# STASIS IN THE LATE PLEISTOCENE GROUND SLOTHS (*PARAMYLODON HARLANI*) FROM RANCHO LA BREA TAR PITS, CALIFORNIA

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**Abstract**—Stasis in Pleistocene mammals in the face of climatic change during the glacial-interglacial cycles has been widely documented. We examined the size and shape changes of the bones of common large ground sloth, *Paramylodon harlani*, from Rancho La Brea. We measured multiple dimensions of most the adult unbroken astragali, patellae, and the major limb bones; only the astragali, patella, and radii were abundant in enough well dated pits for analysis. In every dimension, these bones show stasis in linear dimensions, as well as in robustness of limb elements. Statistical analysis by ANOVA confirmed that the means of all the temporally sequential samples were not significantly different from each other, so stasis prevails. These results, together with those of every common large bird or mammal from Rancho La Brea, show that stasis prevailed in the region from 35,000 to 11,000 years ago, despite climate changes that caused the region to go from oak-chaparral at 35 ka, to closed-cone snowy piñon-juniper forest at peak glacial 21 ka, and then back to oak-chaparral-sage scrub vegetation over the past 10,000 years.

## INTRODUCTION

Despite the classic models of evolution in response to environmental change, based on neontological examples such as Galapagos finches or lab rats, paleontologists have overwhelmingly shown that most fossil metazoans show stasis (Jackson and Cheetham, 1999; Jablonski, 2000, 2008; Gould, 2002; Geary, 2009; Hallam, 2009; Princehouse, 2009; Ruse and Sepkoski, 2009) as predicted by Eldredge and Gould (1972). Even more striking is the fact that fossil species show stasis in the face of dramatic climatic changes (e.g., Coope, 1979; Davis, 1983; Bennett, 1990; Prothero and Heaton, 1996; Prothero, 1999). This has been particularly well documented in Pleistocene mammals (Barnosky, 1994, 2005), which are remarkably stable and unchanging even though they lived through multiple glacial-interglacial cycles and large-scale climate change.

Recently, such stasis has also been well documented in the mammals and birds of the Rancho La Brea tar pits. These include virtually all the common mammals recovered from there, such as the dire wolves (Linden and Prothero, in press), the felids (Madan et al., this volume), the bison (Raymond and Prothero, this volume), and the horses and camels (DeSantis et al., this volume). The five most common birds also show complete stasis, including the golden eagles (Molina and Prothero, this volume), the condors (Syverson and Prothero, 2010), and the bald eagles, caracaras, and turkeys (Fragomeni and Prothero, this volume).

This stasis in the fossils found at Rancho La Brea occurs despite the fact that there is a well-dated climatic record showing significant changes in the mollusks, plants, and isotopes (Warter, 1976; Coltrain et al., 2004; Ward et al., 2005). Heusser (1998) examined the pollen record from high-resolution deep-sea cores taken just offshore, and found significant vegetational change in the region. During Oxygen Isotope Stage (OIS) 3 (59 ka to 24 ka), the region was blanketed in an oak-chaparral woodland, but during the last glacial maximum (24-14 ka), this was replaced by a closed-cone coniferous piñon-juniper forest with significant snowfall in the winter. During the glacial-interglacial transition (14 ka to 10 ka), the vegetation gradually returned to oak and chaparral with significant alders, and in the past 10,000 years of the Holocene, the region was cloaked in the coastal sage scrub vegetation that still lives there today.

Rancho La Brea not only provides a good record of the past 40,000 years of climate in one region, but it also provides outstanding samples of the fauna through that time, with thousands of well-preserved bones (Akersten et al., 1983; Stock and Harris, 1992; Friscia et al.,

2008), each recovered from radiocarbon dated pits (Marcus and Berger, 1984; O'Keefe et al., 2009).

Given that all the other abundant large mammals and birds from Rancho La Brea show stasis through the entire time interval, the question arises as to whether the same is true of the sloths. Prothero and Raymond (2008) documented the lack of size dimorphism in the postcranial bones from two of the three ground sloths found in the region (*Paramylodon harlani, Nothrotheriops shastensis*). The third ground sloth, *Megalonyx jeffersoni*, was too rare to be analyzed in this manner. Of the three sloths from Rancho La Brea, only *P. harlani* is common in enough of the dated pits to be useful in a study of change over time, so it is the only taxon examined in this research. Raymond and Prothero (2010) used these same sloth datasets to determine whether endochondral bones were more or less variable than bones derived from connective tissue, such as sesamoids. Neither of these previous studies on sloth bones discussed their changes through time. However, there are examples of size change documented in edentates outside Rancho La Brea. McDonald (1995) demonstrated that there was a size increase in *Paramylodon* from the Blancan to the Rancholabrean. Hulbert and Morgan (1993) reviewed size changes in Pliocene-Pleistocene pampatheres, as well as older literature about size changes in the glyptodonts.

