

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

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Abstract—A classic example of evolution in action is the Galápagos finches, whose rapid responses to climate change are well documented. In this study, we analyzed a sample of barn owl (*Tyto alba*) fossils from the collections of the La Brea Tar Pits Museum, California, to determine changes in size or shape in response to climate fluctuations over the last 35,000 years. Despite a weak Bergmann's rule effect observed in living barn owls, displaying larger body sizes in colder climates, the La Brea owls demonstrated stasis over this time period, with no statistically significant changes in size or robustness despite the peak glacial maximum 18,000-20,000 years ago, when the environment at Rancho La Brea was predominantly coniferous forests and snowy winters. Our results concur with studies conducted on Rancho La Brea great horned owls, condors, golden eagles, bald eagles, turkeys, and caracaras. It appears that many birds do not respond to changes in climate in a simple fashion, and are adaptable to various ecosystems and can live in a variety of habitats or climates without change in body size or hind limb robustness.

INTRODUCTION

Traditional evolutionary biology features an abundance of examples of adaptive responses to changes in climate, particularly in birds such as the Galápagos finches (Weiner, 1995; Grant and Weiner, 1999; Grant and Grant, 2007). Numerous additional instances of microevolutionary adaptations have been documented in modern birds such as Siberian warblers, English sparrows, cuckoos, cowbirds, and red-winged blackbirds (Weiner, 1995). These studies suggest that bird body mass and robustness respond readily to environmental and climate changes.

Over the last four decades, paleontologists have acknowledged stasis over long time periods in fossil populations (Eldredge and Gould, 1972; Eldredge, 1999; Gould, 2002). Since most fossil metazoans demonstrate evolutionary stasis over millions of years, it may seem as though short-term, small-scale examples of stasis may be less important in terms of macroevolution (Jackson and Cheetham, 1999; Gould, 2002; Jablonski, 2000, 2008; Geary, 2009; Princehouse, 2009; Hallam, 2009; Sepkoski and Ruse, 2009). However, there exists abundant evidence (e.g., Coope, 1979; Davis, 1983; Bennett, 1990; Prothero and Heaton, 1996; Prothero, 1999; Prothero et al., 2012) of stasis over periods of climate change or stress, which should be periods of morphological change given the tenets of evolutionary biology and the kinds of microevolutionary responses to climatic change described above.

The La Brea Tar Pits provide an excellent platform to test the effects of climate change on vertebrate morphology over thousands of years. Over 85,000 specimens of birds representing more than 133 species are known from the tar pits, including 19 extinct species (Howard, 1962). The Tar Pits are renowned for their exquisite preservation of fossil specimens, particularly delicate bird bones, throughout a variety of time intervals (Akersten et al., 1983; Stock and Harris, 1992; Friscia et al., 2008). The temporal sequence of pits has been established by radiocarbon dating, which gives researchers insight into the climate cycles of the Pleistocene.

Based on evidence collected from snails, pollen, plants, and oxygen isotopes, the La Brea Tar Pits themselves record the climate record of southern California at the time the pits formed (Warter, 1976; Coltrain et al., 2004; Ward et al., 2005). However, the most useful and continuous record of this time period is found in pollen from deep-sea cores drilled from the California continental shelf. According to Heusser (1998), pollen grains indicate a shift from oak and chaparral vegetation 59,000 years ago to pine-juniper-cypress woodlands 24,000 years ago, and then to closed-cone juniper-ponderosa forests with harsh, snowy winter conditions during the last glacial maximum 24,000-14,000 years ago. The glacial-interglacial transition 14,000-10,000 years ago altered the landscape back to predominantly oak-chaparral and coastal sagebrush with some alder. Over the last 10,000 years, this region has retained its familiar modern assemblage of oak-chaparral-herbaceous vegetation. Additionally, as established by oxygen and carbon isotope analyses

(Coltrain et al., 2004), the last interglacial and previous glacial periods had increased seasonal aridity.

