

## STASIS IN THE EXTINCT LA BREA FRAGILE EAGLE (*BUTEOGALLUS FRAGILIS*) IN RESPONSE TO CLIMATE CHANGE

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**Abstract**—The evolution of the Galápagos finches is one of the most famous examples of how the environment drives the evolution of traits in birds. Other examples of modern birds also suggest that birds evolve rapidly in response to climate change. However, of all the birds studied so far from the Pleistocene asphalt deposits of Rancho La Brea, none of them show change in the size or proportions due to climate changes of the last glacial maximum and the subsequent Holocene warming, from about 37 ka to 9 ka, when the chaparral typical of today was replaced by the snowy coniferous forests during the peak of the glacial maximum, about 18–20 ka. To test this further, we measured the tarsometatarsus (TMT) of *Buteogallus fragilis*, the extinct La Brea Fragile Eagle. We found complete stasis in both the size and proportion of the leg bones from 37,000 years ago until the end the Pleistocene. Like other La Brea birds, *Buteogallus fragilis* shows no response to the climate changes of the late Pleistocene.

### INTRODUCTION

Rancho La Brea tar pits (RLB) are a good place to test evolutionary models, because there are a large number of fossils preserved in them. Although animals did not get trapped in the tar often, when an animal did, many predators would also get trapped in an attempt to catch the prey. This makes the tar pits a prime example of a predator trap. As a result of the large number of predator and scavengers lured into the tar, there is a large sample size of very well-preserved fossils of a large variety of both birds and mammals which typically would not be as common in the fossil record.

The Rancho La Brea oil seep deposit yields incredible numbers of Pleistocene–Holocene bird fossils, with over 85,000 individual bones representing at least 133 bird species, 19 of which are extinct (Howard, 1962). The tar is great at trapping and preserving their delicate bones, and as a result, there are enormous collections at RLB that represent many different species and many different time intervals ranging from about 37 ka to 9 ka (Akersten et al., 1983; Stock and Harris, 1992; Friscia et al., 2008). Many of the fossils were radiocarbon dated by using multiple specimens from each pit. The ages of the pits are then estimated (Marcus and Berger, 1984; O’Keefe et al., 2009; Fuller et al., 2017).

Rancho La Brea also preserves an excellent climatic record based on data from snails, pollen, plant macrofossils, and oxygen isotopes (Warter, 1976; Coltrain et al., 2004; Ward et al., 2005). Some pollen samples collected from deep-sea cores drilled offshore in the California continental shelf preserve a much better record of the changes in vegetation. Heusser’s (1998) analysis of pollen grains found an alternation between an interglacial oak-chaparral flora and a glacial conifer forest in southern California over the past 60,000 years. About 59 ka, there was a change from oak and chaparral vegetation to pine-juniper-cypress woodlands, culminating about 24 ka, then between 24 and 14 ka (the last glacial maximum), the vegetation changed to a closed-cone juniper-ponderosa forest with abundant winter snow. During the glacial-interglacial transition from 14 to 10 ka, the landscape returned to dominant oak-chaparral and coastal sagebrush with pulses of alder. The region has been covered by the modern assemblage of oak-chaparral-herbaceous vegetation for the past 10,000 years. Oxygen and carbon isotopic analyses suggest there was increased seasonal aridity during the last interglacial and previous glacial (Coltrain et al., 2004).

One model of evolution that could be tested is the notion of how environment drives morphological change, and what

drives speciation. Galápagos finch model has long dominated the thinking of how microevolution occurs, since it is one of the best documented examples of change in morphology over a time scale of years to decades (Weiner, 1997; Grant and Weiner, 1999; Grant and Grant, 2007). In particular, small-scale differences in beaks due to short-term environmental change has been proposed an exemplar of phenotypic response to environmental change. Other examples of microevolutionary change in modern birds include studies of Siberian warblers, English sparrows, and pigeons (Weiner, 1995). English sparrows were found to have had better chances of survival after a severe blizzard if the males were smaller and lighter, or if the females were closer to average in size (Weiner, 1995).

