

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

PATRICK GILLESPIY¹, DONALD R. PROTHERO^{1,2} and VALERIE J. P. SYVVERSON³

¹Dept. Geological Sciences, California State Polytechnic University, Pomona, CA 91678; -email: patrick.gillespy.87@gmail.com;

²Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, CA 90007; -email: donaldprothero@att.net;

³Dept. Geosciences, University of Wisconsin, 1215 W Dayton St., Madison, WI 53706; -email: vsyverson@gmail.com

Abstract—Conventional evolutionary biology suggests that birds evolve rapidly in response to climate change, as exemplified by the Galapagos finches. However, previous studies of birds from the 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 teratorns showed also 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 result also suggests that the Galapagos finch model of rapid change in response to climate may not be appropriate for all birds.

INTRODUCTION

Adaptive responses to climatic and environmental changes are common within conventional evolutionary biology thought. Such responses are made famous by Darwin's Galapagos finches and can be observed as responses to climatic changes, such as competition and drought (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.

For 44 years now, paleontologists have become 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 the 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 trapped and preserved numerous floral and faunal specimens from a variety of time intervals and 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 bird species are extinct (Howard, 1962). The tar pits were particularly suited for trapping and preserving delicate bird bones, typically resulting in large samples of many 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 been conducted and allowed for more accurate estimates of dates (Marcus and Berger, 1984; O'Keefe et al., 2009) together 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 the climatic record in southern California at the time they formed, based upon data from gastropods (snails), pollen, plant macrofossils, and oxygen isotopes (Warter, 1976; Coltrain et al., 2004; Ward et al., 2005). The best record of this time interval comes from 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 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.

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) analyzed the large RLB sample of golden eagles, and found no indication of larger body sizes during the peak glacial interval at 18–20 ka years ago. Syverson and Prothero (2010) found no size differences in the third most common 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*). These are among the five most common birds in the RLB collections, and all of them 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. *T. merriami* tended to be a large-bodied raptorial bird, having much in common with New World vultures and storks, and 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). Another species of *Teratornis*, *T. woodburnensis*, was recovered from Legion Park, near Woodburn, Oregon, dated to about 11,000–12,000 years ago (Campbell and Stenger, 2002). It was slightly larger, with a wingspan over 4 meters (14 feet), suggesting that there was some Bergmann's rule effect at least 11,000–12,000 years ago.

METHODS

We studied the largest known sample of *Teratornis* in the La Brea Tar Pits Museum collections, with a minimum of 63 individuals, which were found in pits ranging from 9 ka to 37 ka. We measured the tarsometatarsus (TMT) because these are among the most robust elements in the bird skeleton, being 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 and those of the other parts of the skeleton, so the TMT is a good proxy for body size, and has been widely used by ornithologists and paleo-ornithologists for just that reason.

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): total 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 mixed together with samples from all the different pits, so we searched the Excel database for all RLB birds by the pit number first. This allowed us 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 here.

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, unidirectional 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 Shapiro-Wilk test were not normally distributed. 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, using the jackknife method ($p > 0.05$). This is apparent in a plot of any of the dimensions (Figs. 2-3) against age. Although the values of individual specimens fluctuate around the mean in Figures 2 and 3, in most cases there are no statistically significant differences between samples of adjacent ages.

The main exceptions to this generality are the samples at 21 ka (Table 2, Fig. 2), which appear to be significantly different in length and midshaft area, but not in the other variables. However, the sample at 18 ka, which is closer to the peak of the last glacial maximum, does not show this same trend, so the results at 21 ka do not lend strong support to the idea that the birds were uniformly larger in all dimensions during the cold of the last glacial maximum.

The sample at 14 ka gave significantly different results in the midshaft width and depth dimensions, but not in the other dimensions, especially not in the midshaft area. This result is surprising because it is the product of width times depth. This odd result is probably a statistical artifact because the 14 ka sample (Pit 4) is by far the largest

TABLE 1. Basic statistics of RLB Teratornis TMTs.