## METHODS

All measurements were made with digital calipers, or with a tape measure for lengths of limb bones, using the anatomical landmarks described by Prothero and Raymond (2008). Only unbroken, adult bones were measured. Although we measured nearly all the common postcranial bones (humeri, radii, ulnae, femora, patellae, tibiae, astragali, and calcanea), only the tibiae, astragali, and patellae were abundant enough in the well-dated pits to allow us to examine size and shape changes through time (actual sample sizes for each bone in each pit are given in Table 1). Data were recorded on Excel spreadsheets, which also allowed us to calculate basic statistics. Additional statistical analyses were performed with XL Stat.

Radiocarbon dates on the pits followed O'Keefe et al. (2009), or Marcus and Berger (1984) for pits that have not been recently redated. As described by Prothero and Raymond (2008), the postcranial bones show no apparent sexual size dimorphism, so this was not a factor in our analysis. Samples were analyzed for normality using the Shapiro-Wilk test, and those samples that were parametric were then analyzed using ANOVA.

TABLE 1. Basic statistics of *Paramylodon harlani* bones analyzed in this study. All measurements in mm.

| Character | Age (ka) | N | Mean | Variance |
|---|---|---|---|---|
| Radius length | 11 | 5 | 288.2 | 158.2 |
| | 14 | 8 | 278.8 | 204.6 |
| | 16 | 1 | 286.0 | — |
| | 18 | 3 | 284.3 | 46.3 |
| | 21 | 1 | 277.0 | — |
| | 35 | 4 | 290.5 | 28.3 |
| Radius midshaft width | 11 | 4 | 24.7 | 6.2 |
| | 14 | 8 | 69.7 | 23.0 |
| | 16 | 1 | 66.0 | — |
| | 18 | 3 | 64.3 | 0.3 |
| | 21 | 1 | 66.0 | — |
| | 35 | 4 | 71.2 | 86.2 |
| Radius midshaft depth | 11 | 4 | 38.7 | 29.5 |
| | 14 | 8 | 36.1 | 14.4 |
| | 16 | 1 | 31.0 | — |
| | 18 | 3 | 35/6 | 86.3 |
| | 21 | 1 | 32.0 | — |
| | 35 | 4 | 37.2 | 8.9 |
| Radius distal width | 11 | 4 | 77.2 | 6.9 |
| | 14 | 8 | 77.1 | 162.9 |
| | 16 | 1 | 76.0 | — |
| | 18 | 3 | 76.0 | 28.0 |
| | 21 | 1 | 71.0 | — |
| | 35 | 4 | 75.7 | 16.2 |
| Patella proximal-distal length | 11 | 7 | 123.2 | 74.2 |
| | 14 | 17 | 118.8 | 96.2 |
| | 16 | 8 | 114.2 | 30.2 |
| | 18 | 13 | 120.5 | 151.7 |
| | 21 | 2 | 123.5 | 220.5 |
| | 35 | 3 | 116.3 | 54.3 |
| Patella lateral width | 11 | 7 | 109.0 | 13.0 |
| | 14 | 17 | 105.5 | 40.6 |
| | 16 | 8 | 103.5 | 7.4 |
| | 18 | 13 | 105.4 | 92.7 |
| | 21 | 2 | 99.0 | 0.0 |
| | 35 | 3 | 109.3 | 52.3 |
| Patella dorsal-plantar depth | 11 | 7 | 62.8 | 6.4 |
| | 14 | 17 | 57.8 | 9.9 |
| | 16 | 8 | 56.0 | 17.7 |
| | 18 | 13 | 56.7 | 31.0 |
| | 21 | 2 | 58.0 | 18.0 |
| | 35 | 3 | 56.6 | 2.3 |
| Astragalus proximal-distal length | 10 | 3 | 128.3 | 94.3 |
| | 11 | 13 | 132.7 | 79.0 |
| | 15 | 19 | 131.1 | 58.4 |
| | 17 | 10 | 126.5 | 72.0 |
| | 27 | 5 | 127.6 | 12.3 |
| | 28 | 20 | 128.3 | 65.0 |
| | 32 | 6 | 119.3 | 308.6 |
| | 35 | 11 | 124.9 | 51.6 |
| Astragalus lateral width | 10 | 3 | 137.0 | 13.0 |
| | 11 | 13 | 138.7 | 58.8 |
| | 15 | 19 | 133.9 | 100.7 |
| | 17 | 10 | 133.0 | 88.6 |
| | 27 | 20 | 135.3 | 63.1 |
| | 28 | 20 | 135.3 | 63.1 |
| | 32 | 6 | 125.1 | 143.7 |
| | 35 | 11 | 132.0 | 88.6 |