By contrast, the punctuated equilibrium model of Eldredge and Gould (1972) predicted morphological stasis in a species despite the environment changing. As Eldredge and Gould (1972) pointed out, a speciation event occurring over a few years to decades is nearly instantaneous on a geologic time scale. Once a species is established, the fossil record shows that there is no net morphological change in that species for a very long time, often thousands to even millions of years. In the 50 years since the original publication of the Eldredge and Gould (1972) paper, studies have found that nearly all multicellular animals show stasis (Jackson and Cheetham, 1999; Gould, 2002; Jablonski, 2000, 2008; Geary, 2009; Princehouse, 2009; Hallam, 2009; Sepkoski and Ruse, 2009; Hunt et al., 2015). Most fossil species have thousands of generations which show little or no change over many thousands to millions of years (Jackson and Cheetham, 1999). Even more surprising, most organisms undergo a stasis for a long time, despite evidence of a changing climate. (e.g., Coope, 1979; Davis, 1983; Bennett, 1990; Prothero and Heaton, 1996; Prothero, 1999; Prothero et al., 2012).

RLB samples spanning long time intervals and encompassing the last glacial-interglacial cycle should be able to determine if the cold conditions of the last peak glacial caused size or shape changes in birds. Bergmann’s rule describes the change in size among a species when there is a change in climate. It would explain why animals that are at higher elevations and in colder regions would have larger body size. This prediction can be made for the birds present at Rancho La Brea. During the glacial maximum about 18–20 ka, one might predict that the specimens may be larger than those which were present during the Holocene. Allen’s rule also might apply to La Brea specimens, since individuals from colder climates tend to have shorter more

robust appendages than those from warmer climates.

Clinal variation in size consistent with Bergmann's rule is present in modern populations of most of the extant birds at RLB. For example, the most common bird in the tar pits, the Golden Eagle (*Aquila chrysaetos*), shows considerable clinal variation today, with larger-bodied subspecies in higher latitudes in both Siberia and North America (Brown, 1968; Johnsgard, 1990). However, Golden Eagles in RLB show no indication of larger body sizes during the peak glacial interval at 18–20 ka (Molina, and Prothero, 2011). There were also no size differences in the third most common bird over the same period, the extinct California Condor *Gymnogyps amplus* (Syverson and Prothero, 2010), nor in the second most common bird, the extinct California Turkey (*Meleagris californica*), the Bald Eagle (*Haliaeetus leucocephalus*), or the La Brea Caracara (*Caracara plancus prelutosus*) (Fragomeni and Prothero, 2011). According to Gillespy et al. (2016) there is no change in size or shape in the huge extinct condor-like *Teratornis merriami*. There was also complete stasis in the size and shape of the Black Vultures (*Coragyps occidentalis*) (Long et al., 2016), in the Great Horned Owls (*Bubo virginianus*) (Madan et al., 2015), in the Barn Owls (*Tyto alba*) (Madan et al., 2016), the Burrowing Owl (*Athene cunicularia*) and the Long-Eared Owl (*Asio otus*) (Madan et al., 2018). Thinking of the Galápagos finches, some people might argue that smaller birds with smaller home ranges might change in response to climate. But even the small birds (Western Meadowlark, *Sturnella neglecta*; Raven, *Corvus corax*; and Yellow-Billed Magpie, *Pica nuttalli*) showed no change during the climate transition (Long et al., 2020). For the last 35 ka, all the commonly preserved birds at RLB have remained the same size and maintained morphological stasis.

With this in mind, we studied one of the other common birds of La Brea, the extinct Fragile Eagle *Buteogallus fragilis*, originally named and described by Miller (1911) from RLB specimens in the University of California Museum of Paleontology. It is a member of the genus *Buteogallus* that includes nine species of extant crab hawks, black hawks, savanna hawks, and the solitary eagle (*B. solitarius*) and Chaco eagle (*B. coronatus*) (Brown, 1968; Johnsgard, 1990). Most of the species are restricted to Central and South America, and some Caribbean islands like Cuba (*B. gundlachii*), where it is a giant (Brown, 1968; Johnsgard, 1990). The common black hawk (*B. anthracinus*) is found in the southwestern United States.

## MATERIALS AND METHODS

We measured the all the well-dated complete adult tarsometatarsi (TMTs) of *Buteogallus fragilis* in the RLB collections. Based on counts of unique skeletal elements, the minimum number of individuals represented in the collection is 83 (Howard, 1962, Table 1).

Using the museum's Excel database for all RLB birds, we determined the pit number of each specimen. Pit 16, which has problematic, widely scattered radiocarbon ages (Marcus and Berger, 1984; O'Keefe et al., 2009), produces a high percentage of the bird bones from RLB (Howard, 1962), but the dating is too poor to be used for time-series studies like this one, so all specimens from Pit 16 were excluded.