Character	Age (ka)	N	Mean	SD	CV
Length	9	1	96.1	—	—
	11	17	91.4	5.4	5.9
	14	13	85.3	3.8	4.5
	16	3	90.8	4.4	4.9
	18	16	88.1	2.9	3.4
	21	6	90.4	3.7	4.1
	35	4	89.4	3.3	3.7
Midshaft depth (antero-posterior)	9	1	14.4	—	—
	11	17	14.3	0.9	6.3
	14	13	14.1	0.8	5.9
	16	3	14.5	0.8	5.3
	18	16	14.1	0.8	5.7
	21	6	14.1	1.0	7.3
	35	4	14.3	1.0	6.9
Midshaft transverse width	9	1	12.0	—	—
	11	17	12.3	0.8	6.9
	14	13	11.6	0.4	4.2
	16	3	12.0	1.1	9.3
	18	16	11.8	0.7	5.9
	21	6	12.1	0.5	4.1
	35	4	12.0	0.8	6.5

in the study (Fig. 2).

The only other significant results were the lengths of the two Holocene samples (Pit 10 at 9 ka), but this difference appeared only in the length and midshaft depth dimensions of both samples, and in the area and robustness of the 9 ka sample. This reduced size can be seen in the plots (Fig. 2), and is consistent with the general trend in size reduction of many mammals and birds in the Holocene (as seen in California condors by Syverson and Prothero, 2010).

Contrary to the expectation of Bergmann's rule, there is very little consistent evidence of larger body size in the samples around the last glacial maximum at 18-20 ka.

The same is true of measures of shape, such as a robustness index (cross-sectional area of the midshaft divided by length), shown in Figure 3. With the exception of Pit 9, the means are all within a narrow band, and the differences are not significant except for the cases noted above (Table 2). In particular, the samples at 16 ka (Pit 13), 18 ka (Pit 3), and 21 ka (Pit 60) show no increase in robustness as would be expected from Bergmann's rule for animals living in colder climates (Fig. 3).

Evaluating models for the time series (Table 3, Fig. 4) confirms the lack of any overall directional change over the time period being measured. Length is best modeled as a random walk, and stasis is the preferred model for both of the midshaft measurements and for the

MsL

MsW

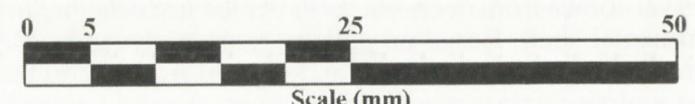


FIGURE 1. Image of a *Teratornis* TMT, showing the measurement landmarks.

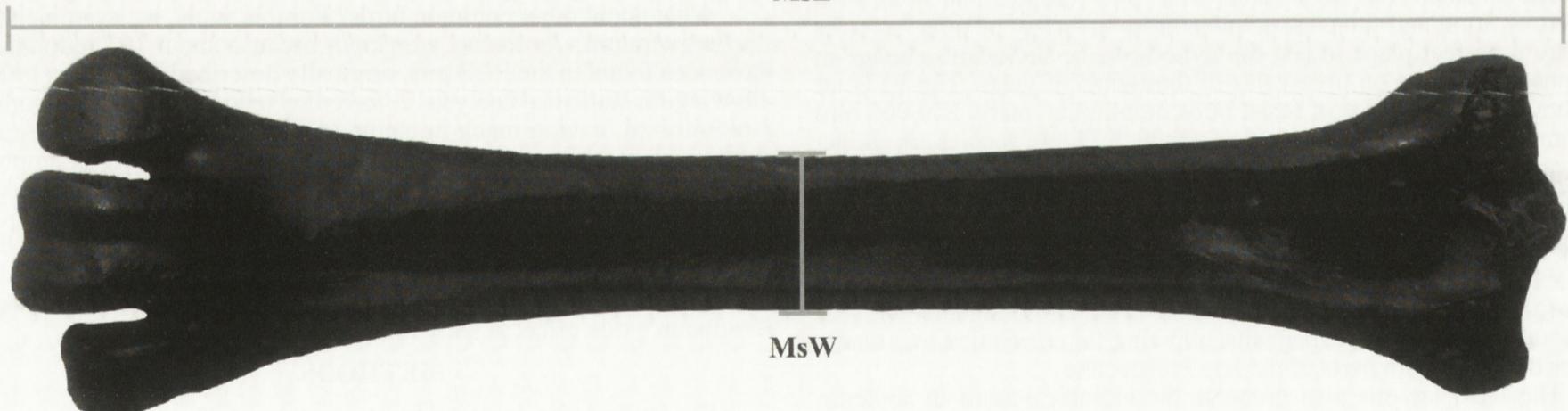


TABLE 2. Kruskal-Wallis test of dimensions of Great Horned Owl TMTs. Instead of straight pooled variation, the jackknife method was used. **Bold face** indicates results that are significantly different at the $p > 0.05$ level. *Italics* indicate that the time interval is represented by a single specimen (pits dated at 26 ka and 35 ka). Degrees of freedom = df.

