STASIS IN TERATORNS FROM THE LA BREA TAR PITS DURING THE LAST GLACIAL-INTERGLACIAL CYCLE

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**Abstract**—Conventional evolutionary biology suggests that birds evolve rapidly in response to climate change, as exemplified by the Galápagos finches. However, previous studies of birds from Rancho La Brea tar pits showed no significant size or shape changes over the last glacial-interglacial cycle, despite significant climate changes during the last 35,000 years. We studied the largest birds at Rancho La Brea, *Teratornis merriami*, to determine if they showed size or shape changes in response to the climate. Even though teratorns seem to exhibit a weak Bergmann’s rule effect, with larger body sizes in colder climates, the Rancho La Brea ~~samples~~ also showed complete stasis over this interval, with almost no statistically significant changes in size or robustness even during the peak glacial interval at 18,000-20,000 years ago, when the climate at Rancho La Brea was dominated by coniferous forests and snowy winters. These results are consistent with earlier studies on all the other large birds at Rancho La Brea. This suggests that the Galápagos finch model of rapid change in response to climate may not be appropriate for all birds.

# INTRODUCTION

Adaptive responses to environmental changes are common within conventional evolutionary biology thought. Such responses are made famous by Darwin’s Galápagos finches and can be observed as responses to climatic and ecological changes, such as drought and resulting competition (Weiner, 1995; Grant and Weiner, 1999; Grant and Grant, 2006, 2007). There are numerous other demonstrated instances of microevolutionary change in modern birds, such as Siberian warblers, English sparrows, cuckoos, cowbirds, red-winged blackbirds, and many others (Weiner, 1995). These studies all suggest that body size and robustness in birds are highly responsive to environmental and climatic changes.

But for 44 years now, paleontologists have been aware of the prevalence of stasis among fossil populations over long time intervals (Eldredge and Gould, 1972; Eldredge, 1999; Gould, 2002). From this perspective, it seems that these short-term examples of small-scale change may not be very important to large-scale macroevolution. Most fossil metazoans show evolutionary stasis over timescales of millions of years (Jackson and Cheetham, 1999; Gould, 2002; Jablonski, 2000, 2008; Geary, 2009; Princehouse, 2009; Hallam, 2009; Sepkoski and Ruse, 2009). There is abundant evidence (e.g., Coope, 1979; Davis, 1983; Bennett, 1990; Prothero and Heaton, 1996; Prothero, 1999; Prothero et al., 2012) of stasis during periods of climatic change and stress, which should be intervals of morphological change according to conventional evolutionary biology.

The Rancho La Brea (RLB) tar pits, which have trapped and preserved numerous floral and faunal specimens from a variety of time intervals beginning around 50 ka, are a perfect place to test the hypothesis of short-term change in response to climate on timescales of thousands of years. The RLB tar pits house large samples of fossil birds numbering nearly 250,000 bird specimens, representing 139 species, of which 23 species are extinct (Howard, 1962). The tar pits are particularly suited to trapping and preserving delicate bird bones, typically resulting in large samples of many disarticulated bones from a variety of time intervals (Akersten et al., 1983; Stock and Harris, 1992; Friscia et al., 2008). Recent radiocarbon dating of pits has allowed accurate estimates of dates (Marcus and Berger, 1984; O’Keefe et al., 2009) along with the temporal sequences of the deposits, allowing for correlation to climatic cycles during certain parts of the late Pleistocene.

The RLB tar pits also preserve proxies for the climatic record in southern California in the form of gastropods (snails), pollen, plant macrofossils, and oxygen isotopes (Warter, 1976; Coltrain et al., 2004; Ward et al., 2005). The best climatic record of this time interval, however, comes from pollen in deep-sea cores drilled just offshore in the California continental shelf. Based on pollen grains analyzed by Heusser (1998), there was a change from oak and chaparral vegetation at about 59 ka to pine-juniper-cypress woodlands at 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. In the past 10,000 years, the region has been vegetated by the modern assemblage of oak-chaparral-herbaceous vegetation. According to oxygen and carbon isotopic analysis (Coltrain et al., 2004), there was increased seasonal aridity during the last interglacial and previous glacial maximum.

