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

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Abstract

# 1. Introduction

The classic neontological model of gradualistic evolution argues 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). Weiner (1995) summarized additional examples of microevolutionary change in recent birds, such as Siberian warblers, English sparrows, cuckoos, cowbirds, red-winged blackbirds, and many others. In all cases, these studies emphasized how quickly birds changed in size and shape in response to external climatic forcing factors.

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 animal and plant species should undergo little net change in size or shape, and instead remain static over millions of years after a speciation event. Hundreds of paleontological studies undertaken since 1972 (Jackson and Cheetham, 1999; Gould, 2002; Jablonski, 2000, 2008; Geary, 2009; Princehouse, 2009; Hallam, 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.

Among Pleistocene mammals, the stability of species through multiple episodes of climate change and instability is well established. As early as 1863 Darwin’s friend, the pioneering mammalian paleontologist Hugh Falconer, warned in a letter to Darwin about stasis observed in mammoths from different Pleistocene deposits. In his 1863 publication, Falconer wrote, “If we cast a glance back on the long vista of physical changes which our planet has undergone since the Neozoic Epoch, we can nowhere detect signs of a revolution more sudden and pronounced, and more important in its results, than the intercalation and subsequent disappearance of the Glacial period. Yet the mammoth lived before it, and passed through the ordeal of all the hard extremities which it involved, bearing his organs of locomotion and digestion all but unchanged” (Falconer, 1863).

In almost 150 years since Falconer’s observations, stasis through climatic change in Pleistocene organisms has become even better documented (Bennett, 1990, 1997; Barnosky, 1994, 2005; Barnosky and Kraatz, 2007; Lister, 2004; and many other papers). Barnosky (1994, p. 173) wrote, “climatic oscillations on the multi-millennial scale may not stimulate speciation much.” Barnosky (2005, p. 247) commented that “despite the increased potential for isolation of populations that should occur with multiple advances and retreats of glaciers and rearrangement of climatic zones, empirical data suggest that speciation rates were neither appreciably elevated for Quaternary mammals, nor strongly correlated with glacial-interglacial transitions.” On p. 257, he wrote, “research that has focused on tracing the morphological characters that had taxonomic significance in these taxa revealed no direct correlation between climate changes and morphologic changes.” Bennett (1990, 1997) suggested that Quaternary climate change did not stimulate speciation in plants, a conclusion that has since been well supported (Kadereit et al., 2004; McKinnon et al., 2004; Willis and Niklas, 2004). Likewise, studies of Pleistocene birds shows very little evolutionary effect of climate change (Avise et al., 1998; Klicka and Zink, 1999; Zink et al., 2004). Nor do fish (Avise et al., 1998), reptiles and amphibians (Avise et al., 1998; Holman, 1995), or insects (Coope, 2004) seem to show major morphological change or speciation in response to Quaternary climate cycles. McGill et al. (2005) argued that Quaternary small mammal communities showed remarkable inertia and resistance to change, despite dramatic climatic changes of the glacial-interglacials cycles.

Yet there are changes in size and body proportions of many Pleistocene and Recent mammals that might be expected to respond to episodes of dramatic cooling or warming. These include well known ecological clines such as Bergmann’s rule, where more cold-adapted species or subspecies tend to have larger body sizes to conserve body heat, and Allen’s rule, where more cold-adapted species or subspecies tend to have shorter more robust limbs and other appendages (such as ears) compared to those of warmer climates. For example, the northern bison subspecies, the wood bison (*Bison bison athabascae*), is much larger and with more robust limbs than the more southerly subspecies, the plains bison (*Bison bison bison*) (McDonald, 1981; Nowak, 1991). 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 (Nowak, 1991; Franklin, 1983). The steppe-dwelling Bactrian camel (*Camelus bactrianus*) weighs about 600-1040 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.

Although not all felids demonstrate Bergmann’s rule of larger body size in colder climates of higher latitudes or altitudes, the American puma (or cougar or mountain lion) (*Felis concolor*) does vary in body size by latitude, with the largest in the higher latitudes of North and South America, and the smallest in the tropics (Agustin Iriarte et al., 1990; Sunquist and Sunquist, 2002). Similarly, among the many subspecies of the tiger (*Panthera tigris*), the largest are the cold-adapted Siberian tigers (227 kg in weight), while the smallest are the tropical subspecies such as the Sumatran tiger (75-140 kg in weight) or the Indochinese tiger (110-140 kg in weight)(Sunquist and Sunquist, 2002).