Of all the skeletal measurements, the tarsometatarsus is by far the most robust element in the bird skeleton and therefore the most likely to be preserved intact. The TMT is considered a good proxy for within-species body size variation and has been widely used by ornithologists and paleo-ornithologists for that purpose. Syverson and Prothero (2010) made a more extensive set of measurements in the La Brea condor (*Gymnogyps amplus*) and found no differences between the trends shown in TMT measurements and those of the other parts of the skeleton. We measured only complete, undeformed adult TMTs to avoid artifacts resulting from breakage or ontogeny.

We measured a total of 80 *Buteogallus fragilis* TMTs with digital metric calipers. Two dimensions were measured (Fig. 1): maximum shaft length between the longest proximal-distal ends of the TMT; and midshaft transverse width of the TMT. These values allowed us to calculate a robustness index, the cross-sectional area (calculated from the width) divided by the length, to examine shape as well as size.



FIGURE 1. Reconstructed skeleton of the Fragile Eagle, *Buteogallus fragilis*, on display at the La Brea Tar Pits Museum.

Once the pit dates had been added to the spreadsheet, we performed basic statistical analysis using Excel and PAST (Hammer et al., 2001). The different pit samples were then compared to determine which ones were different from the pooled sample mean minus that group by the one-way ANOVA (analysis of variance), as well as a Kruskal-Wallis test of ANOVA since one sample was not normally distributed.

## RESULTS

The results of the statistical analysis of the data are shown in Table 1. The data for the TMT length are plotted in Figure 2, and the robustness of the TMT (cross-sectional area/length)

TABLE 1. Basic statistics of La Brea *Buteogallus fragilis* TMTs.  
SD = Standard Deviation; CV = Coefficient of Variation (= 100 x SD/Mean)

Character	Age (ka)	N	Mean	SD	CV
Length	37	3	105.8	1.2	1.1
	25	10	106.6	3.1	2.9
	18	20	105.8	3.5	3.3
	16	12	106.1	3.7	3.5
	14	15	105.4	4.6	4.3
	11	7	106.9	3.5	3.3
	9	7	104.9	2.2	2.1
Midshaft transverse width	37	3	8.7	0.7	7.6
	25	10	8.6	0.8	9.7
	18	20	8.7	0.8	8.7
	16	12	8.8	0.8	8.6
	14	15	8.7	0.9	10.2
	11	7	8.8	0.7	7.6
	9	7	8.8	0.7	8.1



FIGURE 2. Image of La Brea *Buteogallus fragilis* TMT, showing the measurement landmarks. Scale bar in cm.

is shown in Figure 3. The graphs clearly show that there is no obvious trend or difference between the means of the samples from 37 ka (Pit 77) all the way to the youngest sample at 9 ka (Pit 10).

Using PAST software, each sample from a different pit was tested for normality, and all but the oldest sample (only 3 specimens from Pit 77) were parametric. Consequently, it is appropriate to use ANOVA, since nearly all the data are normally distributed. Results of the ANOVA are shown in Table 2. The  $F$  value was 0.3237 ( $p = 0.9225$ ), so  $F$  was greater than  $F_{critical}$ , and thus the ANOVA shows that the medians of each pit sample were not significantly different from the median of the total pooled sample. The variance was also analyzed using the Kruskal-Wallis test for equal medians in PAST (since the Pit 77 sample was not big enough to have a normal distribution). The results were essentially the same. The chi-squared result was 2.1, greater than the  $H_{critical}$  value ( $p = 0.9102$ ), so there is no significant difference between the sample means.

## DISCUSSION

*Buteogallus fragilis* did not show any response to the difference in climate during the last global glaciation. This result is consistent with other birds examined from the La Brea area. Significant clinal size variation due to Bergmann's Rule has been documented in many La Brea birds, as discussed above. Based on this, one might expect an increase in the size and robustness in specimens dated at the last glacial maximum, from 18-20 ka. However, there is no significant change in body size or limb robustness. Even during conditions of coniferous forests with frequent snow around, 18-20 ka, limb size and robustness was not significantly greater than the specimens from the warmer Mediterranean climate with chaparral vegetation around 9 ka.

