-value	Normal
Width:	10	9	72.100	85.100	80.033	3.523	0.148	Yes
	14	3	73.600	78.800	76.333	2.610	0.831	Yes
	16	40	71.400	84.900	79.583	3.599	0.013	No
	24	30	73.000	85.300	80.570	2.994	0.204	Yes
	30	6	65.200	83.100	76.500	6.880	0.410	Yes
	32	17	71.500	85.600	79.788	3.933	0.618	Yes
Length:	10	9	69.900	85.900	80.056	4.782	0.380	Yes
	14	3	74.700	80.200	76.800	2.972	0.258	Yes
	16	40	70.200	87.500	80.075	3.334	0.374	Yes
	24	30	75.600	89.400	82.647	2.690	0.168	Yes
	30	6	72.700	84.500	78.367	5.136	0.341	Yes
	32	17	75.600	86.000	81.488	3.042	0.111	Yes
Depth:	10	9	38.200	54.900	44.067	5.714	0.093	Yes
	14	3	38.000	51.400	44.733	6.700	0.984	Yes
	24	30	37.100	57.400	47.027	5.578	0.356	Yes
	30	6	32.400	54.200	42.367	8.755	0.599	Yes
	32	17	39.300	56.300	48.529	5.533	0.160	Yes
	16	40	32.100	55.400	43,698	5,439	0.148	Yes

TABLE 4. Equus astragali: basic statistics and Shapiro-Wilk normality test.

	Age (Ka)	Sample Size	Minimum	Maximum	Mean	Standard Deviation	p-value	Normal?
Width:	10	33	56.300	69.900	63.542	3.165	0.543	Yes
	16	44	60.100	73.900	67.389	4.024	0.066	Yes
	24	10	59.900	71.600	66.590	4.205	0.331	Yes
	30	2	64.400	66.200	65.300	1.273	1.000	Yes
	32	8	60.900	69.300	64.875	2.383	0.671	Yes
Length:	10	33	66.200	75.900	70.739	2.384	0.618	Yes
	16	44	64.400	77.200	70.377	2.655	0.772	Yes
	24	10	66.100	75.200	72.610	2.651	0.012	No
	30	2	68.500	73.600	71.050	3.606	1.000	Yes
	32	8	70.100	75.100	72.125	1.855	0.393	Yes
Depth:	10	33	54.300	64.200	59.197	2.797	0.146	Yes
	16	44	51.400	65.100	58.241	3.069	0.501	Yes
	24	10	53.800	65.400	59.540	3.633	0.991	Yes
	30	2	52.900	60.500	56.700	5.374	1.000	Yes
	32	8	54.600	63.800	59.713	2.905	0.391	Yes

TABLE 5. ANOVA comparing all samples of *Equus* from well-dated pits with normal distributions.

Measurement	F	F-critical	Significant change?
Mc3: Max Length	2.726864	2.506621	Yes
Mc3: Proximal Depth	2.182404	2.506621	No
Mc3: Midshaft Depth	2.399573	2.506621	No
Patella: Length	3.870308	2.306259	Yes
Patella: Depth	2.621767	2.306259	Yes
Astragalus: Width	5.527535	2.470681	Yes
Astragalus: Depth	1.064654	2.470681	No

TABLE 6. Kruskal-Wallis test comparing the differences between samples of *Equus* from pits of different ages without normal distributions.

Measurement	p-value	Significant change?
Mc3: Proximal Width	0.025	Yes
Mc3: Midshaft Width	0.045	Yes
Mc3: Distal Width	0.123	No
Mc3: Distal Depth	0.060	No
Mt3: Max Length	0.057	No
Mt3: Proximal Width	0.515	No
Mt3: Proximal Depth	0.379	No
Mt3: Midshaft Width	0.454	No
Mt3: Midshaft Depth	0.361	No
Mt3: Distal Width	0.247	No
Mt3: Distal Depth	0.345	No
Patella: Width	0.380	No
Astragalus: Length	0.051	No