In terms of the effects of climate and environmental changes on La Brea birds, including barn owls, we may expect to see a demonstration of Bergmann's rule, wherein larger body sizes occur in colder climates, during times when the La Brea region was coldest 18,000-20,000 years ago at the last glacial maximum. Meiri and Dayan (2003) reviewed data from 94 species of living birds, and found that over 70% showed significant size change with latitude, consistent with Bergmann's rule being applicable to most birds. Some 23 distinct subspecies of *Tyto alba* are recognized around the world; they are the most widespread land bird in the world, living on every continent except Antarctica. In general, the differences between subspecies show a weak Bergmann's rule effect, with the largest in colder climates and the smallest in warmer climates and especially on islands (Bruce, 1999; König et al., 2009; McGillivray, 1989).

The golden eagle (*Aquila chrysaetos*), the most common bird found in the La Brea Tar Pits, demonstrates dramatic clinal variation in present-day populations, where more massive subspecies exist in higher, colder latitudes in Siberia and North America (Brown, 1968; Johnsgard, 1990). However, Molina and Prothero (2011) found results inconsistent with this in the La Brea fossil assemblage of golden eagles during the peak glacial interval 18,000-20,000 years ago. Similar findings were yielded from the extinct California condor (*Gymnogyps amplius*), the extinct California turkey (*Meleagris californica*), the La Brea caracara (*Caracara plancus prelutosus*), and the bald eagle (*Haliaeetus leucocephalus*) (Syverson and Prothero 2010; Fragomeni and Prothero 2011). Madan et al. (2015) found complete stasis in the largest owls from La Brea, the great horned owl (*Bubo virginianus*). All these birds, among which are the most common birds found at La Brea, exhibit morphological stasis over the entire Late Pleistocene.

In this study, we examine morphological changes in barn owls (*Tyto alba*), whose abundance allows for robust statistical analysis.

METHODS

We measured specimens of barn owls from the La Brea Tar Pits and Museum collections, representing hundreds of individuals (Howard 1962, table 1) from almost every pit. We took measurements of the tarsometatarsus (TMT), the most robust element in the skeletons of birds, and therefore the least likely to be broken or distorted by fossilization. No differences in the trends demonstrated by the tarsometatarsus and those from other parts of the skeleton were observed in studies of the La Brea condor (Syverson and Prothero, 2010), making the tarsometatarsus a useful proxy for body size, for which it is commonly used by ornithologists and paleo-ornithologists.

Complete, unbroken adult tarsometatarsi were measured with dial calipers. Three dimensions were measured (Fig. 1): the maximum length from proximal to distal ends, midshaft width, and midshaft depth. Since La Brea bird specimens are not separated by pit in the

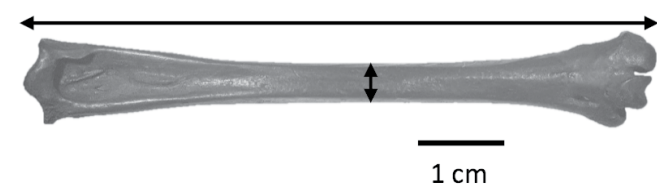


FIGURE 1. Location of measurements (in mm) on a typical TMT of *Tyto alba*.