Among birds examined in this study, the bald eagle (*Haliaeetus leucocephalus*) and the golden eagle (*Aquila chrysaetos*) shows considerable clinal variation, with larger-bodied subspecies in the high latitudes in both Siberia and North America today (Brown, 1968; Johnsgard, 1990). *Caracara plancus*, the extant southern caracara, is well known to have larger body sizes in the southern cold regions of South America than it does in the tropics (Brown, 1968; Johnsgard, 1990). Given these strong size and shape trends in modern populations, there is every reason to suspect that populations that experienced dramatic cooling or warming in the Pleistocene might show similar trends.

This study examines the effects of the changes in the climate on all the mammals and birds from Rancho La Brea that have sufficiently abundant material from the well-dated pits. There are 59 mammal species at Rancho La Brea, some of which are represented by thousands of specimens. These include the dire wolf, *Canis dirus*, the saber-toothed cat *Smilodon fatalis*, the giant “lion” or “jaguar” *Panthera atrox*, the large ground sloth *Paramylodon harlani*, the bison *Bison antiquus*, the western horse (*Equus occidentalis* Leidy, 1865 *sensu* Merriam, 1913; hereafter *E*. “*occidentalis*”) and the western camel *Camelops hesternus*. Other mammals (mammoths and mastodonts, bears, pronghorns, small mammals, etc.) occur as well, but not enough specimens occur in enough well dated pits to allow us to conduct a study of this sort.

The sample of birds in particular is one of the best in the entire fossil record, with over 85,000 individual bones representing at least 133 species, including 19 extinct species (Howard, 1962). The five most common birds include the extinct Pleistocene condor *Gymnogyps amplus*, the bald eagle *Haliaeetus leucocephalus* and golden eagle *Aquila chrysaetos*, the extinct California turkey *Meleagris californica*, and the extinct La Brea caracara (*Caracara plancus prelutosus* according to Banks and Dove, 1992, and Dove and Banks, 1999). There are a few other common birds, but most don’t occur in multiple pits, or are currently under study by others and thus unavailable.

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 addition 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. The most detailed and well-calibrated record comes not from RLB itself, but from deep-sea cores drilled just offshore in the California borderland. According to Heusser (1998), the region changed from oak and chaparral vegetation around 59 ka to pine-juniper-cypress woodlands by 24 ka, then to a closed-cone juniper-ponderosa forest with abundant winter snow during the last glacial maximum (24-14 ka). During the glacial-interglacial transition from 14 to 10 ka, the landscape returned to dominant oak-chaparral and coastal sagebrush with pulses of alder, and in the past 10,000 years, the region has been vegetated by the modern assemblage of oak-chaparral-herbaceous vegetation. Coltrain et al. (2004) performed stable isotope analysis and found evidence of increased seasonal aridity during the last interglacial and previous glacial.

**2. Hypothesis**

The samples from Rancho La Brea give us a unique opportunity to test the changes of all the common members of a Quaternary fauna in a single location with large well dated samples spanning the last 35,000 years of climate changes. Such a dramatic change from warm interglacial scrub brush to snowy glacial pine forests represents a significant transformation of the modern ecological communities and should be expected to have at least some effect on size and robustness in the animals that experienced these changes. In particular, we might expect the samples nearest the peak glacial maximum at about 20 ka to be both larger (Bergmann’s rule) and more robust (Allen’s rule) compared to samples from before and after the peak glacial. In any case, statistically significant changes in size or shape would test the hypothesis that organisms change their size and shape in response to climate. The lack of such a response would support the “punctuated equilibrium” model of species stability.