Stasis is also documented through this climate transition in larger mammals of Rancho La Brea, of which no change has been found in size or shape since 37 ka (Prothero et al., 2012; Prothero and Raymond, 2008, 2011; DeSantis et al., 2011; Raymond and Prothero, 2011; Madan et al., 2011). Numerous studies (Barnosky, 1994, 2005) document stasis in body size in nearly every Pleistocene mammal lineage at other fossil sites, despite many of these species ranging through several glacial-interglacial cycles. Taken together, it is clear that Pleistocene birds and mammals of all sizes show none of the expected

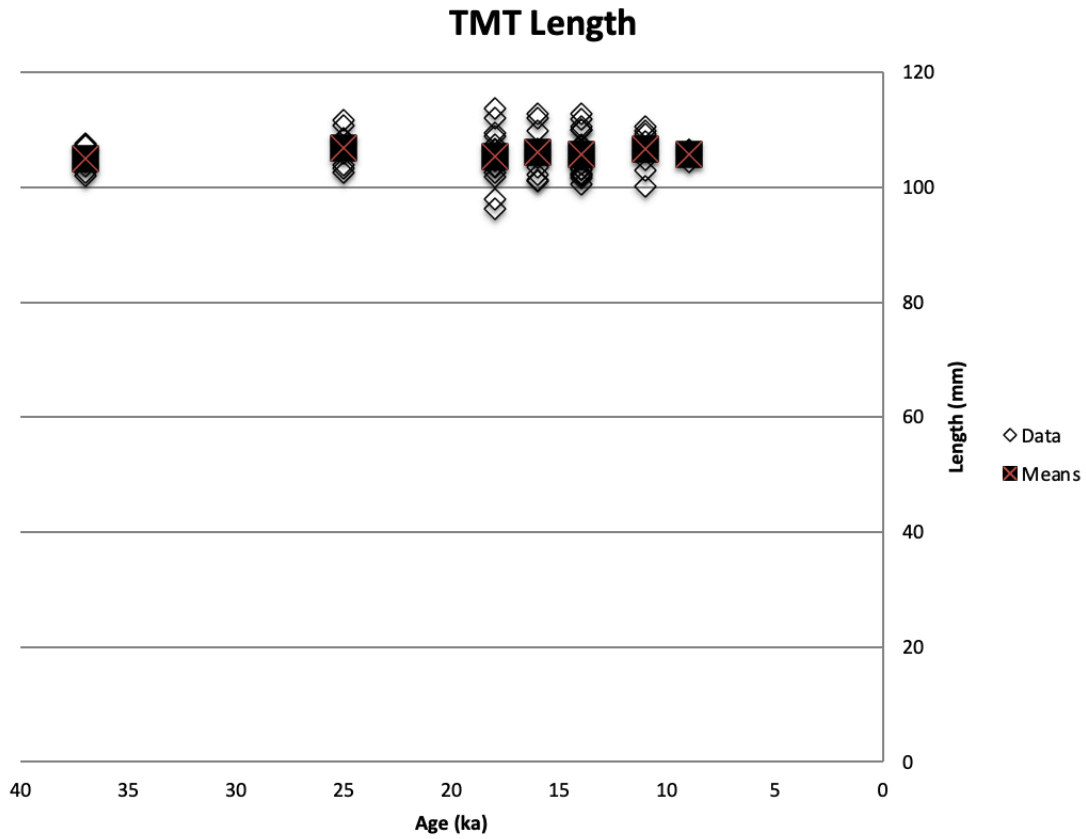


FIGURE 3. Plot of the lengths of *Buteogallus fragilis* TMTs through time. Open diamonds = individual specimens; solid squares = mean for each pit.