So how did climatic and floral changes affect the birds at RLB, including teratorns? Ecogeographic trends might be expected that are consistent with Bergmann’s rule of larger body size in colder climates at the times when Rancho La Brea was at its coldest and snowiest about 18,000-20,000 years ago during the last glacial maximum. The most common bird at RLB, the golden eagle (*Aquila chrysaetos*) shows considerable clinal variation today, with larger-bodied subspecies in the high latitudes in both Siberia and North America (Brown, 1968; Johnsgard, 1990). However, Molina and Prothero (2011) found no indication of larger body sizes in the large RLB sample of golden eagles during the peak glacial interval at 18-20 ka years ago. Syverson and Prothero (2010) similarly found no size differences during the peak glacial interval in the third most common RLB bird, the extinct California condor *Gymnogyps amplus*. Fragomeni and Prothero (2011) found no significant size or robustness changes in the second most common bird, the extinct California turkey (*Meleagris californica*), nor the La Brea caracara (*Caracara plancus prelutosus*), nor the bald eagle (*Haliaeetus leucocephalus*). The five most common birds in the RLB collections thus all exhibit morphological stasis for the entire late Pleistocene.

What about other common birds? For this study, we examined the La Brea teratorn, *Teratornis merriami*, because about 105 individuals have been found in the RLB pits, originally described by Miller (1909), allowing for statistical analysis. *Teratornis* are large-bodied raptorial birds, closely related to New World vultures and storks; *T. merriami* is estimated to have weighed around 13.7 kg (Campbell and Tonni, 1983) with a wingspan of 3.5-3.8 meters (11.5-12.5 feet). A partial skeleton of another species of *Teratornis, T. woodburnensis*, was recovered from Legion Park, near Woodburn, Oregon, dated to 11-12 ka (Campbell and Stenger, 2002). It was slightly larger than the average *T. merriami*, with a wingspan over 4 meters (14 feet), suggesting that there was some Bergmann’s rule effectbetween different latitudes at this time.

# METHODS

We studied the largest known sample of *Teratornis* in the La Brea Tar Pits Museum collections, with a minimum of 63 individuals from pits ranging from 9 ka to 37 ka based on the pit chronology of Marcus and Berger (1984).

We measured the tarsometatarsus (TMT) because these are among the most robust elements in the bird skeleton, less prone to breaking or deforming (Fragomeni and Prothero, 2011). While tibiotarsus measurements have been shown to scale well with body mass in birds, they are often susceptible to breakage, making most measurements difficult to record precisely (Field et al., 2013). Studies of the La Brea condor (Syverson and Prothero, 2010) demonstrated no differences between the trends shown by the TMT measurements in disarticulated pit samples and those showed by the other parts of the skeleton from the same samples, so the TMT is used here as a proxy for body size, as it is widely used by ornithologists and paleo-ornithologists.

Only complete, undeformed adult TMTs were measured, so that there were no artifacts due to breakage or ontogeny. We measured specimens with digital metric calipers. Three dimensions were measured (Fig. 1): maximum shaft length between the longest proximal-distal ends of the TMT; midshaft anteroposterior thickness of the TMT; and midshaft transverse width of the TMT. Unlike the fossil mammal collections in the La Brea Tar Pits Museum, bird fossils are not separated in the trays or in the drawers by pit, but sorted by species instead, so we searched the Excel database for all RLB birds by the pit number first. This was to avoid measuring specimens from pits like Pit 16, which has problematic, widely scattered radiocarbon ages (Marcus and Berger, 1984; O’Keefe et al., 2009), and so could not be used in our study. For unknown reasons, Pit 16 produces a high percentage of the bird bones from RLB (Howard, 1962), but the dating is too poor to be used in a temporal sequence study like this.

Once the pit dates had been added to the spreadsheet, we performed basic statistical analysis using Excel and R for each sample for a well-dated pit. We then tested the samples for normality using the Shapiro-Wilk method. Since most of the data were non-parametric, we used the Kruskal-Wallis test to determine whether each sample was from the pooled mean of all other measurements. Time-series measurements were also fit to evolutionary models (directional random walk, undirected random walk, and stasis) in R using the paleoTS package.

# RESULTS

The basic statistics of the *Teratornis* TMT sample are shown in Table 1. All of the samples that were large enough for the test were not normally distributed, using a Shapiro-Wilk test for normality. Thus, the different pit samples were then compared to see if they were significantly different from the pooled sample mean using the Kruskal-Wallis test. In most cases (Table 2), the differences were not significant at p>0.05. This is apparent in a plot of any of the dimensions against age (Figure 2). Although the values of individual specimens fluctuate around the mean, in most cases there are no statistically significant differences between samples of adjacent ages.

