

STASIS IN LATE QUATERNARY BIRDS FROM THE LA BREA TAR PITS DURING THE LAST GLACIAL-INTERGLACIAL CYCLE

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Abstract—The emphasis on gradual evolution in response to climatic change, as typified by the studies on Galapagos finches, suggests that birds should respond with changes in body size and shape to significant changes in climate. We examined the most commonly fossilized birds at Rancho La Brea to see if there were measurable changes during the last glacial-interglacial cycle. Measurements of the tarsometatarsi of the common birds, such as the bald eagle (*Haliaeetus leucocephalus*), the extinct California turkey (*Meleagris californica*) and the caracara (*Caracara plancus preluosus*) showed complete stasis for the last 35,000 years, with no statistically significant size or robustness changes even during the peak glacial interval at 20,000 years ago, when the climate at Rancho la Brea was dominated by closed-cone coniferous forests and snowy winters. Even though birds such as the bald eagle and caracara show a strong Bergmann's rule effect, with larger body sizes in colder climates, the bald eagles and caracaras at Rancho La Brea did not change in size during the coldest period of the glacial maximum. These results, along with previously documented examples of La Brea condors and golden eagles, suggest that birds are not as sensitive to long-term changes in climate as is traditionally thought.

INTRODUCTION

The Galapagos finches have long been used as exemplars of how evolution takes place on the microevolutionary scale, with well-documented cases of body size and beak shape and size changing within a few decades in response to changes in climate (especially drought and temperature) (Weiner, 1995; Grant and Weiner, 1999; Grant and Grant, 2007). Weiner (1995) summarized additional examples of microevolutionary change in recent birds, such as Siberian warblers, English sparrows, cuckoos, cowbirds, red-winged blackbirds, and many others. In all cases, these studies emphasized how quickly birds changed in size and shape in response to external climatic forcing factors.

Although these neontological case studies are undoubtedly valid, ever since the proposal of the "punctuated equilibrium" model (Eldredge and Gould, 1972; Gould and Eldredge, 1977; Eldredge, 1999; Gould, 2002), paleontologists have come to question whether these short-term examples of small-scale change are really the stuff of macroevolution. Study after study of examples from the fossil record clearly show that most metazoans exhibit stasis over millions of years (Jackson and Cheetham, 1999; Jablonski, 2000, 2008; Gould, 2002; Geary, 2009; Hallam, 2009; Princehouse, 2009; Ruse and Sepkoski, 2009). In addition, many studies (e.g., Coope, 1979; Davis, 1983; Bennett, 1990; Valentine and Jablonski, 1993; Prothero and Heaton, 1996; Prothero, 1999) demonstrate that fossils show stasis even in periods of dramatic climate change, when the neontological models would predict significant changes in body size or shape.

The Rancho La Brea (RLB) sample provides a superlative setting for a study of Ice Age fossils through time. The sample of birds in particular is one of the best in the entire fossil record, with over 85,000 individual bones representing at least 133 species (including 19 extinct species) (Howard, 1962). The tar seeps were ideal for both trapping and preserving delicate bird bones, allowing us to get large samples from different pits from many different time intervals (Akersten et al., 1983; Stock and Harris, 1992; Friscia et al., 2008). These pits are also well dated by radiocarbon methods (Marcus and Berger, 1984; O'Keefe et al., 2009), so the numerical age of each sample can be reliably determined and put in a true temporal order. Prior to the application of radiocarbon dating, the age sequence of the pits was done by comparing sample similarity and presence of extinct species (Howard, 1962), or by the assumption that gradual size change through time provided a sequence

(Menard, 1947; Nigra and Lance, 1947). In reality, the pits oozed up across the RLB area in no particular pattern, with their dates showing that different pits formed at different times, scattered all across the region (Marcus and Berger, 1984).