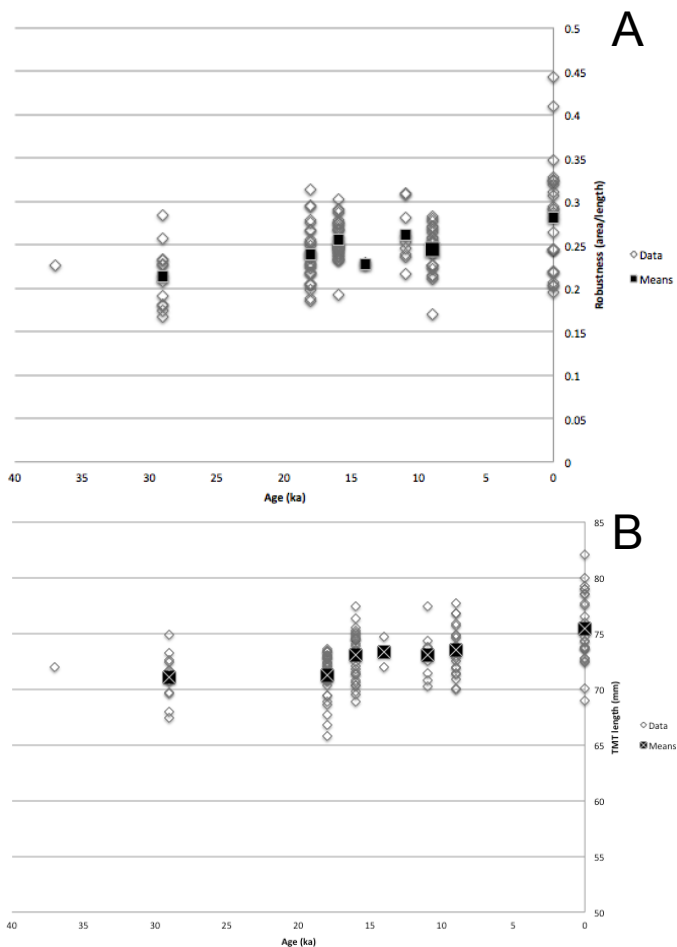


FIGURE 2. Plots of individual TMTs (open diamonds) and the means (solid squares) against age of samples of *Tyto alba*. Age in ka is across the x-axis. **A**, Length. **B**, Robustness index (cross sectional area of the midshaft/ length).

collections, we searched the Excel database by pit number first, in order to avoid specimens from Pit 16 (Marcus and Berger, 1984; O’Keefe et al., 2009), which had a wide scatter of dates and so could not be utilized in this study despite the large number of bird bones recovered from it (Howard, 1962). We also collected measurements from recent barn owl specimens held in the University of California Museum of Vertebrate Zoology (UCMVZ) and the American Museum of Natural History (AMNH) Department of Ornithology.

We performed basic statistical analyses (mean and standard deviation) on age groups once the temporal sequence of specimens was established using Excel and R. For all statistical analyses beyond this, the single specimen at 37 ka was excluded. Then we used the Shapiro-Wilk method to test for normality, and because the data were largely not normally distributed, used the Kruskal-Wallis test to determine if each sample deviated from the pooled mean of all other measurements. For those measurements, which indicated a significant difference of at least one age cohort from the sample mean, a *post hoc* test was conducted by calculating the Mann-Whitney *U* statistic for each interval versus the other measurements in that interval (jackknife resampling by groups) in order to determine which age cohorts were significantly different from

the rest. Time-series measurements were fit to evolutionary models (directional random walk, undirected random walk, stasis, and stasis with a single punctuated change) using the package “paleoTS” in R (Hunt, 2007), and model fits compared using the corrected Akaike information criterion.

RESULTS

The basic statistics are given in Table 1, including means, standard deviations, and coefficients of variation for each variable in each age group, and plotted in Figures 2 and 3. The Kruskal-Wallis test for sample differences (Table 2) indicated that significant differences on the basis of age were present in all five measured and calculated variables, so the *post hoc* Mann-Whitney test was conducted for all of them (Table 3). Applying the appropriate Bonferroni correction for the seven comparisons made with each data set, the significance of these tests was evaluated at $p=(0.05/7)=0.007$. The results from this test indicate that the 0 ka (modern) sample is significantly larger in all dimensions except width; that the 18 ka sample is shorter on average than the rest of the sample (by 2.23 mm) and its midshaft area smaller, although differences in the other values do not reach the significance level; and that the 29 ka sample is smaller in all dimensions than the rest of the sample. The visually apparent difference in several dimensions for the 14 ka sample is not significant because of the small size of this sample ($n=2$). Most importantly, the sample nearest the peak glacial (18 ka) is not larger in body size as predicted by Bergmann’s rule, but actually slightly smaller.

Evaluating the time series with respect to the evolutionary models of directional evolution, stasis, random walk, and punctuated change (single shift) shows that all variables are best modeled as stasis. A model of stasis with punctuational shift was also fitted; however, the short time series means that the number of parameters in the punctuational model (5) is too close to the number of usable time points in the sample (7), which causes the punctuated shift model to be evaluated as very bad in all cases. More data from the 37 ka pit or from other time horizons would extend the time series and make the punctuated change model easier to evaluate.

TABLE 1. Basic statistics of *Tyto alba* TMTs.