The exception to this rule is the lengths of TMTs from the 14ka sample, which are significantly smaller than those from other pits, with a mean length of 85.3 compared to 90.0 for all other pits combined (p=0.016 by ANOVA and 0.026 by K-W). This deviation is clearly visible in Figure 2, and coincides with the onset of deglaciation according to the pollen proxy in Heusser (1998); however, it is only present in this single pit, and the 11 ka sample following it is indistinguishable from the overall mean length.

Contrary to the expectation of Bergmann’s rule, there is no evidence of larger body size or greater robustness in the samples around the last glacial maximum at 18-20 ka.

The same is true of measures of shape, such as cross-sectional area (midshaft width times depth) and robustness(cross-sectional area of the midshaft divided by length), shown in Figure 2. With the exception of the single sample at 9 ka, the means are all within a narrow band, and the differences are not significant except for the case noted above (Table 2). In particular, the samples at 16, 18 ka, and 21 ka show no increase in robustness as would be expected for animals living in colder climates.

Evaluating models for the time series (Table 3) confirms the lack of any overall directional change over the time period being measured. Length is best modeled as stasis, and a random walk is the preferred model for both of the midshaft measurements and for the derived area and robustness indices; however, the AICc values for these two are similar in all cases, indicating that there is little difference in predictive power between the two.

# DISCUSSION

As shown by previous analyses of the RLB golden eagles (Molina and Prothero, 2011), California condors (Syverson and Prothero, 2010), bald eagles, turkeys, and caracaras (Fragomeni and Prothero, 2011), there is no evidence of significant size or shape changes in these birds during the last glacial maximum, despite the dramatic changes in climate and vegetation documented in the region over the past 40,000 years.

This trend is also consistent with nearly all the larger mammals of RLB, which also show no response in size or shape during the maximum climatic changes of the past 35,000 years (Prothero et al., 2012; Prothero and Raymond, 2008, 2011; DeSantis et al., 2011; Raymond and Prothero, 2011; Madan et al., 2011). This is supported by numerous studies (Barnosky, 1994, 2005) that document stasis in nearly every Pleistocene mammal lineage, even though many of these species ranged through several glacial-interglacial cycles. Thus, stasis is a widespread phenomenon in nearly all Pleistocene birds and mammals over the entire span of several glacial-interglacial cycles.

Paleontologists and neontologists have long argued about the significance of stasis despite changes in environment. It is clearly inconsistent with the adaptive sensitivity shown by the Galápagos finches and other recently documented examples of adaptation and microevolution on short time scales (Weiner, 1995). Ideas like stabilizing selection (Estes and Arnold, 2007) are clearly inapplicable and fail to explain this phenomenon, since the environment in this case is changing, not stabilizing (Lieberman and Dudgeon, 1996). Other ideas, such as developmental canalization, have been used to explain this stability, but this model has fallen out of favor in view of the phenotypic plasticity of domesticated animals, such as dogs (Gould, 2002; Eldredge et al., 2005). Bennett (1990, 1997) argued that the climate changes of the Pleistocene were too rapid for organisms to respond, but the Pleistocene fossil record spans tens to hundreds of thousands of years. If the Galápagos finches could show change in just a few years, then evolutionary changes can occur in a matter of years or decades. Although it has been suggested that mean phenotype fluctuates on a time scale rapid enough to appear static, most RLB pits have narrow enough time constraints that they should capture changes on this time scale.

The most widely accepted explanation for long-term stasis is the idea that most organisms that have large geographic ranges are also adapted to a wide spectrum of local environments, so they do not respond to environmental change by means of morphological change (Eldredge, 1999; Lieberman et al., 1995; Lieberman and Dudgeon, 1996; Eldredge et al., 2005). This is consistent with the stasis in the size measurements presented here, which indicate not only that climate change did not result in the expected *evolutionary* adaptations in teratorns and other large birds, but that there were not even *migratory* shifts in the population present in Southern California. This hypothesis might be more appropriate for large birds like *Teratornis,* which ranged all over the Americas from Oregon to Argentina, than for smaller bird species, some of which are restricted to very small ranges. Unfortunately, the sample of most smaller birds at RLB is insufficient to test this hypothesis. In the case of small mammals, however, there is stasis through climate changes during the Pleistocene as well (Barnosky, 2005). Such stasis is also apparent in small mammal populations during late Eocene-Oligocene climate changes (Prothero and Heaton, 1996). Thus, a comprehensive model of expected morphological response to dramatic climate change on thousand-year timescales still eludes us, and much further research is required.