Another valuable aspect of RLB for this kind of study is that the climatic record is excellent, with data from snails, pollen, other plant fossils, and oxygen isotopes (Warter, 1976; Coltrain et al., 2004; Ward et al., 2005). The most detailed and well-calibrated record comes not from RLB itself, but from deep-sea cores drilled just offshore in the California borderland. According to Heusser (1998), the region changed from oak and chaparral vegetation around 59 ka to pine-juniper-cypress woodlands by 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, and in the past 10,000 years, the region has been vegetated by the modern assemblage of oak-chaparral-herbaceous vegetation. Coltrain et al. (2004) performed stable isotope analysis and found evidence of increased seasonal aridity during the last interglacial and previous glacial.

So how did birds at RLB respond to all this climatic and vegetational change? At the very least, a response due to Bergmann's rule of larger body size in colder climates might be expected when Rancho La Brea (RLB) reached its coldest, snowiest period 20,000 years ago during the last glacial maximum. The golden eagle (*Aquila chrysaetos*) shows considerable clinal variation, with larger-bodied subspecies in the high latitudes in both Siberia and North America today (Brown, 1968; Johnsgard, 1990). Yet Molina and Prothero (this volume) found no evidence of larger body sizes during the peak glacial interval at 20,000 years ago in the large sample of golden eagles, which are the most common bird known from RLB. Likewise, Syverson and Prothero (2010) detected no size change in the third most common bird, *Gymnogyps amplus*, an extinct relative of the California condor. This raises the question: do any of the other common birds show any significant size or shape changes during the past 40,000 years as sampled at RLB?

METHODS

In this study, we sampled the Page Museum collections of several of the most common birds at RLB, after the golden eagles and the condors. These included the second most common bird, the extinct Califor-

nia turkey (*Meleagris californica*), which has been recently monographed by Bochenski and Campbell (2006). In addition, we measured the La Brea caracara (*Caracara plancus prelutosus* according to Banks and Dove, 1992, and Dove and Banks, 1999), and the bald eagle (*Haliaeetus leucocephalus*). These birds were chosen because they were relatively common in the census of Howard (1962, table 1), with at least 175 individuals, including a sample from the oldest pit, Pit 77 (35 ka), so a wide span in time was represented with specimens from every known age. Howard (1962, table 1) reported at least 175 individuals of bald eagles in the sample, and 289 caracaras, along with 599 turkeys, making them the second, fourth, and the fifth most common birds at RLB.

We measured the tarsometatarsus (TMT), since it is the most robust and commonly preserved element, typically showing little or no breakage. It is by far the most robust element in the bird skeleton, which aids in its excellent preservation. When we studied the entire skeleton of the La Brea condor (Syverson and Prothero, 2010), we found no differences between the trends shown by the TMT measurements and those of the other parts of the skeleton, so we feel confident in assuming that the TMT tracks the overall body size.

Only complete unbroken, undeformed adult TMTs were measured to minimize variability due to ontogeny or taphonomic effects. Measurements were made with digital metric calipers. For the caracaras, we used digital interface software that allowed us measure seven dimensions of the bone (maximum length, proximal maximum depth and width, midshaft maximum depth and width, distal maximum depth and width) following the conventions used by Bochenski and Campbell (2006). Unlike the Page Museum fossil mammal collection, however, the bird fossils are not separated in the drawers by pit, so we ended up measuring many specimens from pits like Pit 16, which has problematic radiocarbon ages (Marcus and Berger, 1984; O’Keefe et al., 2009), and so could not be used in our study. As Howard (1962) noted, for some reason Pit 16 produces a high percentage of the bird bones from RLB, so it is unfortunate that they are so poorly dated and cannot be used. Consequently, the bald eagles were measured by looking up the pit number of a specimen in the RLB bird Excel database provided by K. Campbell, so that we didn’t measure specimens from Pit 16 or other poorly dated pits, and waste time with data we could not use. All data were then entered into Excel spreadsheets so that basic statistics could be calculated.

