STASIS IN RED-TAILED HAWKS (*BUTEO JAMAICENSIS*) FROM LA BREA TAR PITS DURING THE LAST GLACIAL-INTERGLACIAL CYCLE

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Abstract—Conventional evolutionary theory suggests that species acquire small modifications to their bodies on a short time scale when there is a shift in environmental conditions. According to this model, new species evolve as a result of the accumulation of such minor adaptive changes. Birds present a number of classic examples of this type of evolution, with rapid adaptive evolution recorded in a variety of bird species over decades to centuries. However, the punctuated equilibrium model predicts that these small changes do not add up to new species, but are just fluctuations around a mean and will appear as stasis over geological time scales. The rich fossil bird assemblage at Rancho La Brea is a good place to see how birds have adapted to climate changes of the last 35,000 years, including the last glacial-interglacial cycle. In this study, we assess size and shape change in the red-tailed hawks (*Buteo jamaicensis*) from Rancho La Brea. Body size and limb robustness of the red-tailed hawks show no morphological change since the last glacial maximum about 18,000-20,000 years ago, when the southern California chaparral was replaced by snowy coniferous forests. These findings are consistent with all the other studies of La Brea fossil birds, which also exhibit stasis over the climate changes over the last glacial-interglacial cycle.

INTRODUCTION

The Galápagos finch model of evolution is widely cited in evolutionary biology as an example of how organisms rapidly adapt to changes in their environment. Decades of research has demonstrated that the mean size of their beaks and body of a species can shift over a few years in response to environmental changes (Weiner, 1995; Grant and Weiner, 1999; Grant and Grant, 2007). This model of evolution has been demonstrated in many other birds, including Siberian warblers, English sparrows, cuckoos, cowbirds, red-winged blackbirds, and many others (Weiner, 1995). These data seem to suggest that evolution in organisms (especially birds) occurs rapidly, within a few generations, and is very responsive to environmental change.

The punctuated equilibrium model, however, predicts morphological stasis among species (Eldredge and Gould, 1972). Punctuated equilibrium theory states that over long timescales of thousands to millions of years, gradual morphological change is rare or non-existent, and most species exhibit stasis over long time scales (Eldredge and Gould, 1972; Eldredge, 1999; Gould, 2002). Most traits in most fossil metazoans show evolutionary stasis over timescales of millions of years (*e.g.,* Jackson and Cheetham, 1999; Gould, 2002; Jablonski, 2000, 2008; Geary, 2009; Princehouse, 2009; Hallam, 2009; Sepkoski and Ruse, 2009; Hunt et al., 2015). Many studies have shown that periods of climatic change and stress produce stasis rather than significant morphological change (*e.g.* Coope, 1979; Davis, 1983; Bennett, 1990; Prothero and Heaton, 1996; Prothero, 1999; Prothero et al., 2012). These instances of stasis on long time scales show clearly that small-scale evolutionary changes in modern species do not accumulate straightforwardly into major morphological change and speciation over longer time scales as was previously thought.

The Rancho La Brea (RLB) tar pit Lagerstätte provides an extraordinarily rich Pleistocene-Holocene fossil collection with which to test this hypothesis of bird evolution in response to climate change (Howard, 1962). Bird skeletons are delicate and have low preservation potential in most taphonomic environments, but the RLB asphalt seeps preserve an exceptional variety of different bird species: over 133 species of birds are represented by over 85,000 individually preserved bones from deposits with ages ranging from 50 ka to 9ka (Akersten et al., 1983; Stock and Harris, 1992; Friscia et al., 2008).

Based on data from snails, pollen, plant macrofossils, and oxygen isotopes, Rancho La Brea also preserves an excellent climatic record (Warter, 1976; Coltrain et al., 2004; Ward et al., 2005), although the records are from a few individual pits and do not produce a detailed high-resolution continuous climate record. The best climate proxy, however, comes not from the RLB plants directly, but from deep-sea cores. 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 shifted 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 ka. Oxygen and carbon isotopic analyses suggest there was increased seasonal aridity during the last interglacial and previous glacial periods (Coltrain et al., 2004). Many of the pits have been individually radiocarbon dated (Marcus and Berger, 1984; O'Keefe et al., 2009; Fuller et al., 2015), so the age of most of the pits is known and they can be assigned to the relevant late Pleistocene climatic conditions.

So how might climate change affect the birds of Rancho La Brea? One prediction would be a change in body size of animals, consistent with Bergmann's rule which predicts larger body size in colder climates. Thus, body size should peak when Rancho La Brea was at its coldest and snowiest during the last glacial maximum about 18-20 ka. In addition, Allen's rule predicts that limb elements and other extremities should get shorter and more robust in times when it is cold and organisms need to conserve heat.