## RESULTS

Basic statistics for all our measurements are given in Table 1. Our plots of the astragalar dimensions through time are shown Figure 1. Many variables were measured and could have been plotted and shown in this paper, but the proximal-distal length (Fig. 1A) and transverse width (Fig. 1B) are representative. As can be seen by visually tracking the mean values (large open squares) through the plot, there is very little change from one sample to the next, and no net increase in size in the dimensions of samples around the glacial maximum at 20 ka (as might be expected if sloths followed Bergmann's rule of larger body sizes in colder climates).

The pit samples that were large enough were analyzed using a Shapiro-Wilk test for normality, and all proved to be parametric. Thus, they could be analyzed using ANOVA. The ANOVA (Table 2) does not falsify the null hypothesis that any of the samples is significantly different from the mean.

Three variables were measured on the patellae (see Prothero and Raymond, 2008), and a representative plot of patellar length is shown in Figure 1C and patellar width in Figure 1D. As was the case with the astragalus, the means from the patellae track within a narrow range in every pit from 35 ka to 11 ka, with no significant departures from the average values. These data also passed a Shapiro-Wilk normality test, so they could be analyzed using parametric tests. ANOVA results (Table 2) also showed that none of the samples is significantly different from the mean of the entire population, so there is no significant size change through time in the patellae.

Finally, the only limb bone that yielded more than a few specimens per pit was the radius. Samples were much more limited than those of smaller bones like astragali or patellae, but did occur in enough pits to

be useful in this study. Even with this smaller sample size, the mean values in Figure 2A do not deviate from each other. These data were normally distributed, so the ANOVA was run (Table 2) and showed that none of the pit samples was significantly different from the mean for the population.

Another possibility is that limb bones might become more or less robust, even if overall linear dimensions are not changing. To address this, we took the midshaft area of the radius and divided it by the length of the same bone to produce a robustness index. When these are plotted (Fig. 2B), the data are a bit noisier (since the samples are small, and ratios are much more sensitive to changes than linear dimensions), but there appears to be stasis in the means. This is confirmed by ANOVA (Table 2), so there were no significant changes in robustness of the limbs of these ground sloths, even when climate and vegetation are very different at the last glacial maximum 21,000 years ago.