For the turkeys, Z. Bochenski and K. Campbell graciously provided us with the original database compiled for their 2006 study (Bochenski and Campbell, 2006). In this case, we extracted the TMT measurements, and then compiled the metric data with the pit number from the RLB bird database file, and then the pit ages from O’Keefe et al. (2009). All specimens from Pit 16 and other poorly dated pits, along with partial or immature specimens, were then eliminated from the database before calculations were performed.

Once the pit dates had been plugged into the spreadsheet, we performed basic statistical analysis (mean, standard deviation) of each sample for a well-dated pit. We then tested the samples for normality using the Shapiro-Wilk method. For samples that were normally distributed, we used ANOVA to determine if the temporally sequential samples were statistically significant from one another or not. If the data were non-parametric, we used the Kruskal-Wallis test to determine whether each temporally sequential sample was significantly different or not.

RESULTS

Caracaras

The basic statistics of the RLB caracara TMT sample are shown in Table 1. All of the samples that were large enough for the test were normally distributed, using a Shapiro-Wilk test for normality. Thus, the different pit samples were then compared to see if they were significantly different in size using ANOVA. In every case (Table 2), the calculated F value was less than the $F_{critical}$ value, indicating that the differences were not significant. This is apparent in a plot of any of the dimensions

TABLE 1. Basic statistics of RLB caracara TMTs.

Character	Age (ka)	N	Mean	Variance
Length	9	4	90.2	13.5
	11	7	86.8	4.4
	16	19	87.9	6.39
	18	38	87.9	7.70
	21	3	89.6	6.03
	35	4	89.4	5.61
Proximal width	9	3	13.6	0.23
	11	7	13.4	0.41
	16	19	13.3	2.00
	18	39	13.5	0.59
	21	3	13.4	0.41
	35	4	13.8	0.52
Proximal depth	9	4	7.1	0.07
	11	7	7.1	0.27
	16	21	7.5	2.76
	18	38	7.3	0.28
	21	3	7.2	0.23
	35	4	7.5	0.34
Midshaft width	9	4	4.9	0.37
	11	7	5.1	0.16
	16	21	5.2	0.11
	18	38	5.3	0.21
	21	3	5.4	0.04
	35	4	5.2	0.20
Midshaft depth	9	4	4.4	0.10
	11	7	4.3	0.22
	16	21	4.4	0.25
	18	38	4.4	0.15
	21	3	4.7	0.01
	35	4	4.8	0.18
Distal width	9	4	14.2	0.24
	11	7	13.9	0.18
	16	20	14.1	0.73
	18	38	14.0	0.48
	21	3	14.4	0.16
	35	4	14.3	0.37
Distal depth	9	4	8.4	0.38
	11	7	8.0	0.63
	16	21	8.3	0.91
	18	38	8.5	0.74
	21	3	9.1	0.19
	35	4	8.7	0.15

TABLE 2. ANOVA of dimensions of caracara TMTs. Degrees of freedom = 5.

Variable	F	$F_{critical}$	p	Significant
Maximum length	1.26	2.34	0.28	No
Proximal width	0.69	2.34	0.62	No
Proximal depth	0.27	2.34	0.92	No
Midshaft width	0.50	2.34	0.77	No
Midshaft depth	0.84	2.34	0.52	No
Distal width	0.20	2.34	0.41	No
Distal depth	1.08	2.34	0.37	No
Robustness	0.62	2.34	0.04	No

(Fig. 1) against age. Although individual samples fluctuate around the mean in Fig. 1, there are no statistically significant differences between samples of adjacent ages. Contrary to the expectation of Bergmann’s rule, there is no evidence of larger body size in the samples around the last glacial maximum at 20 ka. Yet *Caracara plancus*, the extant southern caracara, is well known to have larger body sizes in the southern cold regions of South America than it does in the tropics (Brown, 1968; Johnsgard, 1990). The sample from Pit 3 (18,593 radiocarbon years, according to O’Keefe et al., 2009) and Pit 60 (21,383 radiocarbon years) are statistically identical, as is the sample at Pit 13 (16,192 radiocarbon years), showing that there is no real difference in size through the last glacial maximum or the glacial-interglacial transition.