Length	<u>Age (ka)</u>	<u>χ^2</u>	<u>df</u>	<u>p-value</u>
0	12.82676060	1		0.0003416968
9	12.83721500	1		0.0003397930
11	0.63399701	1		0.4258929630
14	3.58398964	1		0.0583388823
16	0.25524760	1		0.6134040835
18	2.76540435	1		0.0963223452
21	12.03368270	1		0.0005224775
26	2.00925221	1		0.1563423633
29	0.07589799	1		0.7829352742
35	0.44221311	1		0.5060562125

Midshaft Width

<u>Age (ka)</u>	<u>χ^2</u>	<u>df</u>	<u>p-value</u>
0	36.34184361	1	1.655707e-09
9	3.14471741	1	7.617319e-02
11	1.71158867	1	1.907794e-01
14	8.98105065	1	2.727937e-03
16	1.84712659	1	1.741180e-01
18	0.13427349	1	7.140416e-01
21	6.91932316	1	8.526924e-03
26	0.12280212	1	7.260150e-01
29	0.18241932	1	6.693023e-01
35	0.03070053	1	8.609102e-01

Midshaft Depth

<u>Age (ka)</u>	<u>χ^2</u>	<u>df</u>	<u>p-value</u>
0	39.562811030	1	3.176756e-10
9	8.448544827	1	3.653356e-03
11	0.202183065	1	6.529645e-01
14	6.524930332	1	1.063727e-02
16	0.027069138	1	8.693163e-01
18	0.120472536	1	7.285226e-01
21	0.218056942	1	6.405244e-01
26	0.001227625	1	9.720499e-01
29	1.065036011	1	3.020694e-01
35	1.772690917	1	1.830494e-01

Midshaft Area

<u>Age (ka)</u>	<u>χ^2</u>	<u>df</u>	<u>p-value</u>
0	0.31836112	1	0.572594220
9	6.73567635	1	0.009450339
11	0.25012428	1	0.616987585
14	0.25503450	1	0.613552232
16	0.59741840	1	0.439564722
18	0.01335272	1	0.908006039
21	3.91298700	1	0.047914365
26	0.03061471	1	0.861102745
29	0.53088479	1	0.466235114
35	0.82782166	1	0.362903177

Robustness

<u>Age (ka)</u>	<u>χ^2</u>	<u>df</u>	<u>p-value</u>
0	0.10231579	1	0.74906810
9	4.91878652	1	0.02656617
11	0.28166667	1	0.59561090
14	0.03498134	1	0.85163476
16	0.49837037	1	0.48021704
18	0.21362637	1	0.64393982
21	2.06390805	1	0.15082293
26	0.39673469	1	0.52878043
29	0.63947368	1	0.42390145
35	0.76530612	1	0.38167307

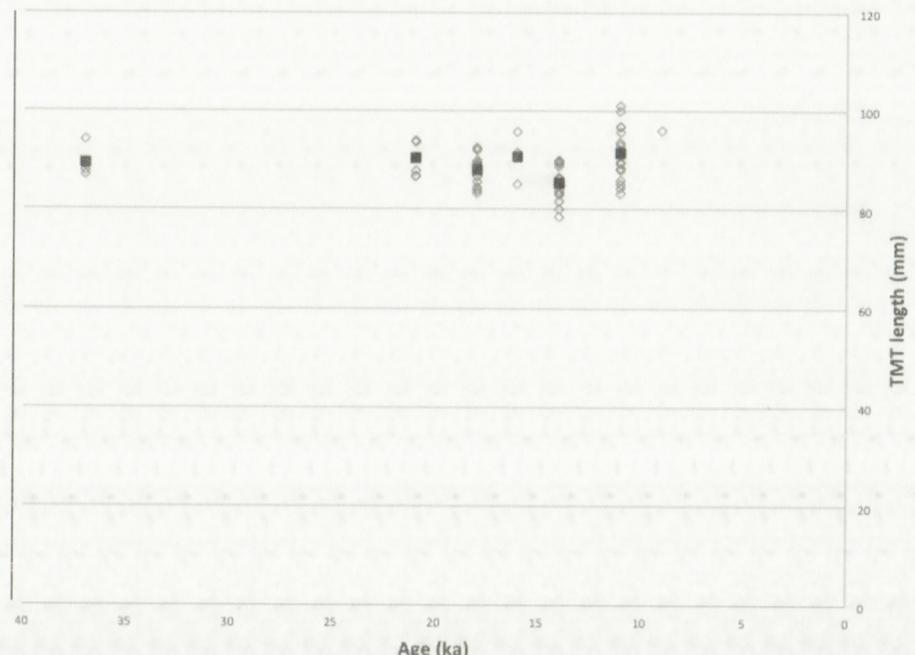


FIGURE 2. Plot of the length of *Teratornis* TMTs through time. Open diamonds = individual specimens; solid diamonds = mean for each pit.

