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

MEENA MADAN[1], DONALD R. PROTHERO[2] and V. J. P. SYVERSON[3]

[1]School of Earth Sciences, University of Bristol, Bristol, BS8 1TQ, UK -email: mm13970@my.bristol.ac.uk;
[2]Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, CA 90007;
[3]University of Michigan Museum of Paleontology, 1109 Geddes Ave., Ann Arbor, MI 48109

Abstract—Conventional evolutionary biology highlights examples like the Galapago finches, which show rapid responses to climatic change. We studied the sample of Great Horned Owls (*Bubo virginianus*) from the Page Museum collections from Rancho La Brea to determine if they showed size or shape changes in response to the climate changes of the last 35,000 years. Even though living Great Horned Owls exhibit a weak Bergmann's rule effect, with larger body sizes in colder climates, the Rancho La Brea owls 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 La Brea Condors, Golden Eagles, Bald Eagles, Turkeys, and Caracaras. Apparently, many birds do not respond to long-term changes in climate in a simple fashion, but are ecologically flexible and live in a wide range of habitats and climates without change in size or limb robustness.

INTRODUCTION

Conventional evolutionary biology has long featured examples of adaptive responses to climatic change, especially in birds such as the Galapagos finches (Weiner, 1995; Grant and Weiner, 1999; Grant and Grant, 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 43 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 are a perfect place to test the hypothesis of short-term change in response to climate on timescales of thousands of years. The tar pits produce a huge sample of fossil birds with over 85,000 individual bones representing at least 133 species (including 19 extinct species)(Howard, 1962). The tar pits were particularly suited for trapping and preserving delicate bird bones, so there are typically large samples of many bones from a variety of time intervals (Akersten et al., 1983; Stock and Harris, 1992; Friscia et al., 2008). Many of the pits have also been radiocarbon dated (Marcus and Berger, 1984; O'Keefe et al., 2009), so we know the temporal sequence of the pits, and which ones correspond to certain parts of the late Pleistocene climatic cycles. Before radiocarbon dating, the age of pits was merely guesswork, or they were given a sequence based on "trends" in size between pits (Menard, 1947; Nigra and Lance, 1947) that have not proven to be real (Madan et al., 2011; Prothero et al., 2012). Thus, Husband (1924) measured many variables on the RLB Great Horned Owl collection, but could not address the difference in age between pits, or their true temporal sequence.

The RLB tar pits also preserve a climatic record for southern California at the time they formed, as reconstructed from the data from 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 vegetational change affect the birds at RLB, including the Great Horned Owls? We might expect to see changes 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). Yet 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. 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 Great Horned Owl (*Bubo virginianus*) because it is relatively common in most of the pits, allowing for statistical analysis. McGillavray (1989) documented a weak Bergmann's rule effect in the living Great Horned Owls of North America, so some size change during colder times might be expected.

METHODS

We studied the large sample of Great Horned Owls in the Page Museum collections, which represent at least 128 individuals according to Howard (1962, Table 1). They have been found in almost every pit, including the oldest pit, Pit 77 (35 ka).

We measured the tarsometatarsus (TMT), which is by far the most robust element in the bird skeleton, and is very often preserved intact and undeformed at RLB. 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): maximum shaft length between the longest proximal-distal ends of the TMT; midshaft anteroposterior thickness of the TMT;

TABLE 1. Basic statistics of RLB Great Horned Owl TMTs.

Character	Age (ka)	N	Mean	SD	CV
Length	0	19	62.1	2.3	3.8
	9	10	61.0	1.9	3.1
	11	3	65.0	1.6	2.6
	14	31	64.6	1.8	2.8
	16	9	65.6	2.2	3.5
	18	8	65.9	2.7	4.2
	21	12	66.3	1.8	2.8
	26	1	60.0	—	—
	29	3	62.4	3.8	6.1
	35	1	62.9	—	—
Midshaft depth (antero-posterior)	0	19	7.4	0.8	10.2
	9	10	5.4	0.7	12.2
	11	3	6.0	0.4	5.9
	14	31	5.9	0.6	9.7
	16	9	6.0	0.6	9.2
	18	8	6.0	0.6	9.9
	21	12	6.2	0.5	8.3
	26	1	6.1	—	—
	29	3	5.6	0.6	10.9
	35	1	5.3	—	—
Midshaft transverse width	0	19	6.9	1.1	15.8
	9	10	8.1	0.8	10.4
	11	3	9.4	0.7	7.4
	14	31	9.2	0.9	9.7
	16	9	9.2	1.0	10.7
	18	8	8.8	0.9	10.7
	21	12	9.5	0.8	8.1
	26	1	9.1	—	—
	29	3	8.4	0.9	11.0
	35	1	8.5	—	—

FIGURE 1. Image of a Great Horned Owl TMT, showing the measurement landmarks.

and midshaft transverse width of the TMT. Unlike the fossil mammal collections in the Page 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 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. We also obtained measurements of TMTs of modern Great Horned Owls from the Natural History Museum of London in Tring, from other online data sources, and from Bochenski and Campbell (2010).