CONCLUSION

Although evolutionary theory suggests that organisms are delicately responsive to changes in their environment, this study shows no statistically significant size or shape changes in the Rancho La Brea horses or camels over the last 40,000 years despite the climate and vegetational changes due to the last glacial-interglacial cycle. This is despite the fact that both modern horses and camelids exhibit a tendency

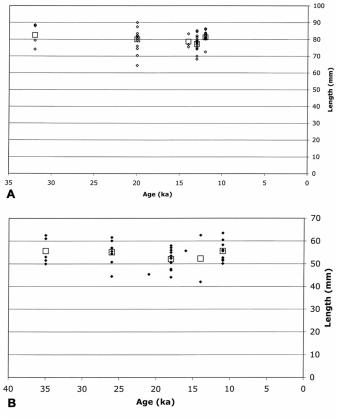


FIGURE 3. Representative plots of *Camelops* ankle bone dimensions through time. Symbols as in Figs. 1 and 2. **A**, Astragalus. **B**, Cuboid.

TABLE 7. Basic statistics of *Camelops* astragali, calcanea, and cuboids measured in this study.

Element	Age (ka)	N	Mean	St.Dev.
Astragalus length	11	19	81.2	3.5
	16	22	77.2	4.4
	18	3	78.6	3.4
	26	17	80.1	6.4
	35	4	82.5	6.1
Astragalus width	11	21	56.5	3.9
	16	20	56.3	6.3
	18	4	57.4	4.6
	26	20	57.7	3.0
	35	3	54.8	3.5
Astragalus depth	11	21	42.4	3.9
	16	19	43.4	3.7
	18	4	43.1	5.5
	26	19	43.2	1.9
	35	3	41.2	1.9
Calcaneum length	11	7	148.7	11.7
Ü	16	5	147.9	18.3
	18	15	129.4	15.3
	26	10	131.9	20.3
Calcaneum width	11	13	50.0	3.9
	14	6	42.9	4.7
	16	5	47.9	6.3
	18	10	49.2	9.5
	26	9	46.5	6.9
	35	3	41.6	2.4
Calcaneum depth	11	13	25.1	2.5
	14	6	27.9	2.3
	16	5	26.7	2.7
	18	9	26.9	2.1
	26	9	26.3	1.9
	35	3	24.2	0.9
Cuboid length	11	10	54.6	5.1
	16	5	57.3	2.2
	18	12	52.0	4.1
	26	4	52.4	5.6
	35	5	55.6	5.1
Cuboid width	11	10	28.8	3.8
Cuoda widai	16	5	29.9	1.2
	18	12	26.6	2.9
	26	4	27.7	1.1
	35	5	27.4	2.5
Cuboid depth	11	10	38.8	4.5
саоола асран	16	5	41.0	0.8
	18	12	38.0	2.7
	18 26	4	36.6	5.9
	26	4	30.0	5.9

TABLE 8. ANOVA of different pit samples of the different dimensions of *Camelops* astragali, calcanea, and cuboids, showing that none of the dated pit samples are significantly different ($F > F_{critical}$) from one another, and that stasis prevails.

Element	F	$\mathbf{F}_{\mathrm{crit}}$	Significant?
Cuboid: proximal-distal length	1.324	2.678	No
Cuboid: lateral width	1.357	2.678	No
Cuboid: dorsal-plantar depth	0.673	2.678	No
Calcaneum: max proximal-distal length	2.887	2.892	No
Calcaneum: max lateral width	1.519	2.456	No
Calcaneum: dorsal-plantar depth	1.795	2.456	No
Astragalus: proximal-distal length	2.015	2.533	No
Astragalus: lateral width	0.803	2.522	No
Astragalus: dorsal-plantar depth	0.406	2.522	No

toward larger body sizes in colder climates, yet the cold climates at La Brea 20,000 years ago were insufficient to cause a measurable change in body size or limb robustness. Such stasis, along with the examples documented from nearly all other Pleistocene mammals and birds, argues that organisms are not as responsive to environmental change as classicial Neo-Darwinian theory predicts.