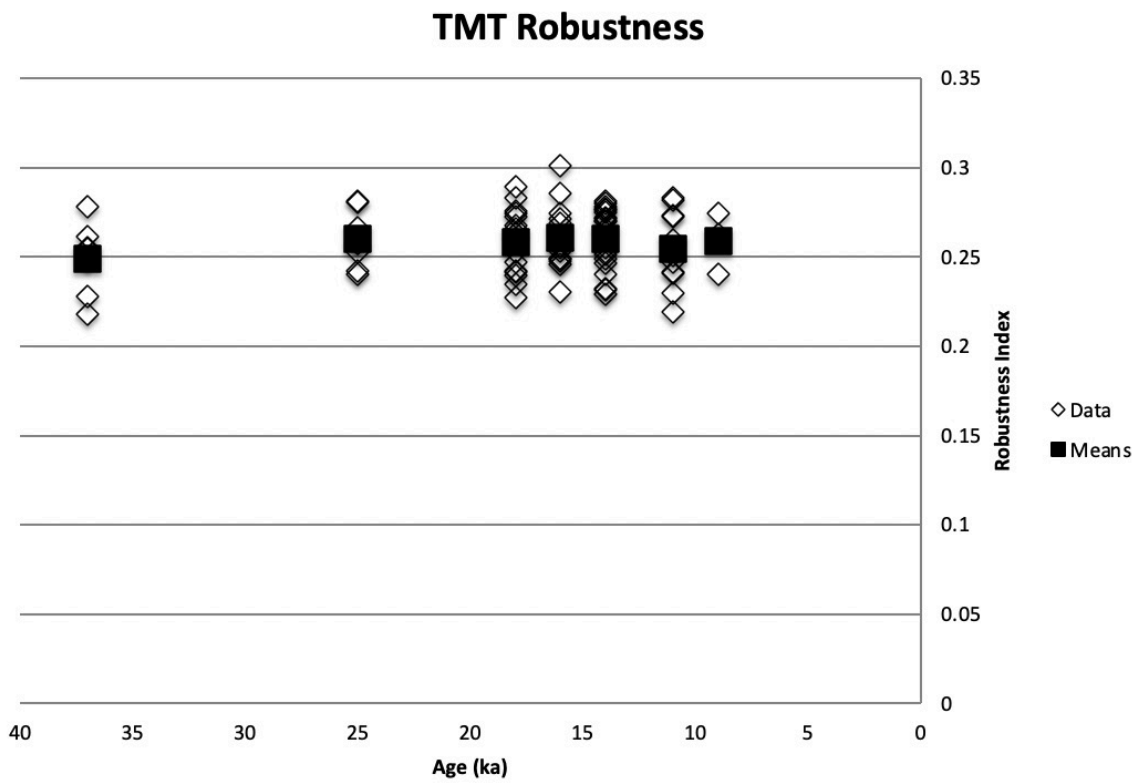


FIGURE 4. Plot of the robustness (midshaft cross-sectional area divided by length) of *Buteogallus fragilis* TMTs through time. Symbols as in Figure 3.

increases in size or robustness during climate changes over the entire span of several glacial-interglacial cycles.

Since the original “punctuated equilibria” model was introduced by Eldredge and Gould (1972), the function of how evolution occurs and what the prevalence of stasis means have been debated. Conventional neontologists have focused on small-scale changes like the beak sizes in Galápagos finches and other small birds as the prime example of how evolution occurs in birds and other animals (Weiner, 1995). However the evidence of long-term stasis in all the birds and mammals of RLB, despite strong selection from climate change, conflicts with the idea that these changes power evolutionary change. Hunt et al. (2015) found that 38% of a wide range of time series of fossil organisms best fit by a stasis model across a wide range of temporal resolutions, but especially for time series driven by sub-million-year fluctuations in global temperature.

How do we explain such stasis? Stabilizing selection (Estes and Arnold, 2007) does not work in this case because the environment is rapidly changing, not stable (Lieberman and Dudgeon, 1996). The idea that developmental canalization might constrain gradual morphological change has been proposed, but no longer is very popular (Gould, 2002; Eldredge et al., 2005). Bennett (1990, 1997) argued that organisms might not respond to the climate changes of the Pleistocene because they are too rapid for adaptation. However, this is contradicted by observation of population means shifting over just a few years, such as in the Galápagos finches, whereas the Pleistocene fossil record spans tens to hundreds of thousands of years. Uyeda et al. (2011) examined at a wide range of morphological time series from paleontological and neontological studies on scales from years to tens of millions of years. They found that the small-scale changes seen by neontologists over the periods of years to decades amounted to no more than small deviations around a mean, which were generally constrained and did not accumulate over long periods of time. These were what they called “bounded fluctuations”. True lasting evolutionary changes only occurred over longer time scales (>1 million years), when rare but considerable bursts of phenotypic change go beyond the normal bounded fluctuations. Uyeda et al. (2011) argued that these bursts of change represent shifts in adaptive zones, but that the small-scale changes seen in Galápagos finches and other small birds do not add up to permanent evolutionary changes.

#### ACKNOWLEDGMENTS

We thank Aisling Farrell and Gary Takeuchi for allowing access to the La Brea Tar Pits Museum collection of birds. We thank Li Zhi Heng and Vanesa DePietri for reviewing the manuscript. DRP is grateful to the late Les Marcus for teaching him biometrics, and for introducing him to the wonders of Rancho La Brea.

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