Clinal variation in size consistent with Bergmann's rule is present in modern populations of most of the birds at RLB. For example, within the tar pits the most common bird is the Golden Eagle (*Aquila chrysaetos*), which shows considerable clinal variation by latitude and temperature today. Extant populations of Golden Eagles have larger-bodied subspecies in higher latitudes in both Siberia and North America, and smaller ones

near the tropics (Brown, 1968; Johnsgard, 1990). Yet Golden Eagles of RLB do not show indication of larger body sizes at 18-20 ka, during the peak glacial interval (Molina and Prothero, 2011). The second most common bird, the extinct California turkey (*Meleagris californica*), shows no size variation over the same period, nor does the third most common bird, the extinct California Condor *Gymnogyps amplus* (Syverson and Prothero, 2010). The fourth and fifth most common birds, the Bald Eagle (*Haliaeetus leucocephalus*) and the La Brea Caracara (*Caracara plancus prelutosus*) (Fragomeni and Prothero, 2011) show no size variation through the climate cycle, either. According to Gillespy et al. (2016), there are no shape or size modifications in the huge extinct condor-like *Teratornis merriami*. Stasis also occurs in the Black Vultures (*Coragyps occidentalis*) (Long et al., 2016), the Great Horned Owls (*Bubo virginianus*)(Madan et al., 2015), the Barn Owls (*Tyto alba*) (Madan et al., 2016), the Burrowing Owl (*Athene cunicularia*) and in the Long-Eared Owl (*Asio otus*)(Madan et al., 2018). Even the smallest common birds (Western Meadowlark, *Sturnella neglecta*; Raven, *Corvus corax*; and Yellow-Billed Magpie, *Pica nuttalli*) showed no significant variation in body size or limb proportions during the climate transition (Long et al., 2020). Therefore, for the last 35 ka, all studies of the birds preserved at RLB indicate that size and morphological stasis occurred, despite the dramatic climate change around 18-20 ka ago during the peak glacial maximum, when RLB was covered in ponderosa pine forests and experienced heavy winter snows.

Among the common birds at RLB that has not yet been studied is the Red-Tailed Hawk (*Buteo jamaicensis*). Extant Red-Tailed Hawks ranges all the way from the Arctic in the summer to Central America in the winter. It exhibits considerable clinal variation over latitude, with as many as 14 different subspecies recognized (Brown, 1968; Johnsgard, 1990; Fitzpatrick and Dunk, 1999) on the basis of both skeletal and plumage differences. The current occurrence of such clinal variation could imply that *B. jamaicensis* are sensitive to climate change. Thus, due to the changes in climate over the past 60 ka, there should be significant morphological differences between specimens at RLB. Specifically, we would expect to find larger body sizes and more robust limb dimensions among the specimens from pits in the 18-20 ka range, during the last glacial maximum, than in extant populations from warmer climates.

MATERIALS AND METHODS

Of all the skeletal measurements, the tarsometatarsus (TMT) 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. For this study, we measured only complete, undeformed adult TMTs to avoid artifacts resulting from breakage or ontogeny. For comparison, we also measured 10 TMTs from 5 recent *Buteo jamaicensis* individuals from University of California Museum of Comparative Zoology.

We measured all the well-dated complete adult tarsometatarsi (TMTs) of the Red-Tailed Hawk (*Buteo jamaicensis*) in the RLB collections, a total of 88 specimens. Based on counts of unique skeletal elements, the minimum number of *Buteo jamaicensis* individuals represented in the collection of TMTs is 108 (Howard, 1962, Table 1). Two dimensions were measured using digital metric calipers (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 of midshaft cross-sectional area

divided by length.

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.

Once the pit dates had been added to the spreadsheet, we performed basic statistical analysis using Excel and R. Since none of the samples from any pit were normally distributed (Shapiro-Wilk method, threshold $p<0.05$), we used the nonparametric Kruskal-Wallis test to determine whether any pit sample was significantly different from the pooled mean of all other measurements. The different pit samples were then compared to determine which ones were different from the pooled sample mean minus that group by the Mann-Whitney U test. The time series of each measurement was also fit to evolutionary models (directional random walk, undirected random walk, stasis, and strict stasis) in R using the paleoTS package.
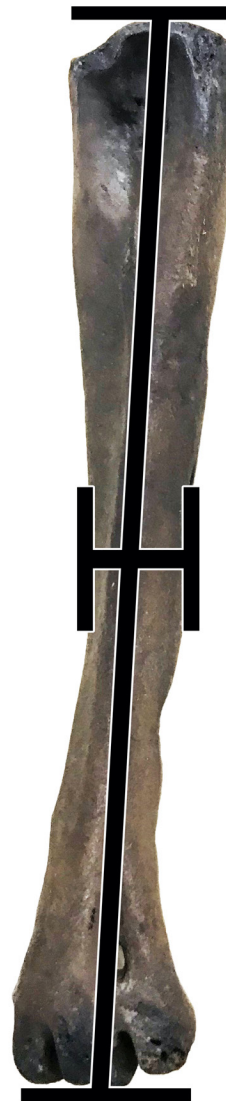

FIGURE 1. Image of *Buteo jamaicensis* TMT, showing the measurement landmarks.