# 3. Materials and Methods

We used dial and digital calipers to measure the most abundant postcranial bones with adequate sample sizes from enough pits. As described in detail in the papers on each animal (Syverson and Prothero, 2010, on condors; Molina and Prothero, 2011, on golden eagles; DeSantis et al., 2011 on horses and camels; Madan et al., 2011, on felids; Fragomeni and Prothero, 2011, on bald eagles, turkeys, and caracaras; Prothero and Raymond, 2011, on ground sloths; Raymond and Prothero, 2011, on bison; Linden, 2011, on dire wolves), the measurements encompassed most of the dimensions of the bones that were appropriate for their respective shapes.

For analysis, 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 parametric 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 performed multivariate analysis using the XL Stat program of Microsoft Excel.

Additionally, in this paper we reanalyzed the whole corpus of data using log-likelihood methods to create models for the time-series of each individual measurement, e.g. “*Gymnogyps amplus*, femur, distal width”. Timeseries were modeled as a directional trend (Dir), a random walk (RW), and variance around a static optimum (Stasis); the Akaike information criterion (AIC) for the three models was computed and the relative weights compared to give a ratio of support for each model. These analyses were performed in R using the “paleoTS” package. Results are reported here as a triple, the means of the three relative weights for a group of measurements taken on a given set of bones.

We studied samples only from pits with good radiocarbon dates and relatively small error estimates (Marcus and Berger, 2004; O’Keefe et al., 2009), which excluded samples from Pits 4 and 16. Although the error estimates on some pits have changed somewhat(O’Keefe et al., 2009), their mean pit ages are still sufficiently different that scholars continue to treat each sample as distinct in age (O’Keefe, 2009).

We measured only 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.

# 4. Results

*4.1. Dire Wolves—*The dire wolf, *Canis dirus*, is by far the most common mammalian fossil at Rancho La Brea, represented by thousands of individual bones from nearly every pit. Linden (2011) presented preliminary results of his research into dire wolves, and full documentation will be published elsewhere. He sampled all the common bones the skeleton of *Canis dirus*, especially femora, humeri, tibiae, astragali, and metapodials. He found no significant differences in size or shape between the pits, with the exception of Pit 13 (16 ka in age), which yielded aberrantly small specimens. This is the same conclusion obtained by O’Keefe (2009), who found that the Pit 13 dire wolf skull sample also seemed small and stunted compared to all other pit samples. The full reason behind this anomalous sample from 16 ka is not understood, but it is important to note that it is not the sample closest in age to the peak glacial maximum (20 ka) or any other significant climatic event, all of which are statistically indistinguishable from one another. Thus, the dire wolf sample shows stasis in all but one sample, and does not match the climate hypothesis of larger more robust specimens about 20 ka.

For this study, we examine two aspects of the data set not discussed by Linden (2011). Following the model described in Madan et al. (2011), we subjected the two largest limb bones (humerus and femur) to principal components analysis (PCA) to see if there were shape changes among pits of different ages. The results (Figs. 1-3) are very similar to those obtained by Madan et al. (2011) for *Smilodon*. In every case, the loadings were 70-90% on the first factor/ first PC, showing that most of the variability is explained by this single component. Typically, in PCA that are done on variable biological samples, PC1/factor 1 is usually a proxy of size. The second PC/ second factor explained typically 20% or less of the variability, so there does not seem to be much of a shape component in these data; the third PC/ third factor explained typically less than 5% of the data, and the loading on the remaining factors was negligible.

Looking at circular plots of the first vs. second PC/ factor (Figs. 2-3), there is no consistent trend in data from sequential pits. No single variable consistently sticks out of the general cluster of vectors on the second PC/ second factor axis, so there does not appear to be a consistent change in shape through time. This is exactly what we found when we analyzed the femora and limbs of *Smilodon* as well. Thus, we find no evidence of consistent shape change through time, either in the plots of limb robustness of Linden (2011) or in our own multivariate analysis, nor is there any evidence that limbs in samples near 20 ka in age are larger or more robust, as would be expected if the climatic cooling had an effect on these animals.

Timeseries analysis fails to detect any signal of either directional change or stasis in the *Canis* limb bones (mean AIC weights: Dir 0.003, RW 0.97, stasis 0.03). Results for the astragali are more equivocal between stasis and random walk, but likewise show no support for any directional trend (Dir 0.02, RW 0.46, stasis 0.52).