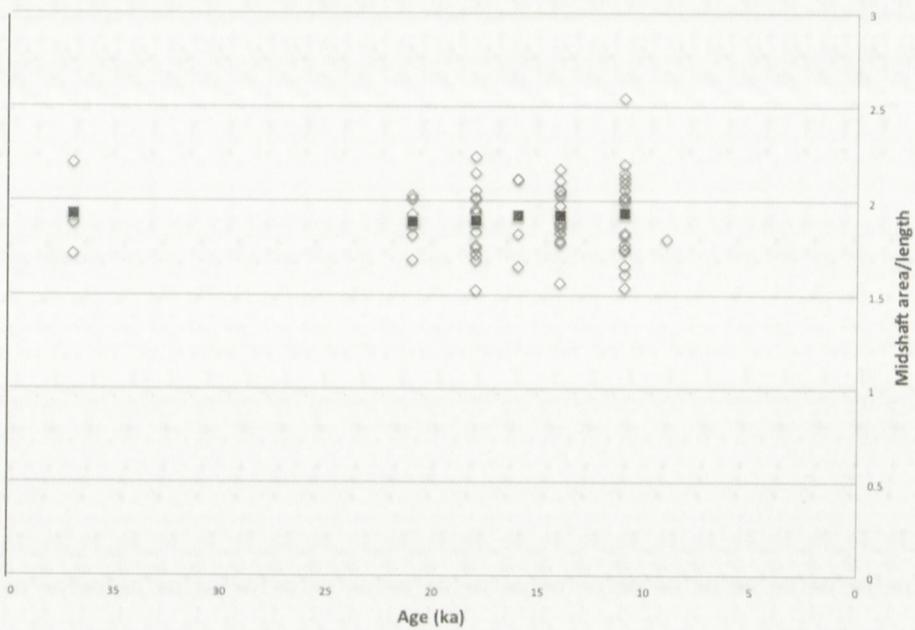


FIGURE 3. Plot of the robustness (midshaft cross-sectional area divided by length) of *Teratornis* TMTs through time. Symbols as in Figure 2. derived robustness index.

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 peak of the last glacial period, 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 and Raymond, 2008, 2011; DeSantis et al., 2011; Raymond and Prothero, 2011; Madan et al., 2011; Prothero et al., 2012). This result is supported 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

TABLE 3. Time-series analysis, given in Akaike weights. GRW = general random walk; URW = unidirectional random walk. The winner of each analysis is shown in bold face. In each case, the variables show either complete stasis (midshaft width, midshaft depth, robustness) or unidirectional random walk (length, midshaft area).

	GRW	URW	Stasis
Length	0.104	0.712	0.184
MidshaftW	0.044	0.271	0.685
MidshaftD	0.004	0.013	0.983
MidshaftA	0.157	0.477	0.366
Robustness	0.101	0.285	0.614