Character	Age (ka)	N	Mean	SD	CV
Length	0	26	75.4	3.1	4.1
	9	23	73.5	2.1	2.8
	11	8	73	2.1	2.9
	14	2	73.4	1.9	2.6
	16	30	71.3	2.2	2.9
	18	30	71.3	2.1	2.9
	29	12	71.1	2	2.9
	37	1	72	—	—
Midshaft depth (antero-posterior)	0	26	4.8	0.6	11.9
	9	23	4.6	0.2	5.6
	11	8	4.7	0.2	4.6
	14	2	4.5	0.1	1.6
	16	30	4.7	0.3	6.1
	18	30	4.5	2.9	6.6
	29	12	4.3	0.3	7.9
	37	1	4.4	—	—
Midshaft transverse width	0	26	4.3	0.7	15.0
	9	23	3.9	0.3	7.9
	11	8	4.1	0.3	8.0
	14	2	3.8	0.1	1.9
	16	30	3.9	0.3	7.1
	18	30	3.8	0.3	8.5
	29	12	3.5	0.4	11.2
	37	1	3.7	—	—

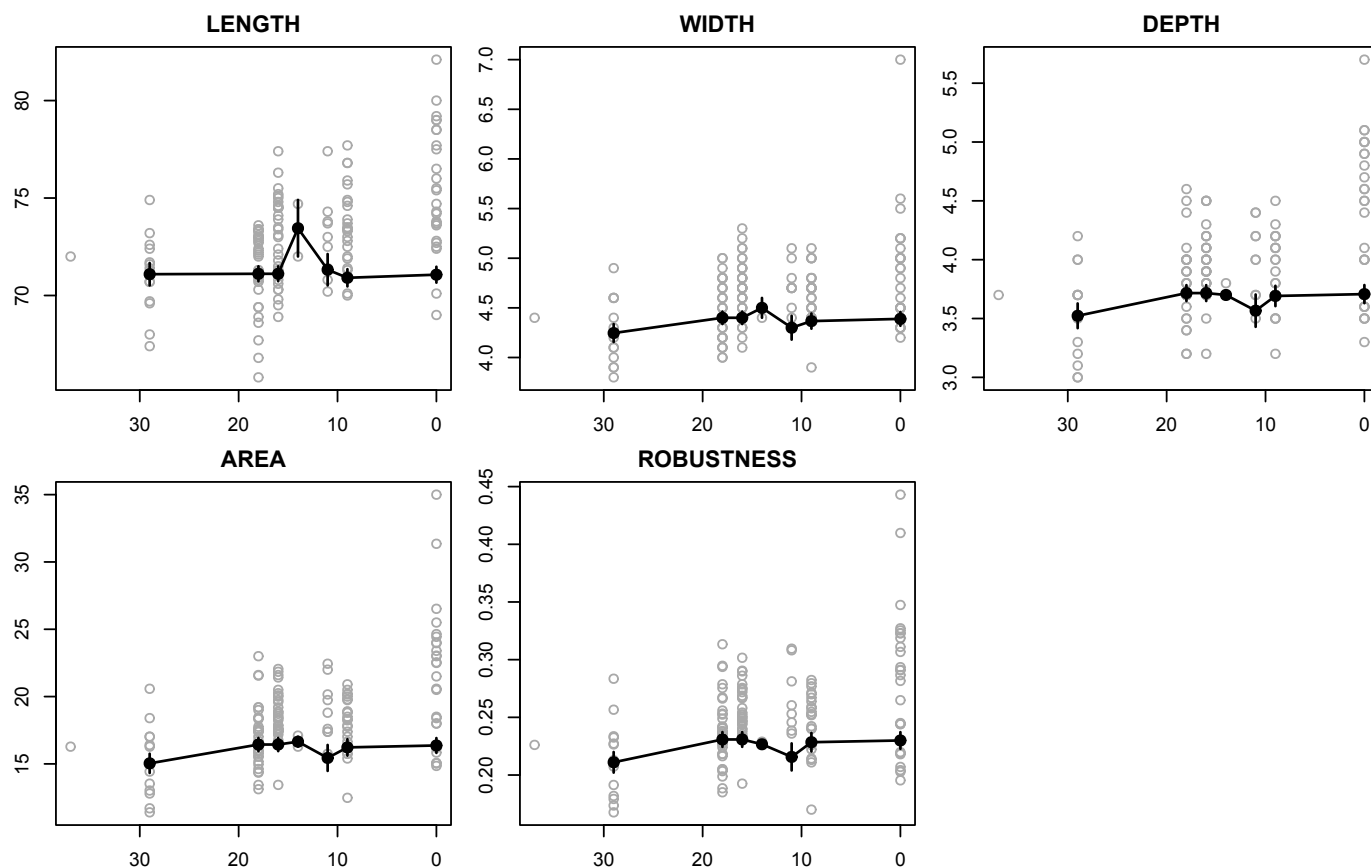


FIGURE 3. Plots of the measured and calculated dimensions of *Tyto alba* TMTs through time. Open circles = individual specimens; solid circles = mean for each pit; error bars indicate variance (± 1 SE). As is apparent from the statistical analysis (Table 3), all dimensions are best modeled by either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

TABLE 2. Results of Kruskal-Wallis tests for sample difference on each measured dimension and calculated index. All are significant at $p < 0.05$.

Measurement	χ^2	df	p-value
Length	37.73	6	1.27E-06
Width	25.81	6	2.41E-04
Depth	23.12	6	7.57E-04
Area	31.52	6	2.02E-05
Robustness	25.02	6	3.39E-04

DISCUSSION

As demonstrated by previous studies on La Brea golden eagles, California condors, bald eagles, turkeys, caracaras, and great horned owls (Molina and Prothero, 2011; Syverson and Prothero, 2010; Fragomeni and Prothero, 2011; Madan 2015), there was no significant evidence of size or shape changes in barn owls during the last glacial

peak at 18,000–20,000 years ago, in spite of the extreme shifts in climate and ecology over the last 40,000 years. Given the dramatic variability in the La Brea owl assemblage (Husband, 1924), and even more so in modern owls (McGillivray, 1989), detecting any significant changes would be unlikely. Therefore, it is unsurprising that barn owls reveal a pattern of stasis during the peak glacial interval in the same way as do other birds from La Brea.