*4.2. Felids—*Madan et al. (2011) measured multiple dimensions of most of the common limb bones of both *Smilodon fatalis* and *Panthera atrox* from Rancho La Brea, including humeri, femora, patellae, tibiae, astragali, third metacarpals (MC3) and third metatarsals (MT3). They found no statistically significant changes in either size or robustness of any of the variables from any of these elements among all the pits sampled. Prior to this study, no one had attempted a similar analysis on any Rancho La Brea fossil except Menard’s (1947) analysis of *Smilodon*. Menard claimed to be able to detect a slight size trend in the metapodials, which he interpreted as a chronocline. Unfortunately for Menard’s (1947) hypothesis, when radiocarbon dates became available, the age sequence of the pit samples he postulated did not match the dates. Madan et al. (2011) measured many more MC3 and MT3 specimens than did Menard (1947), and plotted their data using the modern radiocarbon ages (Fig. 4). They found no statistically significant differences between any individual pit sample and the overall pool of data using ANOVA, and thus no statistically significant size trend through time. The time series analysis backs this up, finding an overall pattern of stasis in all measurements on *Smilodon* metapodials and astragali (mean AIC weights: Dir 0.03, RW 0.34, Stasis 0.63).

Madan et al. (2011) also performed a PCA on the humeri and femora of *Smilodon*. As in the case with *Canis dirus* above, the loadings were overwhelmingly on the first PC/first factor, with very little on the second, third or remaining factors/PCs. Madan et al. (2011, Figs. 6 and 7) plotted PC1 vs. PC2 on circular plots (as in Fig. 2-3 of this paper), and found that there was no consistent pattern of the variables loading on PC2/factor 2. In addition, a random walk model is most strongly supported for all limb bone measurements individually (mean AIC weights: Dir 0.03, RW 0.82, Stasis 0.15). Once again, this suggests that there is no clear trend in change of shape through time in the limb bones of *Smilodon*, just as there was no trend in dire wolves.

Although the sample of *P. atrox* was much smaller than that of *Smilodon*, nevertheless there were enough patellae and astragali from enough different pits that a statistical analysis was possible. In every case, there was no evidence of significant size change of *P. atrox* from one pit sample to the next, and no support for any pattern other than random walk (Dir 0.001, RW 0.995, Stasis 0.004).

*4.3. Horses*—DeSantis et al. (2011) measured the most common elements of the La Brea horse: the cannon bones (MC3 and MT3), astragali, and patellae. As in the previous examples, there was no statistically significant difference between any of the pit samples as established by ANOVA. Astragali and metapodials are dominated by a random-walk pattern (Dir 0.003, RW 0.98, Stasis 0.02) and patellae by stasis (Dir 0.02, RW 0.13, Stasis 0.86).

*4.4. 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 some bones, specifically astragali, calcanea, cuboids, and patellae (Webb, 1965). When these were plotted by radiocarbon age, there were no statistically significant differences between samples in any of these bones (DeSantis et al., 2011), and no suggestion of any pattern other than a random walk (Dir 0.01, RW 0.89, Stasis 0.09).

*4.5. Ground sloths—*Prothero and Raymond (2011) analyzed all the common bones of the large ground sloth *Paramylodon harlani* at Rancho La Brea. Only the radius, patella, and astragalus were sufficiently abundant in enough well dated pits for this type of analysis. As in every other case, the ground sloth bones showed complete stasis in both size and shape through the entire glacial-interglacial cycle, with no evidence of any statistically significant size changes as established by ANOVA, and equivocal support for a stasis or random-walk pattern (Dir 0.04, RW 0.66, Stasis 0.30).

*4.6. Bison—*Raymond and Prothero (2011) analyzed the sample of *Bison antiquus* from Rancho La Brea. Only the MC3-4 and MT3-4 metapodials (cannon bones), calcanea, astragali, patellae, and humeri were sufficiently abundant in enough well dated pits for this kind of analysis. As in all the previous studies, there were no statistically significant differences in size among any of the pits samples of bison from Rancho La Brea, and shape (as measured by robustness of the long bones) was also static, based on ANOVA of the entire sample. All measurements on astragali, patellae, calcanea, and humeral condyle width follow a random-walk (Dir 0.01, RW 0.85, Stasis 0.14), but metapodials have stronger support for a pattern of stasis (Dir 0.03, RW 0.29, Stasis 0.68).