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 significantly different 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 Great Horned Owl 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 case (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 owls 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 is surprising since it is the product of width and depth. This odd result is probably a statistical artifact of the fact that the 14 ka sample (Pit 4) is by far the largest in the study (Fig. 3).

The only other significant results were the lengths of the two Holocene samples (Pit 10 at 9 ka, and modern owls), 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, but does not follow temperature trends (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 as compared to samples from warmer intervals of the Pleistocene. Yet living Great Horned Owls apparently demonstrate a Bergmann's rule effect, with generally large body sizes in colder climates (McGillavray, 1989).

The same is true of measures of shape derived from these measurements. Figure 3 shows a robustness index calculated by dividing cross-sectional area of the midshaft by length. 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 Allen's rule for animals living in colder climates (Fig. 3). Thus, the Great Horned Owls show no evidence of significant size or robustness changes, despite dramatic climatic changes in the region.

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

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

Age (ka)	x^2	df	p-value
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

Age (ka)	x^2	df	p-value
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

Age (ka)	x^2	df	p-value
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

Age (ka)	x^2	df	p-value
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

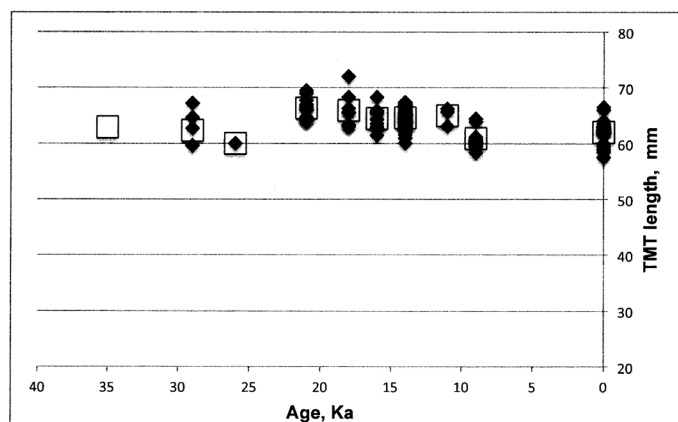| Age (ka)	x^2	df	p-value
0	0.10231579	1	0.74906810
9	4.91878652	1	**0.02656617**
11	0.28166667	1	0.59561090
14	0.03498134	1	0.85163476
16	0.49837037	1	0.48021704
18	0.21362637	1	0.64393982
21	2.06390805	1	0.15082293
26	*0.39673469*	*1*	*0.52878043*
29	0.63947368	1	0.42390145
35	*0.76530612*	*1*	*0.38167307*

FIGURE 2. Plot of the length of Great Horned Owl TMTs through time. Solid diamonds = individual specimens; large open squares = mean for each pit.
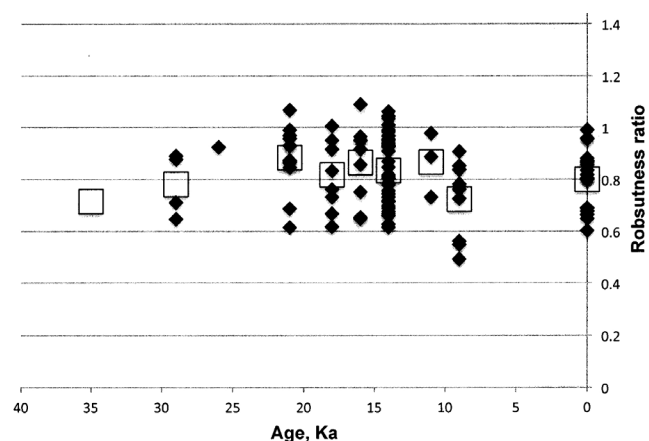

FIGURE 3. Plot of the robustness (midshaft cross-sectional area divided by length) of Great Horned Owl TMTs through time. Symbols as in Figure 2.

preferred model for both of the midshaft measurements and for the derived robustness index.

DISCUSSION

Previous analysis of the RLB Golden Eagles (Molina and Prothero, 2011), California Condors (Syverson and Prothero, 2010), Bald Eagles, Turkeys, and Caracaras (Fragomeni and Prothero, 2011) show that there is no evidence of significant size or shape changes in these birds during the peak of the last glacial, despite the dramatic changes in climate and vegetation documented in the region over the past 40,000 years. Husband (1924) and Howard (1949) suggested that there was a decrease in size in Holocene Great Horned Owls compared to the RLB sample. Our more rigorous statistical analysis only weakly supports this suggestion. Indeed, given the huge range of variability within the RLB owl sample (Husband, 1924), and an even larger range of variability of living owls (McGillivray, 1989), it would be surprising that any real difference could be detected. Thus, it comes as no surprise that Great Horned Owls show the same pattern as the other common birds from RLB.