## DISCUSSION

As shown by the plots in Figures 1 and 2 and the data in Table 2, there is no statistically significant evidence of changes in the size or shape of the bones of the ground sloth *Paramylodon harlani* through the climatic and vegetational changes at Rancho La Brea over the past 40,000 years. These results are consistent with the data recovered from dire wolves (Linden and Prothero, in press), saber-toothed cats and Ice Age lions (Madan et al., this volume), bison (Raymond and Prothero, this volume), horses and camels (DeSantis et al., this volume), and the five most common birds at Rancho La Brea (Syverson and Prothero, 2010; Fragomeni and Prothero, this volume; Molina and Prothero, this volume). They are also consistent with the trends generally observed for Pleistocene mammals across the world (Barnosky, 1994, 2005).
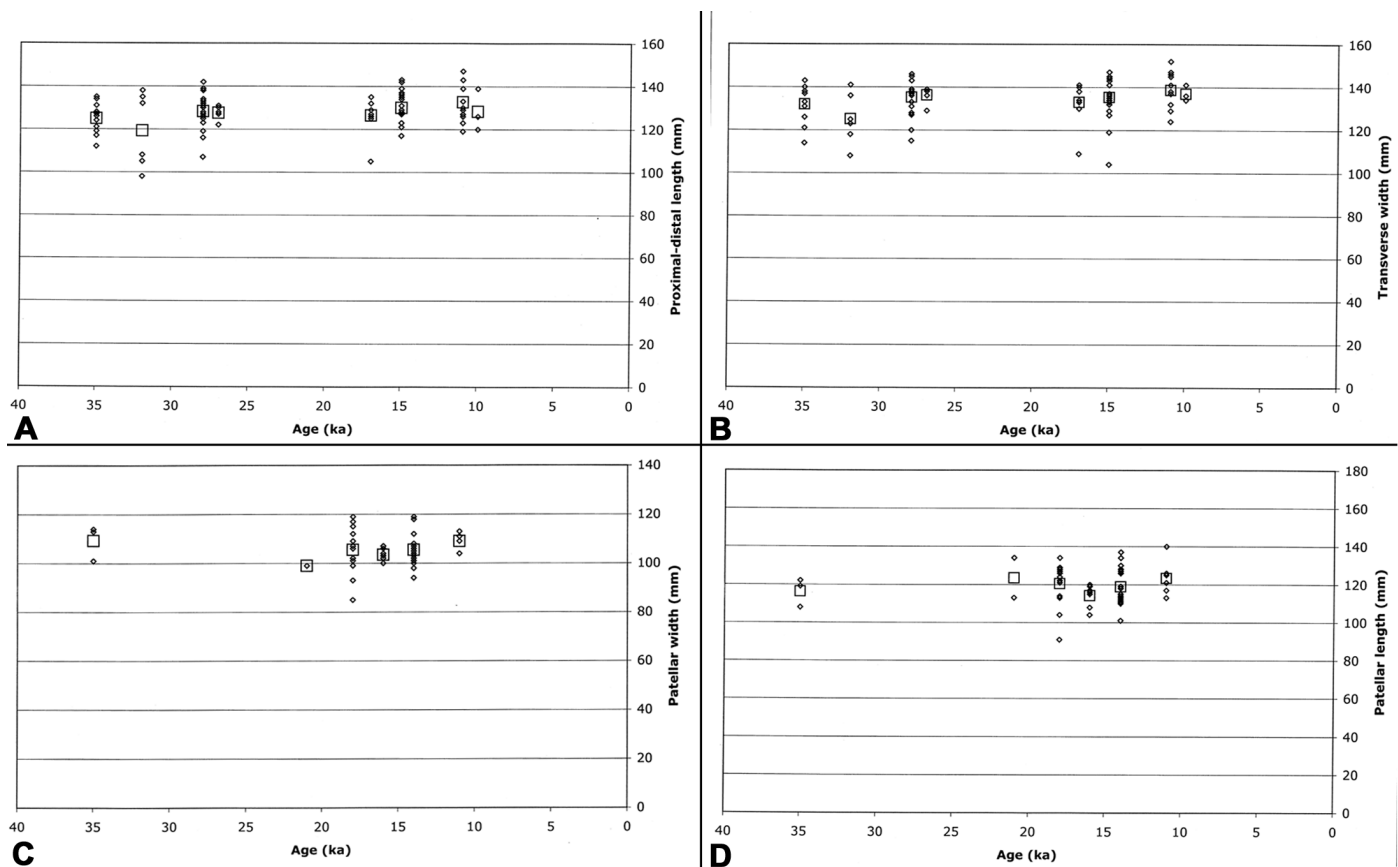


FIGURES 1. **A-D**, Plots of dimensions of *Paramylodon* bones against the age of the pit sample. Open diamonds indicate individual specimens; open squares are the means for each time interval. **A**, Astragalus proximal-distal length. **B**, Astragalus transverse width. **C**, Patellar length. **D**, Patellar width.

TABLE 2. ANOVA of dimensions of *P. harlani* bones analyzed in this study.