The same is true of measures of shape, such as robustness index (cross-sectional area of the midshaft divided by length), shown in Figure 2. The means are all within a narrow band, and the differences are not significant (Table 2). Once again, 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. 2). Thus, the caracaras show no evidence of significant size or robustness changes, despite dramatic climatic changes in the region.

Turkeys

The statistical data for turkey TMTs are summarized in Table 3. Visual inspection of the data plotted against the age of the pit once again shows no obvious trends in body size (Fig. 3) or in shape indices like

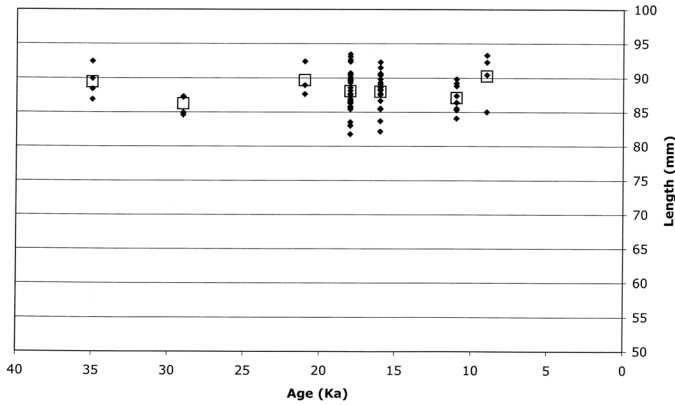


FIGURE 1. Plot of the length of caracara TMTs through time. **Solid diamonds** = individual specimens; **large open squares** = mean for each pit.

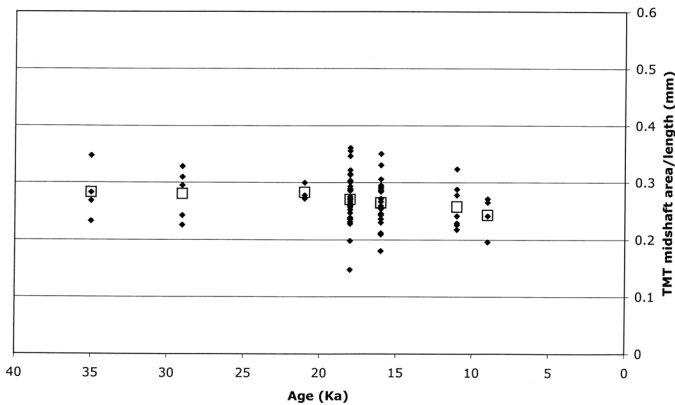


FIGURE 2. Plot of the robustness (midshaft cross-sectional area divided by length) of caracara TMTs through time. Symbols as in Figure 1.

robustness (Fig. 4). The raw size dimensions (Fig. 3) show some bimodality, consistent with the sexual dimorphism in turkeys reported by Bochenski and Campbell (2006, fig. 32). Thus, ANOVA could not be used for these non-parametric data, and a Kruskal-Wallis test was conducted instead. The tests showed (Table 4) that the differences between samples were not significant (K_{obs} was always less than K_{crit} at the 95% confidence level, 8 degrees of freedom), again supporting the idea that there is no change in body size or shape in response to climate change. The Pit 60 sample at 21,383 radiocarbon years appears to be slightly larger and more robust at the time of peak cooling in the region, but the Kruskal-Wallis test (Table 4) shows that these differences are not significant. In summary, there are no statistically significant data to support the idea that turkeys responded to climatic changes by changes in body size or limb robustness.