As was the case with Golden Eagles (Molina and Prothero, 2011) and the Bald Eagles and Caracaras (Fragomeni and Prothero, 2011), Great Horned Owls also exhibit clinal variation in size over latitude following Bergmann's rule (Brown, 1968; Johnsgard, 1990; McGillivray, 1989). Yet at RLB, even conditions of coniferous forests and frequent snow at 20-18 ka did not cause measurable increases in body size in any of these birds.

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

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

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 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, since the environment in this case is changing, not stabilizing (Lieberman and Dudgeon, 1996). Developmental canalization has been proposed as an explaination for this stability, but this model has fallen out of favor in light of the phenotypic plasticity exhibited by 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 the thousand-year time scale of Pleistocene climatic changes.

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 might be appropriate for the larger birds like the Great Horned Owl that range all over the Americas, 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. However, 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 Great Horned Owls of 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. 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 (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 in other localities also demonstrate stasis.
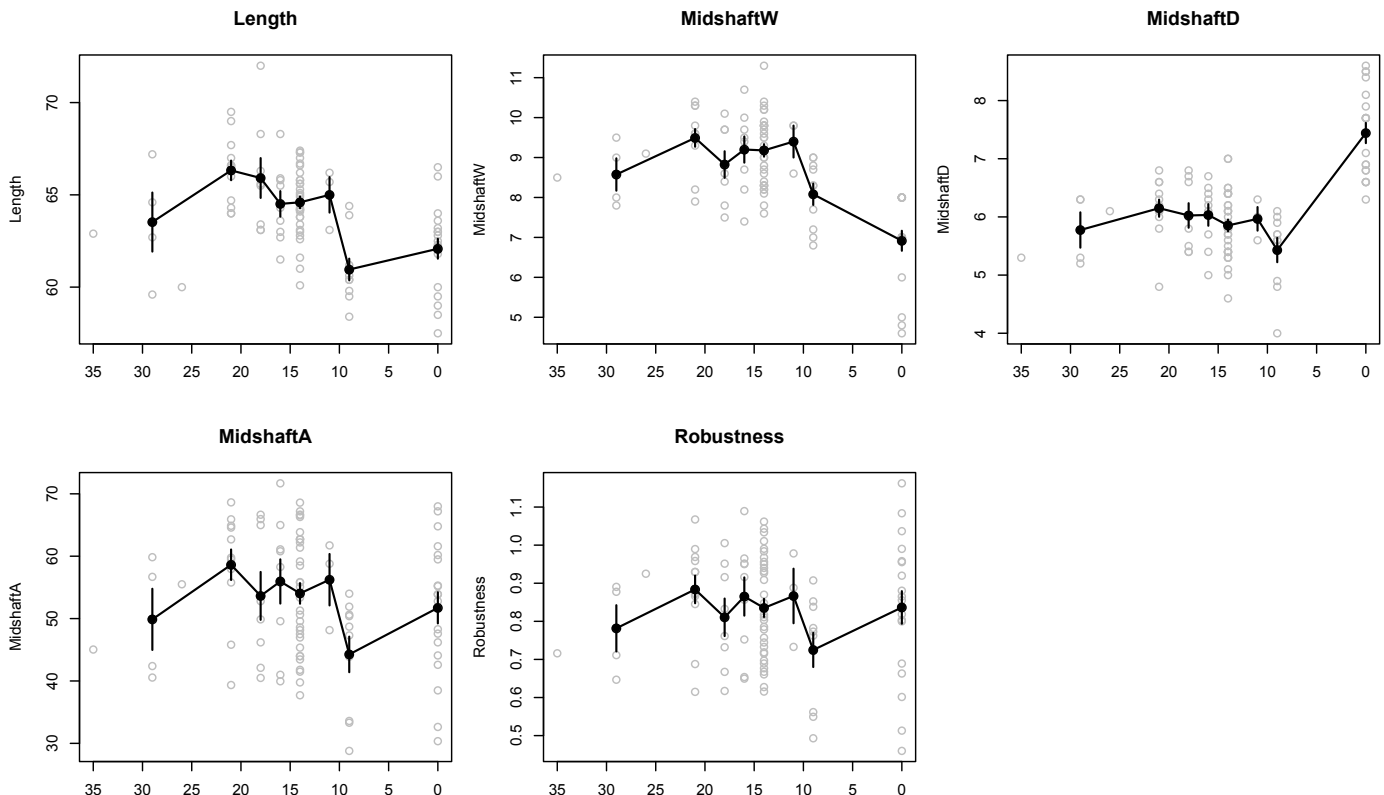

FIGURE 4. Time-series analysis of Great Horned Owls through the last 35 ka at RLB. As is apparent from the model comparisons (Table 3), all the time series are best modeled as either an undirected random walk or complete stasis.

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