# CONCLUSIONS

Statistical analysis of size and shape variables of *Teratornis merriami* from RLB demonstrates almost no significant size or robustness change in response to the dramatic cooling and vegetational change of the peak glacial period 20,000 years ago or to the subsequent deglaciation. This is consistent with previous studies showing stasis in golden eagles, bald eagles, condors, turkeys, and caracaras, despite their strong tendency to follow Bergmann’s rule in modern populations (Molina and Prothero, 2011; Fragomeni and Prothero, 2011; Syverson and Prothero, 2010). This agrees with the evidence that all RLB mammals with sufficient sample sizes also show complete stasis over the last 40,000 years of climatic change, a phenomenon that is still not well explained (Prothero et al., 2012). Although the stasis exhibited by larger mammals and birds might be explained by wide geographic spread and environmental flexibility, this model does not yet explain why environmentally restricted mammals and birds with small body sizes and home ranges also demonstrate morphological stasis during the climate changes of the Late Pleistocene.

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TABLE 1. Basic statistics for measurements on RLB teratorn TMTs (SD=standard deviation, CV=coefficient of variation).

| **Character** | **Pit age (ka)** | **N** | **Mean** | **SD** | **CV** |
| --- | --- | --- | --- | --- | --- |
| Length | 9 | 1 | 96.1 | – | – |
|  | 11 | 17 | 91.4 | 5.4 | 5.9 |
|  | 14 | 14 | 85.3 | 3.8 | 4.5 |
|  | 16 | 4 | 90.8 | 4.4 | 4.9 |
|  | 18 | 17 | 88.1 | 2.9 | 3.4 |
|  | 21 | 6 | 90.4 | 3.7 | 4.1 |
|  | 35 | 4 | 89.4 | 3.3 | 3.7 |
| Midshaft depth (a-p) | 9 | 1 | 14.4 | ­— | — |
|  | 11 | 17 | 14.3 | 0.9 | 6.3 |
|  | 14 | 14 | 14.1 | 0.8 | 5.9 |
|  | 16 | 4 | 14.5 | 0.8 | 5.3 |
|  | 18 | 17 | 14.1 | 0.8 | 5.7 |
|  | 21 | 6 | 14.1 | 1 | 7.3 |
|  | 35 | 4 | 14.3 | 1 | 6.9 |
| Midshaft width (lateral) | 9 | 1 | 9 | 1 | 12 |
|  | 11 | 17 | 11 | 17 | 12.3 |
|  | 14 | 14 | 14 | 13 | 11.6 |
|  | 16 | 4 | 16 | 3 | 12 |
|  | 18 | 17 | 18 | 16 | 11.8 |
|  | 21 | 6 | 21 | 6 | 12.1 |
|  | 35 | 4 | 35 | 4 | 12 |

TABLE 2. Kruskal-Wallis tests on each measurement and calculated variable for teratorn TMTs.. **Bold face** indicates results that are significantly different at the p > 0.05 level. Degrees of freedom = df.

|  |  |  |  |
| --- | --- | --- | --- |
| **Variable** | **χ2** | **df** | **P-value** |
| **Length** | **14.34** | **6** | **0.03** |
| Width | 1.79 | 6 | 0.94 |
| Depth | 6.06 | 6 | 0.42 |
| Area | 4.64 | 6 | 0.59 |
| Robustness | 0.96 | 6 | 0.99 |

TABLE 3. Time-series analysis of TMT measurements and derived values, given in Akaike weights (corrected Akaike information criterion in parentheses). The winner of each analysis is shown in bold face. All time series are best modeled by either a random walk or stasis.

|  | **Directional** | **Random walk** | **Stasis** |
| --- | --- | --- | --- |
| Length | 0.017 (39.4) | 0.455 (32.8) | **0.528 (32.5)** |
| Width | 0.020 (13.8) | **0.573 (7.1)** | 0.406 (7.8) |
| Depth | 0.022 (16.9) | **0.582 (10.4)** | 0.396 (11.2) |
| Midshaft area | 0.020 (47.2) | **0.530 (40.6)** | 0.450 (40.9) |
| Robustness (area/length) | 0.025 (-4.0) | **0.697 (-10.6)** | 0.278 (-8.7) |

FIGURE 1. Image of a *Teratornis* TMT, showing the measurement landmarks.

FIGURE 2. Plots of the measured and calculated dimensions of *Teratornis* TMTs through time. Open circles = individual specimens; solid circles = mean for each pit; error bars indicate variance (±1 SE). As is apparent from the statistical analysis (Table 3), all dimensions are best modeled by either undirected random walk or stasis.