Bald eagles

The basic statistics of the bald eagle sample are shown in Table 5. Bald eagles, like golden eagles and caracaras, are notable for their clinal variation in size due to Bergmann's rule, so that Alaska specimens weigh about 7.5 kg, while those from Florida average only 2.3 kg (Brown, 1968; Johnsgard, 1990). For that reason, the populations north of 38° north latitude (about the latitude of San Francisco) are currently placed in the subspecies *H. l. washingtonensis*, while those south of 38° north latitude are in the nominate subspecies, *H. l. leucocephalus* (Johnsgard, 1990). As in other eagles, the females average slightly larger than males, but as in our study of golden eagles (Molina and Prothero, this volume), the differences are slight and completely overlapping, and there is no apparent bimodality in male vs. female samples.

TABLE 3. Basic statistics of RLB turkey TMTs (full statistics of pooled samples given in Bochenski and Campbell, 2006).

Character	Age (ka)	N	Mean	SD
Length	9	4	139.4	15.48
	11	17	140.1	18.36
	16	122	143.3	4.00
	18	10	122.4	12.79
	21	22	132.3	11.51
	26	6	136.7	8.07
	29	12	126.9	14.22
	35	7	134.3	9.57
Proximal width	9	4	12.9	1.38
	11	17	12.5	1.28
	16	122	12.6	1.31
	18	10	11.7	1.20
	21	22	12.1	1.17
	26	6	13.3	0.93
	29	12	12.8	1.04
	35	7	12.4	1.28
Proximal depth	9	4	7.8	1.03
	11	17	7.8	0.97
	16	122	7.8	0.89
	18	10	7.3	0.74
	21	6	8.3	0.62
	26	12	8.0	0.78
	29	7	7.5	0.74
	35	4	8.3	0.88

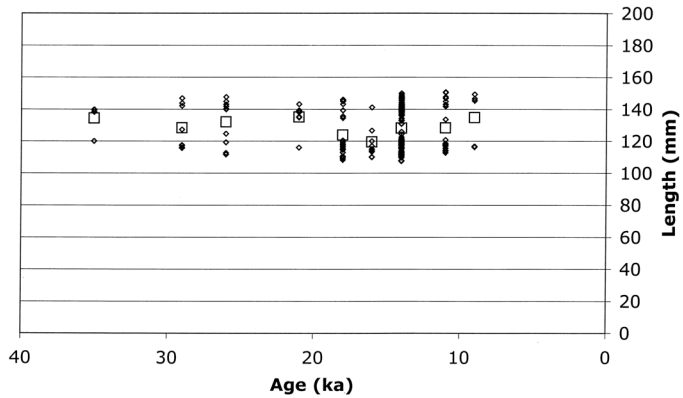


FIGURE 3. Plot of the length of turkey TMTs through time. **Open diamonds** = individual specimens; **large open square** = mean for each pit sample.

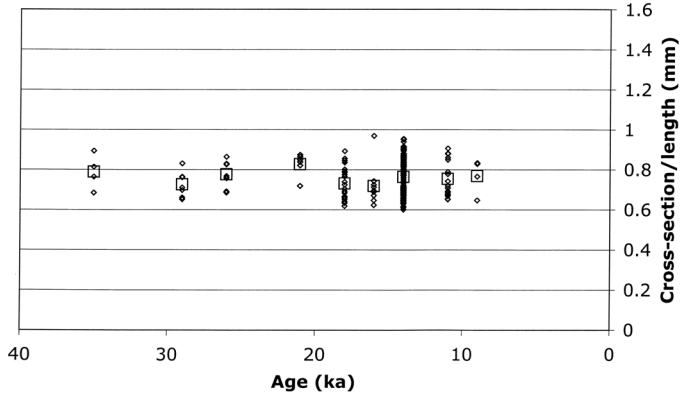


FIGURE 4. Plot of the robustness (midshaft cross-sectional area divided by length) of turkey TMTs through time. Symbols as in Figure 3.

Plots of TMT dimensions through time (Fig. 5) show that the samples fluctuated a bit around a mean, but there is no net trend, nor is there any evidence of the predicted larger size in the samples dated around the glacial maximum at 20 ka, even though our samples range from 35 ka to a Holocene sample from Pit 10 that is only 9 ka in age. Likewise, the robustness of the TMT (Fig. 6) does not change in any significant manner.