This stasis was also relevant to another area of dispute, regarding the size reduction of bison in the early Holocene from *B. antiquus* to modern *B. b. bison*. The two competing hypotheses argue that this size reduction was due to some sort of climatic or habitat change in the southern Plains during the early Holocene, or pressure due to human hunting in the earliest Holocene. Our data showed that RLB *B. antiquus* was unresponsive to the major climate changes of the last glacial-interglacial cycle. This undermines the climatic hypothesis and supports the human hunting pressure hypothesis. Ironically, Hill et al. (2008) even had measurements in their data sets and plots of some of the same Rancho La Brea bison as we studied, yet they failed to remark about the stasis over the past 40,000 years while focusing just on the interval of the Pleistocene-Holocene transition.

*4.7. Birds*—A number of studies have addressed size and shape changes through time in Pleistocene mammals, but there have been much fewer such studies in birds, since their fossil record is much more fragmentary. The five most common birds at Rancho La Brea (Howard, 1962) are the golden eagle, the California turkey, the La Brea condor, the bald eagle, and the caracara (along with the teratorn, which is currently under study by K. Campbell, Jr.).

Molina and Prothero (2011) analyzed the huge sample of right tarsometatarsi (TMT), the lower leg bone, which is the most common skeletal element in most fossil birds. They measured five variables in almost 700 specimens from numerous pits, and found no statistically significant differences between the pit samples as determined by ANOVA. The time series for all five variables are strongly consistent with stasis (Dir 0.06, RW 0.21, Stasis 0.73).

Syverson and Prothero (2010) looked at many different skeletal elements of the Pleistocene condor, *Gymnogyps amplus*. In addition to showing that this species is valid and can be clearly distinguished from the modern California condor, *G. californicus*, Syverson and Prothero looked at the change in the size and shape of TMTs through time, and using ANOVA, found no evidence of pit samples which were statistically separated from the rest of the specimens. Further analysis of this data set confirms that all TMT measurements follow a pattern strongly consistent with stasis and weakly consistent with a random walk (Dir 0.03, RW 0.32, Stasis 0.65), as do humeral measurements (Dir 0.30, RW 0.00, Stasis 0.70). The best models for other skeletal measurements on RLB *G. amplus* are split between stasis and a random walk (mean AIC weights for all *G. amplus* measurements: Dir 0.06, RW 0.65, Stasis 0.30). They also found evidence that the large *G. amplus* survived into the early Holocene and did not immediately reduce in size to *G. californicus*, as had long been assumed.

Fragomeni and Prothero (2011) looked at three other birds that are common at Rancho La Brea. They measured multiple dimensions of the TMTs of the bald eagle and caracara, and found no evidence of size or shape changes in these limb bones through the entire time span. They also analyzed the data set measured by Bochenski and Campbell (2006) of California turkeys, and found that they too show stasis over the entire span of the dated pits at Rancho La Brea.

# 5. Discussion

Despite the expectations that there should be significant size and/or shape change at the peak glacial at 20 ka in the mammals and birds of Rancho La Brea, the data revealed no statistically significant directional trends in the change of the size or shape in any mammal or bird over the last 40,000 years. Even though the pollen shows dramatic cooling and development of a snowy juniper-pine forest at the peak the last glacial-interglacial cycle at 20 ka, the measured shape and size of Rancho La Brea mammals and birds 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). Of the complete RLB data set, about one-third measurement time series were best modeled by stasis and the remainder by a random walk; in no case was directional evolution found to be the best model for the time series of any trait.

This lack of change 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 increase with latitude and colder climate, and Allen’s rule, which predicts shorter and more robust limbs in colder climates. As we pointed out at the beginning of the paper, lack of directional phenotypic response through dramatic climate changes seems to be a prevalent occurrence among Pleistocene species despite the rapid changes of their environment and habitats (Barnosky, 1994, 2005).

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 severely 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).