RESULTS

The size and shape distributions of TMTs of *B. jamaicensis* are remarkably static through the entire interval. This is apparent even before analysis when looking at the data plots (Figures 2 and 3). The results of the basic statistical analysis are given in Table 1, the Kruskal-Wallis test in Table 2, and the time series analysis in Table 3. All the statistical results are consistent with a stable population mean size and shape throughout the interval. The Kruskal-Wallis analysis of variance produces p-values above 0.5 for all three values (length, midshaft width, and robustness), even when the 0 ka sample is included. Evidently, the red-tailed hawks of Rancho La Brea have remained extremely steady in size and robustness over the last 37 ka as the environment cycled between glacial and interglacial climatic conditions.

DISCUSSION

Our analysis reveals that, like the other RLB birds previously studied, the red-tailed hawks did not change their mean size or shape in response to climate change associated with the last glacial maximum. *B. jamaicensis* exhibits even stronger stasis than most of the RLB bird populations during both the last glacial maximum (20-18 ka) and the Pleistocene-Holocene transition (9-0 ka). This is notable given the pronounced ecogeographic variation among and within species of extant red-tailed hawks, including specifically in TMT length (Fitzpatrick and Dunk, 1999).

This surprising result is nonetheless consistent with results on other birds of prey from RLB. Significant clinal size variation

has been documented in modern populations of these other species, which include Golden Eagles (Molina and Prothero, 2011), Bald Eagles and Caracaras (Fragomeni and Prothero, 2011), Great Horned Owls (Madan et al., 2015), Barn Owls (Madan et al., 2016), and Burrowing Owls (Duncan, 2003; König and Weick, 2008). Bergmann's rule would lead us to expect a decrease in robustness and size during the time covered by the RLB specimens, which lasted through the last glacial maximum and the early Holocene. However, during the conditions of coniferous forests and frequent snow at low elevations around 20-18 ka, none of the previously mentioned birds possessed a greater body size or limb robustness than during the near-modern hot Mediterranean climate and chaparral vegetation about 9000 years ago.

In fact, during the same climate transition, similar stasis has also been documented in larger mammals of RLB. Interestingly, all the large mammals from RLB also either remained a constant size or shape or drifted randomly in size and shape in during the past 35 ka (Prothero et al., 2012; Prothero and Raymond, 2008, 2011; DeSantis et al., 2011; Raymond and Prothero, 2011; Madan et al., 2011). Studies of other fossil sites from the same time interval (Barnosky, 1994, 2005) record stasis in body size in almost every Pleistocene mammal lineage, despite many of these species ranging through several glacial-interglacial
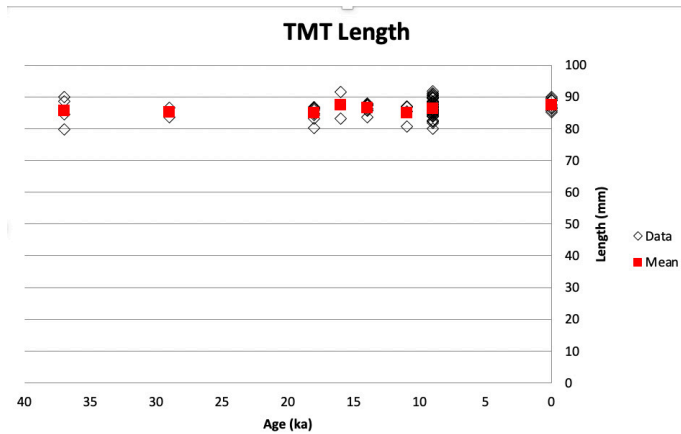