These visual impressions of stasis are confirmed by statistical analysis. The Shapiro-Wilk test showed that the samples were all nor-

TABLE 4. Kruskal-Wallis statistics of RLB turkey TMTs. **df** = degrees of freedom; **Signif?** = are the sample differences statistically significant from one another at the 95% confidence level?

Character	K _{obs}	K _{crit}	df	p	0.05	Signif?
Length	10.97	15.507	8	0.20	0.05	no
Proximal width	10.23	14.06	8	0.17	0.05	no
Proximal depth	13.27	15.50	8	0.10	0.05	no

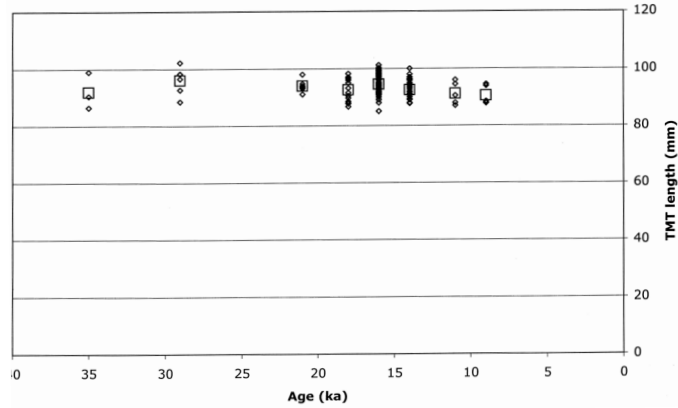


FIGURE 5. Plot of the length of bald eagle TMTs through time. **Open diamonds** = individual specimens; **large open squares** = mean for each pit.

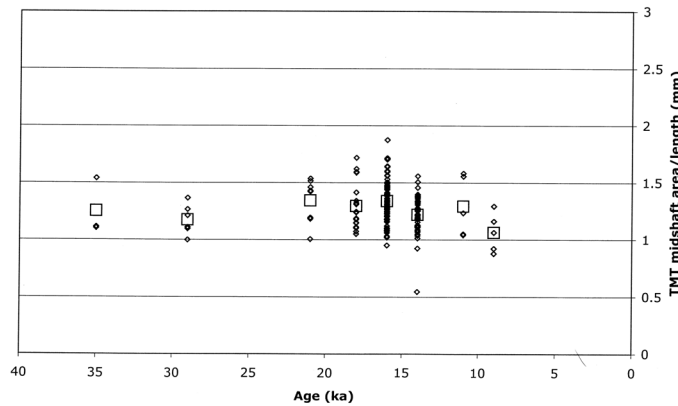


FIGURE 6. Plot of the robustness (midshaft cross-sectional area divided by length) of bald eagle TMTs through time. Symbols as in Figure 3.

mally distributed, so we performed ANOVA on the samples. In each variable (Table 6), the differences between samples are not statistically significant. Even the apparent fluctuation of some of the means is within the range of statistical noise. Thus, there is no statistically significant evidence of size change in bald eagles even during the coldest episodes of the peak glacial at RLB about 20 ka.

DISCUSSION

As the previous analyses of RLB golden eagles (Molina and Prothero, this volume) and condors (Syverson and Prothero, 2010) showed, 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. Even though Howard (1947) thought there was a decrease in size in Holocene eagles (based only on visual inspection of a few specimens, not statistics), Molina and Prothero (this volume) found no evidence for any net size change, even compared to the modern golden eagle population. Thus, it comes as no surprise that some of the other common birds from RLB show no evidence of sensitivity to climate change, either.

TABLE 5. Basic statistics of RLB bald eagle TMTs.