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REFERENCES

- Akersten, W.A., Shaw, C.A. and Jefferson, G.T., 1983, Rancho La Brea: status and future: Paleobiology, v. 9, p. 211-217.
- Barnosky, A.D., 1994, Defining climate's role in ecosystem evolution: clues from late Quaternary mammals: Historical Biology, v. 18, p. 173-190.
- Barnosky, A.D., 2005. Effects of Quaternary climatic change on speciation of mammals: Journal of Mammalian Evolution, v. 12, p. 247-264.
- Bennett, K.D., 1990, Milankovitch cycles and their effects on species in ecological and evolutionary time: Paleobiology, v. 16, p. 11-21.
- Bennett, K.D., 1997, Evolution and ecology: the pace of life: Cambridge, Cambridge University Press, 260 p.
- Coltrain, J.B., Harris, J.M., Cerling, T.E., Ehleringer, J.R., Dearing, M., Ward, J. and Allen, J., 2004, Rancho La Brea stable isotope biogeochemistry and its implications for the palaeoecology of the late Pleistocene, coastal southern California: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 205, p. 199-219.
- Coope, G.R., 1979, Late Cenozoic fossil *Coleoptera*: evolution, biogeography, and ecology: Annual Reviews of Ecology and Systematics, v. 10, p. 247-267.
- Davis, M., 1983, Quaternary history of deciduous forests of eastern North America and Europe: Annals of the Missouri Botanical Garden, v. 20, p. 550-563.
- Eldredge, N. and Gould, S.J. 1972, Punctuated equilibria: an alternative to phyletic gradualism; *in* Schopf, T.J.M., ed., Models in paleobiology: San Francisco, Freeman, p. 82-115.
- Eldredge, N., Thompson, J.N., Brakefield, P.M., Gavrilets, S., Jablonski, D., Jackson, J.B.C., Lenski, R.E., Lieberman, B.S., McPeek, M.A. and Miller III, W., 2005, The dynamics of evolutionary stasis: Paleobiology, v. 31, p. 133-145.
- Estes, S. and Arnold, S.J., 2007, Resolving the paradox of stasis: models with stabilizing selection explain evolutionary divergence on all timescales: American Naturalist, v. 169, p. 227-244.
- Franklin, W.D., 1983, Contrasting socioecologies of South America's wild camelids: the vicuña and the guanaco: American Society of Mammalogists, Special Publication 7, p. 573-629.
- Friscia, A.R., Van Valkenburgh, B., Spencer, L. and Harris, J.M., 2008, Chronology and spatial distribution of large mammal bones in Pit 91, Rancho La Brea: Palaios, v. 23, p. 35-42.
- Geary, D.H., 2009, The legacy of punctuated equilibrium; *in* Allmon, W.D., Kelley, P.H. and Ross, R.M., eds., Stephen Jay Gould: reflections on his view of life: Oxford, Oxford University Press, p. 127-147.
- Gould, S.J., 2002, The structure of evolutionary theory: Cambridge, Harvard University Press, 1464 p.
- Grant, P.R. and Weiner, J., 1999, The ecology and evolution of Darwin's finches: Princeton, Princeton University Press, 512 p.
- Grant, P.R. and Grant, B.R., 2007, How and why species multiply: the