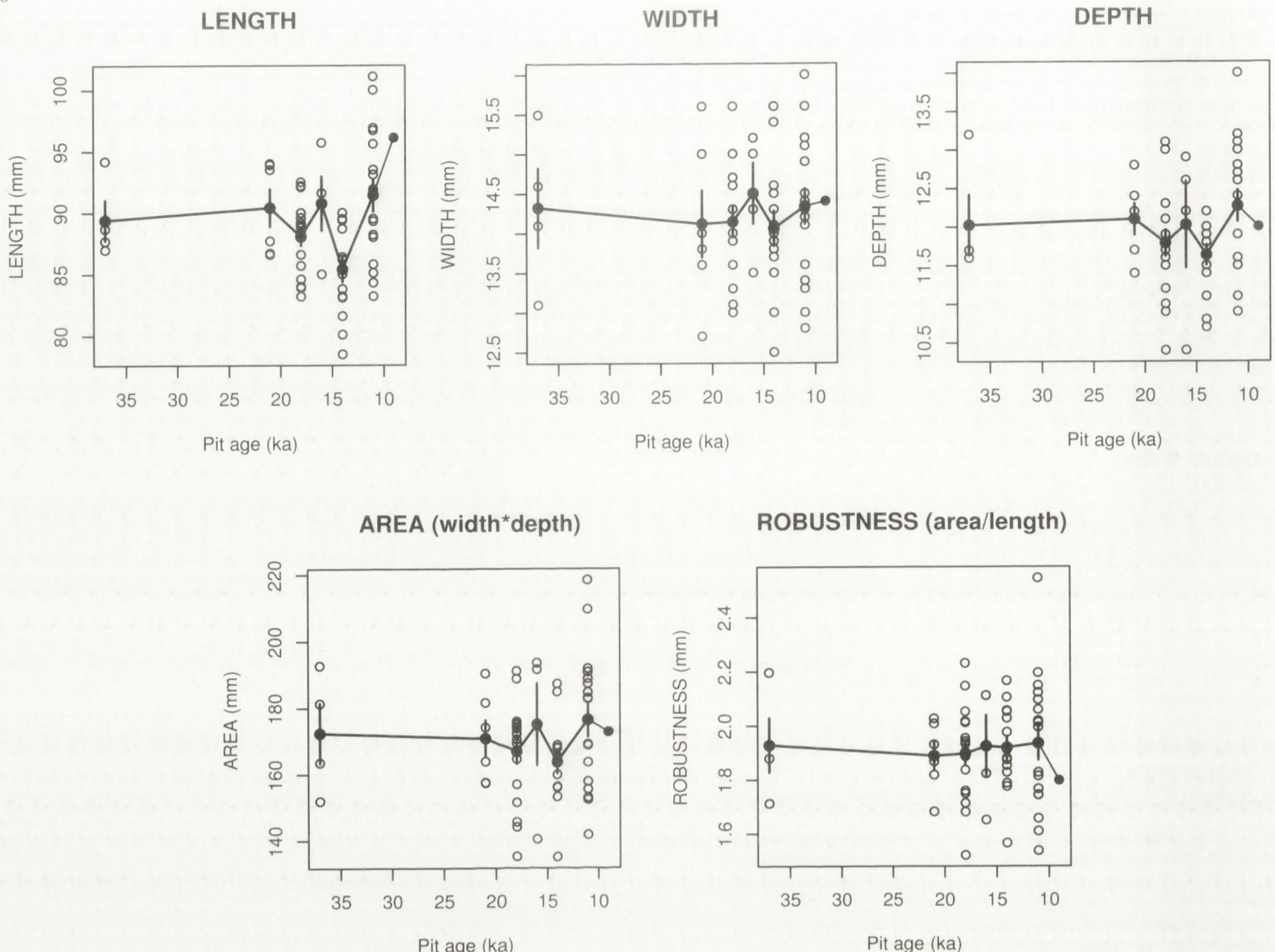


FIGURE 4. Time-series analysis of *Teratornis* through the last 35 ka at RLB. As is apparent from the statistical analysis (Table 3), they exhibit either an unidirectional random walk or complete stasis.

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 notion of adaptive sensitivity shown by the Galapagos 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, because 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 Galapagos 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 (Lieberman et al., 1995; Lieberman and Dudgeon, 1996; Eldredge, 1999; Eldredge et al., 2005). This might be appropriate for the larger birds like the teratorns that ranged all over the Americas from Oregon to Argentina, but not for the smaller birds, some of which live in very small areas. Unfortunately, the sample of most smaller birds at RLB

is insufficient to test this hypothesis. Likewise, the idea of stasis in the smaller birds is not consistent with the size stasis despite to colder climates seen in bald eagles, turkeys, golden eagles, and caracaras. In the case of small mammals, there is stasis through climate changes during the Pleistocene as well (Barnosky, 2005). Such stasis in the small mammal populations is also apparent during late Eocene-Oligocene climate changes (Prothero and Heaton, 1996). Thus, a comprehensive explanation for stasis in the face of dramatic climate changes on thousand-year timescales still eludes us, and much further research is required.

CONCLUSIONS

Statistical analysis of size and shape variables of the teratorns of RLB demonstrates almost no significant changes in size or robustness in response to the dramatic cooling and vegetational change of the peak glacial period 20,000 years ago. This result is consistent with previous studies showing stasis in other RLB birds, despite their strong tendency to follow Bergmann's rule (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 stasis.

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