**7. 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 common Rancho La Brea mammals or birds 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 many of these mammals and birds exhibit a tendency toward larger body sizes (Bergmann’s rule) and shorter more robust limbs (Allen’s rule) 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 classical Neo-Darwinian theory predicts.

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# References

Agustin Iriarte, J., Franklin, W.J., Johnson, W.E., Redford, K.H. 1990, Biogeographic variation of food habits and body size of the American puma: Oecologia 85(2): 185-190.

Akersten, W.A., Shaw, C.A. and Jefferson, G.T., 1983, Rancho La Brea: status and future: Paleobiology, v. 9, p. 211-217.

Avise, J.C., Walker, D., and Johns, G.C. 1998. Species durations and Pleistocene effects on vertebrate phylogeography. Proceedings of the Royal Society of London, B 265:1707-1712.

Banks, R.C., and Dove, C.J., 1992, The generic name for the crested caracaras (Aves: Falconidae): Proceedings of the Biological Society of Washington, v. 105, no. 3, p. 420-425.

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 (1/2), p. 247-264.

Barnosky, A.D., and Kraatz, B.P. 2007. The role of climate change in the evolution of mammals. BioScience 57: 523-532.

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 University Press, Cambridge.

Bochenski, Z.M., and Campbell Jr., K.E., 2006, The extinct California turkey, *Meleagris californica*, from Rancho La Brea: comparative osteology and systematics: Contributions in Science, Natural History Museum of Los Angeles County, v. 509, p. 1-92.

Brown, L., 1968, Eagles, Hawks, and Falcons of the World. McGraw-Hill, New York.

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.

DeSantis, S.N., Prothero, D.R., and Gage, G.L. 2011. Size and shape stasis in late Pleistocene horses and camels from Rancho La Brea during the last glacial-interglacial cycle. *New Mexico Museum of Natural History Bulletin* 53:505-510.

Dove, C.J., and Banks, R.C., 1999, A taxonomic study of the crested caracaras (Falconidae): Wilson Bulletin, v. 111(3): 330-339.

Eldredge, N., 1999, The Pattern of Evolution: W. H. Freeman, New York.

Eldredge, N., and Gould, S.J. 1972, Punctuated equilibria: An alternative to phyletic gradualism, p. 82-115, *in* Schopf, T.J.M. (ed.), Models in Paleobiology: Freeman, San Francisco,

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.

Falconer, H. 1863. On the American fossil elephant. Natural History Review 1863: 43–114.

Fragomeni, A., and Prothero, D.R., 2011. Stasis in late Quaternary birds from the La Brea tar pits during the last glacial-interglacial cycle. *New Mexico Museum of Natural History Bulletin* 53:511-516.

Franklin, W.D.,1983, Contrasting socioecologies of South America’s wild camelids: the vicuña and the guanaco: American Society of Mammalogists Special Publication, v. 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, p. 127-147, *in* Allmon, W.D., Kelley, P.H., and Ross, R.M., eds., Stephen Jay Gould: Reflections on His View of Life: Oxford University Press, Oxford.

Gould, S.J., 2002, The Structure of Evolutionary Theory: Harvard University Press, Cambridge, Massachusetts.

Grant, P.R. and Grant, B.R., 2007, How and Why Species Multiply: The Radiation of Darwin’s Finches: Princeton University Press, Princeton.

Grant, P.R. and Weiner, J., 1999, The Ecology and Evolution of Darwin’s Finches: Princeton University Press, Princeton.

Groves, C.P., 1974, Horses, Asses, and Zebras in the Wild: David and Charles Publishers, Newton Abbott, England.

Hallam, A., 2009, The problem of punctuational speciation and trends in the fossil record, p. 423-432, *in* Ruse, M., and Sepkoski, D. (eds.), The Paleobiological Revolution: University of Chicago Press, Chicago.

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.

Holman, J.A. 1995, Pleistocene Reptiles and Amphibians in North America. Oxford University Press, Oxford, UK.

Howard, H., 1962, A comparison of avian assemblages from individual pits at Rancho La Brea, California: Contributions in Science, Natural History Museum of Los Angeles County, v. 58, p. 1-24.

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](javascript:%20void%200): 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 14, p. 72-77.