FIGURE 2. Plot of the length of *Buteo jamaicensis* TMTs through time. Open diamonds = individual specimens; solid squares = pit means.
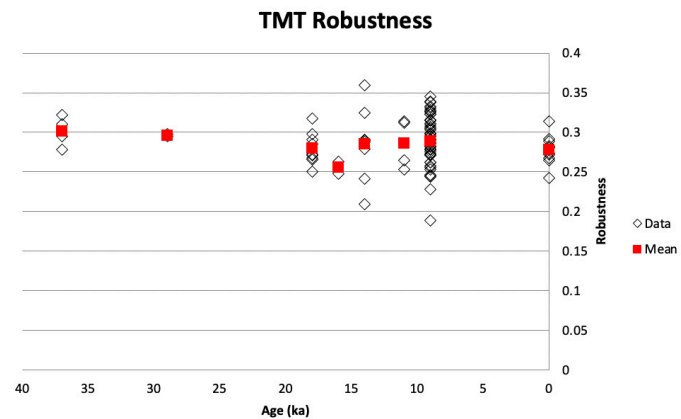

FIGURE 3. Plot of the robustness of *Buteo jamaicensis* TMTs through time. Open diamonds = individual specimens; solid squares = pit means.

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

Character	Age.ka	N	Mean	SD	CV
Length	37	4	85.7	4.58144	18.70591
	29	2	85.1	2.08597	40.79637
	18	9	84.9	2.12868	39.88387
	16	2	87.4	5.94677	14.69705
	14	8	86.5	1.42563	60.67493
	11	4	85	2.90269	29.28318
	9	49	86.4	2.64388	32.67924
	0	10	87.5	1.68091	52.05514
Width	37	4	8.2	0.58054	14.12478
	29	2	8	0.24749	32.32454
	18	9	7.6	0.62301	12.19884
	16	2	7.1	0.78489	9.04585
	14	8	7.9	1.35262	5.84052
	11	4	7.7	1.02883	7.48423
	9	49	7.9	0.90749	8.70533
	0	10	7.7	0.53385	14.42353

TABLE 2. Nonparametric analysis of variance (Kruskal-Wallis test) for *B. jamaicensis* TMTs. No measurement had a significant difference between any two pit samples, so no further analysis was performed.

	K-W chi-squared	df	p-value	significant (p<0.00625)
LENGTH	5.96	7	0.5442	0
WIDTH	5.18	7	0.6375	0
ROBUSTNESS	6.22	7	0.5138	0

TABLE 3. Results of time series analysis. No directional trend was supported for either measurement; all three time series were best fit by a strict stasis model. The same model was supported in all cases even when the modern 0 ka sample was omitted (not shown).

	GRW	URW	Stasis	StrictStasis
LENGTH	0.164	0.098	0.13	**0.609**
WIDTH	0.015	0.116	0.116	**0.752**
ROBUSTNESS	0.054	0.143	0.18	**0.623**

cycles. Overall, it is evident that Pleistocene birds and mammals of all sizes do not undergo any overall change in body size or robustness over the entire span of several glacial-interglacial cycles.

Since Eldredge and Gould (1972) introduced the original "punctuated equilbria" model, there has been a long debate over what the conditions of stasis mean and how evolution takes place. Neontologists dictate that evolution occurs in birds and all other animals alike on a micro-scale, e.g., in beak sizes of the Galápagos finches or other small birds (Weiner, 1995). Yet, the evidence of long-term stasis sampled from all birds and mammals of the RLB conflicts with this notion of the changes generating evolutionary change. These results, however, are consistent with an emerging consensus about the prevalence of stasis over paleontological timescales. Looking at a wide array of paleontological time series, Hunt et al. (2015) found that 38% of them best fit by a stasis model across a wide range of taxa and temporal resolutions, but especially for time series driven by sub-million-year fluctuations in global temperature.

Then how is stasis explained? Stabilizing selection has been put forward as a possible explanation for stasis (Estes and Arnold, 2007), but is not an appropriate answer in this case. In contrast to the model of stabilizing selection, the RLB environment is not stabilizing but changing dramatically (Lieberman and Dudgeon, 1996). Past suggestions indicated that developmental canalization inhibited small-scale change. Yet, this idea has gone out of favor (Gould, 2002; Eldredge et al., 2005). Some have suggested that organisms might not respond to the extremely rapid climate changes of the Pleistocene (Bennett, 1990, 1997). 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. More recently, Uyeda et al. (2011) observed a wide range of morphological time series on scales from years to tens of millions of years from paleontological and neontological studies. They recognized that the small-scale changes seen by neontologists over the periods of years to decades come to be nothing more than fluctuations around a mean. This mean was generally constrained and did not accumulate over long periods of time (what they called "bounded fluctuations"). Therefore, true lasting evolutionary changes only occurred over macro scales (>1 million years), when rare but substantial bursts of phenotypic change go beyond the normal bounded fluctuations. These rare bursts of change represent shifts in adaptive zones but the small-scale changes seen in Galápagos finches and other small birds do not add up to permanent evolutionary changes (Uyeda et al., 2011).

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