- radiation of Darwin's finches: Princeton, Princeton University Press, 256 n
- Groves, C.P., 1974, Horses, asses, and zebras in the wild: Newton Abbot, David and Charles Publishers, 192 p.
- Hallam, A., 2009, The problem of punctuational speciation and trends in the fossil record; *in* Ruse, M. and Sepkoski, D., eds., The paleobiological revolution: Chicago, University of Chicago Press, p. 423-432.
- Heusser, L., 1998, Direct correlation of millennial-scale changes in western North American vegetation and climate with changes in the California Current system over the past 60 kyr: Paleoceanography, v. 13, p. 252-262.
- Jablonski, D., 2000, Micro- and macroevolution: scale and hierarchy in evolutionary biology and paleobiology: Paleobiology, v. 26, p. 15-52.
- Jablonski, D., 2008, Species selection: theory and data: Annual Review of Ecology, Evolution, and Systematics, v. 39, p. 501-524.
- Jackson, J.B.C. and Cheetham, A.H., 1999, Tempo and mode of speciation in the sea: Trends in Ecology and Evolution, v. 14, p. 72-77.
- Lieberman, B.S. and Dudgeon, S., 1996, An evaluation of stabilizing selection as a mechanism for stasis: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 127, p. 229-238.
- Lieberman, B.S., Brett, C.E. and Eldredge, N., 1995, A study of stasis and change in two species lineages from the Middle Devonian of New York State: Paleobiology, v. 21, p. 15-27.
- Marcus, L.F. and Berger, R., 1984, The significance of radiocarbon dates for Rancho La Brea; in Martin, P.S. and Klein, R.G., eds., Quaternary extinctions: a prehistoric revolution: Chicago, University of Chicago Press, p. 159-188.
- Nowak, R.M., 1991, Walker's mammals of the world, 5th edition: Baltimore, Johns Hopkins University Press, 1712 p.
- O'Keefe, F.R., Fet, E.V. and Harris, J.M., 2009, Compilation, calibration, and synthesis of faunal and floral radiocarbon dates, Rancho La Brea, California: Contributions in Science, Natural History Museum of Los Angeles County, v. 518, p. 1-16.
- Princehouse, P., 2009, Punctuated equilibrium and speciation: what does it mean to be a Darwinian?; in Ruse, M. and Sepkoski, D., eds., The paleobiological revolution: Chicago, University of Chicago Press, p. 149-175.
- Prothero, D.R., 1999, Does climatic change drive mammalian evolution?: GSA Today, v. 9, p. 1-5.
- Prothero, D.R. and Heaton, T.H., 1996, Faunal stability during the early Oligocene climatic crash: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 127, p. 239-256.
- Prothero, D.R. and Raymond, K.R., 2008, Variability and sexual size dimorphism in Pleistocene ground sloths (Xenarthra): New Mexico Museum of Natural History and Science, Bulletin, 44, p. 331-334.

- Prothero, D.R., Raymond, K.R., Syverson, V.J. and Molina, S., 2009, Stasis in late Pleistocene birds and mammals from La Brea tar pits over the last glacial-interglacial cycle: Cincinnati Museum Center Scientific Contributions, v. 3, p. 291-292.
- Ruse, M. and Sepkoski, D., eds., 2009, The paleobiological revolution: Chicago, University of Chicago Press, 584 p.
- Stock, C. and Harris, J.M., 1992, Rancho La Brea: a record of Pleistocene life in California: Natural History Museum of Los Angeles County, Science Series, v. 37, p. 1-113.
- Syverson, V.J. and Prothero, D.R., 2010, Evolutionary patterns in late Quaternary California condors: PalArch Journal of Vertebrate Paleontology, v. 7, p. 1-18.
- Ward, J.W., Harris, J.M., Cerling, T.E., Wiedenhoeft, A., Lott, M.J., Dearing, M., Coltrain, J.B. and Ehleringer, J.R., 2005, Carbon starvation in glacial trees recovered from the La Brea tar pits, southern California: Proceedings of the National Academy of Sciences, v. 102, p. 690-694.
- Warter, J.K., 1976, Late Pleistocene plant communities evidence from Rancho La Brea tar pits: symposium proceedings on the plant communities of southern California: Native Plant Society, Special Publication 2, p. 32-39.
- Webb, S.D., 1965, The osteology of *Camelops*: Bulletin of the Los Angeles County Museum, Science, v. 1, p. 1-54.
- Weiner, J., 1995, The beak of the finch: a story of evolution in our own time: New York, Vintage, 352 p.