Johnsgard, P.A., 1990, Hawks, Eagles, and Falcons of North America: Smithsonian Institution Press, Washington, DC.

Kadereit, J.W., Griebeler, E.M., and Comes, H.P. 2004. Quaternary diversification in Alpine plants: pattern and process. Philosophical Transactions of the Royal Society of London B 359: 265-274.

Klicka, J., and Zink, R.M. 1999. Pleistocene effects on North American songbird evolution. Proceedings of the Royal Society of London B 266: 695-700.

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.

Lister, A.M. 2004. The impact of Quaternary ice ages on mammalian evolution. Philosophical Transactions of the Royal Society of London B 359:221-241.

Madan, M., Prothero, D.R., and Sutyagina, A. 2011. Did felids from Rancho La Brea change size or shape in the last Pleistocene? *New Mexico Museum of Natural History Bulletin* 53:554-563.

Marcus, L.F. and Berger, R., 1984, The significance of radiocarbon dates for Rancho La Brea, p. 159-188, *in* Martin, P.S. and Klein, R.G. (eds.), Quaternary Extinctions: A Prehistoric Revolution: University of Chicago Press, Chicago.

McDonald, J.N. 1981. North American Bison—Their Classification and Evolution. University of California Press, Berkeley.

McGill, B.J., Hadly, E.A., and Maurer, B.A. 2005. Community inertia of Quaternary small mammal assemblages in North America. Proceedings of the National Academy of Sciences USA 102: 16701-16706.

McKinnon, G.E., Jordan, G.J., Vaillancourt, R.E., Steane, D.A., and Potts, B.M. 2004. Glacials refugia and reticulate evolution: the case of the Tasmanian eucalypts. Philosophical Transactions of the Royal Society of London B 359:257-284.

Menard, H.W., Jr., 1947, Analysis of measurements in length of the metapodials of *Smilodon*: Bulletin of the Southern California Academy of Sciences, v. 46: 127-131.

Molina, S., and Prothero, D.R. 2011. Evolutionary stasis in late Pleistocene golden eagles. *New Mexico Museum of Natural History Bulletin* 53:564-569.

Nigra, J.O. and Lance, J.F., 1947, A statistical study of the metapodials of the dire wolf group from the Pleistocene of Rancho La Brea: Bulletin, Southern California Academy of Sciences, v. 46, p. 26-34.

Nowak, R.M., 1991. Walker’s Mammals of the World (5th ed.): Johns Hopkins University Press, Baltimore.

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? p. 149-175, *in* Ruse, M., and Sepkoski, D. (eds.), The Paleobiological Revolution: University of Chicago Press, Chicago.

Prothero, D.R., 1999, Does climatic change drive mammalian evolution? GSA Today, v. 9(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. 2011. Stasis in late Pleistocene ground sloths (*Paramylodon harlani*) from Rancho La Brea, California. *New Mexico Museum of Natural History Bulletin* 53:624-628.

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.

Raymond, K.R., and D.R. Prothero. 2011. Did climate change affect size in late Pleistocene bison? *New Mexico Museum of Natural History Bulletin* 53:636-640.

Ruse, M., and Sepkoski, D. (eds.), 2009, The Paleobiological Revolution: University of Chicago Press, Chicago.

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.

Sunquist, M., and Sunquist, F., 2002, Wild Cats of the World: University Of Chicago Press, Chicago.

Syverson, V.J., and Prothero, D.R., 2010, Evolutionary patterns in late Quaternary California condors: PalArch Journal of Vertebrate Paleontology, v. 7(10), 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(3), 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, v. 2, p. 32-39.

Webb, S.D., 1965, The osteology of *Camelops*: Bulletin of the Los Angeles County Museum, Science, v. 1: 1-54.

Weiner, J., 1995, The Beak of the Finch: A Story of Evolution in our Own Time: Vintage. New York.

Willis, K.J., and Niklas, K.J. 2004. The role of Quaternary environmental change on plant macroevolution: the exception or the rule? Philosophical Transactions of the Royal Society of London B 359: 159-172.

Zink, R.M., Klicka, J., and Barber, B.R. 2004. The tempo of avian diversification during the Quaternary. Philosophical Transactions of the Royal Society of London B 359: 215-220.