| Variable | F | F$_{critical}$ | p | df | Significant? |
|---|---|---|---|---|---|
| Radius length | 0.74 | 2.90 | 0.60 | 5 | no |
| Radius midshaft width | 1.07 | 2.90 | 0.41 | 5 | no |
| Radius midshaft depth | 0.64 | 2.90 | 0.66 | 5 | no |
| Radius distal width | 0.24 | 2.90 | 0.93 | 5 | no |
| Patella proximal-distal length | 0.80 | 2.42 | 0.54 | 5 | no |
| Patella lateral width | 1.08 | 2.42 | 0.38 | 5 | no |
| Patella dorsal-plantar depth | 1.65 | 2.42 | 0.03 | 5 | no |
| Astragalus proximal-distal length | 1.89 | 2.12 | 0.08 | 7 | no |
| Astragalus lateral width | 1.64 | 2.12 | 0.13 | 7 | no |
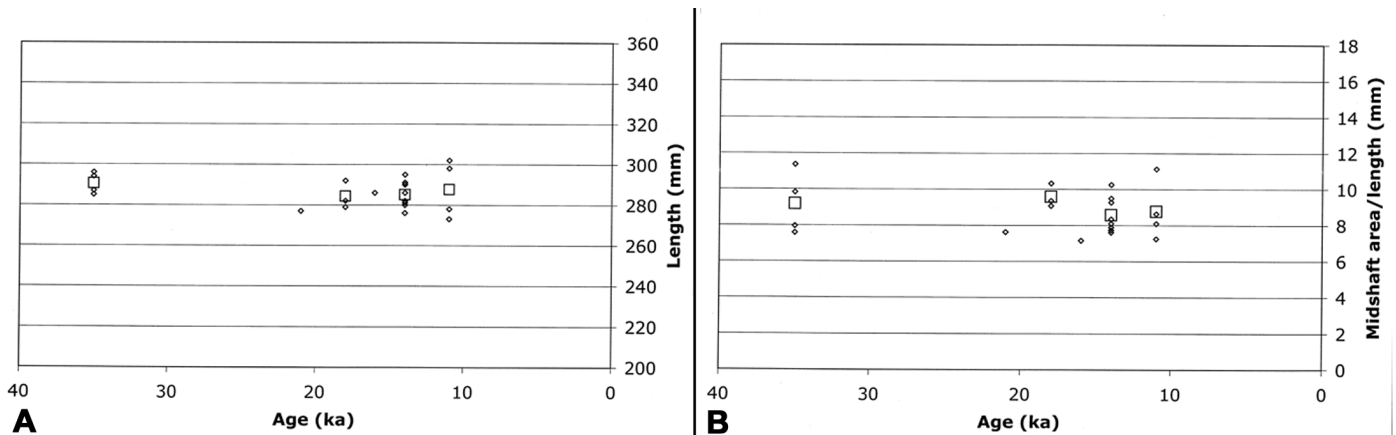


FIGURE 2. **A**, Plot of *Paramylodon* radius length through time. Symbols as in Fig. 1. **B**, Plot of ratios of *Paramylodon* radius robustness (midshaft cross-sectional area divided by the length) against the age of the pit sample. Symbols as in Fig. 1.

Why do Pleistocene mammals and birds show so little evidence of morphological changes in response to well documented climate change? This question is related to the larger question of why we find stasis in nearly all metazoans, despite changes in the environment. We can rule out the stabilizing selection model (Estes and Arnold, 2007), because these environments are changing, not stabilizing (Liebermann and Dudgeon, 1996). For a long time, the idea of developmental constraints and canalization (Eldredge and Gould, 1972) was popular, although it has diminished in popularity as more examples of evolutionary plasticity (such as domesticated dogs) have been documented (Gould, 2002).

Currently, the most popular model is the notion that organisms are very broadly adapted and can live in a wide variety of habitats with minimal morphological change (Lieberman et al., 1995; Eldredge et al., 2005). This may work for the larger mammals and birds of Rancho La Brea, which are widely distributed over North America in the late Pleistocene (Kurtén and Anderson, 1980). However, it is hard to reconcile with the fact that many of these animals (wolves, horses, bison, eagles, caracaras) show clinal variation in size (Bergmann's rule) in response to colder climates, and we see no such change at the coldest period at Rancho La Brea. In addition, *Paramylodon harlani* showed clinal variation in size following Bergmann's rule in the Pleistocene (McDonald et al., 2004). It also does not explain the stasis in small mammal fossils (which have small geographic ranges and are much more sensitive to their environment) over large-scale climate changes, documented both from the Pleistocene (Lich, 1990; Barnosky, 1994, 2005) and other time periods, such as the Eocene-Oligocene transition (Prothero and Heaton, 1996; Prothero, 1999).

## CONCLUSIONS

Like all the other common large mammals and birds at Rancho La Brea, the bones of the ground sloth *Paramylodon harlani* show no significant changes in size or shape through the last 35,000 years of climate change in the region. Such stability is prevalent among nearly all Pleistocene mammals and birds, despite the tremendous variations in climate over the glacial-interglacial cycles. This stasis cannot be explained by stabilizing selection, nor by developmental constraints and canalization. The currently popular explanation is the broad habitat preferences and environmental flexibility of most of these large mammals and birds. However, this explanation does not account for the lack of size change in colder climates (Bergmann's rule), nor does it explain the stasis found in small mammals with much smaller ranges and greater environmental sensitivity.

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