Like the other birds measured from La Brea, barn owls exhibit clinal variations in size over wide latitudes (Bruce, 1999; König et al., 2009; McGillivray, 1989; Meiri and Dayan, 2003). However, at La Brea, during the dominance of coniferous forests and frequent snowfall 18,000–20,000 years ago, they did not have any significant increases in body size or robustness during that time interval, nor did body sizes decrease into the present; indeed, modern barn owls are larger and more robust on average than the RLB specimens. Barn owls from RLB before 16 ka appear to have been significantly more gracile, corresponding to the beginning of the last glaciation, rather than its peak. This suggests that, if a shift toward larger body sizes did occur as the last glacial

TABLE 3. Mann-Whitney U tests of each measurement for each age group versus all other data. “Difference” indicates the amount by which the mean value of each measurement within each age group exceeds the mean value of that measurement in the rest of the sample excluding that age group. Those differences that are significant (at the Bonferroni-corrected p value of $0.05/7 = 0.007$) are given in bold.

	0 ka		9 ka		11 ka		14 ka		16 ka		18 ka		29 ka	
	diff.	p	diff.	p	diff.	p	diff.	p	diff.	p	diff.	p	diff.	p
Length	3.00	6.54E-06	0.62	2.04E-01	0.01	9.72E-01	0.35	7.60E-01	0.02	6.53E-01	-2.23	5.25E-05	-2.13	5.07E-03
Width	0.28	2.38E-02	0.02	5.58E-01	0.11	2.20E-01	-0.18	3.67E-01	0.11	5.79E-02	-0.20	9.71E-03	-0.40	4.39E-04
Depth	0.49	1.03E-03	-0.10	5.78E-01	0.07	4.19E-01	-0.20	5.21E-01	0.03	1.94E-01	-0.19	4.00E-02	-0.44	2.10E-03
Area	3.59	5.27E-04	-0.46	9.89E-01	0.71	3.50E-01	-1.70	3.24E-01	0.43	8.57E-02	-1.69	5.55E-03	-3.49	3.10E-04
Robustness	0.04	3.70E-03	-0.01	7.13E-01	0.01	3.37E-01	-0.02	2.43E-01	0.01	9.66E-02	-0.02	6.04E-02	-0.04	4.92E-04

TABLE 4. Results of paleoTS time series hypothesis testing. The first number (“Weight”) given for each model is the proportional support for that model; the second (“AICc”) is the corrected Akaike information criterion. When these three models are compared, stasis is the best model for all variables.

	Directional		Random walk		Stasis		Single shift	
	Weight	AICc	Weight	AICc	Weight	AICc	Weight	AICc
Length	0.02	21.83	0.246	16.85	0.734	14.66	0	54.38
Width	0.032	-2.40	0.216	-6.22	0.752	-8.71	0	30.96
Depth	0.034	-1.05	0.201	-4.62	0.765	-7.30	0	32.45
Area	0.033	22.53	0.19	19.03	0.777	16.21	0	55.91
Robustness	0.034	-29.26	0.173	-32.54	0.794	-35.59	0	4.10

interval began, it did not reverse after the glaciers receded into the present interglacial. More complete understanding of this pattern will require specimens older than the RLB fossil record.

Large mammals from La Brea show no morphological responses to climate changes over the last 35,000 years (Prothero et al., 2012; Prothero and Raymond, 2008, 2011; DeSantis et al., 2011; Raymond and Prothero, 2011; Madan et al., 2011). Numerous studies have documented stasis in most Pleistocene mammal lineages (Barnosky, 1994, 2005), even in spite of the fact that these animals lived through several glacial-interglacial cycles. Stasis seems to be a common phenomenon across most Pleistocene birds and mammals over numerous glacial-interglacial cycles.

The significance of stasis in the face of a changing environment has been a subject of debate among paleontologists and neontologists for a long time. This is a clear inconsistency with the rapid adaptive responses shown by Galápagos finches, among many other documented examples of adaptations and microevolution on small time scales (Weiner, 1995). Suggestions such as stabilizing selection (Estes and Arnold, 2007) are unsuitable explanations and fail to account for this phenomenon, since the environment in this instance is changing, and not stabilizing (Lieberman and Dudgeon, 1996). Ideas such as developmental canalization have been suggested to account for this stability, but due to the phenotypic plasticity of domesticated animals like dogs, this model has fallen out of favor (Gould, 2002; Eldredge et al., 2005). Though Bennett (1990, 1997) claimed that Pleistocene climate changes occurred too rapidly for organisms to respond, the fossil record in this period spans ten to hundreds of thousands of years; if Galápagos finches can measurably adapt in only a few years, then it would follow that evolutionary changes can occur in a matter of years or decades. It has been suggested, however, that mean phenotype fluctuates slowly enough to seem static, but most La Brea pits have time frames narrow enough that they should capture changes on this scale.

By far the most common explanation for stasis over long periods is that many organisms have wide geographic ranges and as such are well-adapted to a wide variety of environments, making morphological changes in response to environmental shifts unnecessary (Eldredge, 1999; Lieberman et al., 1995; Lieberman and Dudgeon, 1996; Eldredge et al., 2005). This may explain larger birds such as owls, whose habitats range all over North America, but not smaller birds that live in small geographic areas, however there does not exist a large enough sample size of smaller birds at La Brea to test this. Additionally, stasis in smaller birds is inconsistent with size stasis in spite of colder climates seen in bald eagles, turkeys, golden eagles, caracaras and great horned owls. Small mammals also demonstrate stasis across climate changes during the Pleistocene (Barnosky, 2005), as is also apparent during late Eocene-Oligocene climate changes (Prothero and Heaton, 1996). It seems as though a comprehensive explanation for stasis despite extreme climate changes over thousands of years is elusive, and further investigation is required.

CONCLUSIONS

Our statistical analysis of size and shape in Rancho La Brea barn owls exhibits little to no significant changes in size or robustness in response to the climatic fluctuations of the peak glacial period 20,000 years ago. This evidence is consistent with previous studies done on golden eagles, bald eagles, condors, turkeys, and caracaras, despite their general propensity to follow Bergmann’s rule (Molina and Prothero, 2011; Fragomeni and Prothero, 2011; Syverson and Prothero, 2010). This is also consistent with results of studies on La Brea mammals that show stasis over the last 40,000 years of climate change (Prothero et al., 2012). Though this may be possible to explain by a wide geographic

range or environmental adaptability, this model is not able to account for why environmentally restricted mammals and birds with small body masses and geographic regions also exhibit stasis.

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