Character	Age (ka)	N	Mean	Variance
Length	9	5	90.5	11.2
	11	5	91.2	15.5
	14	45	92.5	8.8
	16	71	94.5	12.5
	18	19	92.6	16.2
	21	8	94.0	3.9
	29	6	96.0	23.2
Midshaft width	35	3	92.0	40.8
	9	5	10.9	0.6
	11	5	11.5	2.9
	14	45	11.4	1.2
	16	71	12.3	1.4
	18	19	11.9	2.1
	21	8	12.1	1.1
Midshaft depth	29	6	12.0	0.7
	35	3	11.9	5.1
	9	5	8.7	0.8
	11	5	10.1	0.3
	14	45	9.8	0.7
	16	71	10.2	0.6
	18	19	9.9	0.5
	21	8	10.3	0.6
	29	6	9.3	0.6
	35	3	9.6	0.5

TABLE 6. ANOVA of dimensions of bald eagle TMTs. Degrees of freedom = 7.

Variable	F	F _{critical}	p	Significant
Maximum length	1.88	2.07	0.007	No
Midshaft width	2.01	2.07	0.005	No
Midshaft depth	2.06	2.07	0.002	No

This is particularly surprising in the case of the golden eagles (Molina and Prothero, this volume) and the bald eagles and caracaras (this paper), both of which exhibit strong clinal variation in size over latitude following Bergmann’s rule (Brown, 1968; Johnsgard, 1990). Yet at RLB, even conditions of coniferous forests and frequent snow at 20 ka did not cause measurable increases in body size in either eagle.

This trend is also consistent with nearly all the larger mammals of RLB, which also show no response in size or shape change during the maximum climatic changes of the past 35,000 years (Prothero and Raymond, 2008; Prothero et al., 2009; DeSantis et al., this volume; Raymond and Prothero, this volume). It is also consistent with numerous studies (Barnosky, 1994, 2005) that document stasis in just about every Pleistocene mammal lineage, despite the fact that 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.

The general phenomenon of stasis despite changes in environment has long been a puzzle to both paleontologists and neontologists, and 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. Neontological models like stabilizing selection (Estes and Arnold, 2007) are clearly inapplicable and fail to explain this phenomenon, since the environment is changing not stabilizing (Lieberman and Dudgeon, 1996). For a long time, models of developmental canalization were invoked 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 in fact the record spans tens to hundreds of thousands of years. If the Galapagos finch model is to be taken seriously, evolutionary changes can occur in a matter of years or decades.

The currently popular model for long-term stasis is the notion that most organisms have large geographic ranges in which they are adapted to a wide spectrum of local environments, and thus do not require much morphological change to adapt to most environmental changes (Eldredge, 1989; Lieberman et al., 1995; Lieberman and Dudgeon, 1996; Eldredge et al., 2005). This might be appropriate for the larger birds like the eagles that range all over North America and Europe, but not for the smaller birds, some of which live in very small areas. Unfortunately, the sample of smaller birds at RLB is insufficient to test

this hypothesis. Likewise, it is not consistent with the size variation due to colder climates seen in bald eagles, golden eagles, and caracaras. In the case of small mammals of the late Pleistocene, there is stasis through climate changes as well (Barnosky, 2005), as well as the small mammal populations during the late Eocene-Oligocene climate changes (Prothero and Heaton, 1996). Thus, a comprehensive explanation for stasis in the face of dramatic climate changes still eludes us, and much further research is required.

CONCLUSIONS

Statistical analysis of size and shape variables of the common birds of RLB, including the caracara, bald eagle, and turkey, shows no evidence of size or shape 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 despite their well-known tendency to follow Bergmann's rule (Molina and Prothero, this volume), and in condors as well (Syverson and Prothero,

2010). It is consistent with the fact that nearly all RLB mammals show complete stasis over the last 40,000 years of climatic change, a phenomenon that is still not well explained. Although the models of stasis due to wide geographic spread and environmental flexibility might explain stasis in the larger mammals and birds, it does not yet explain why environmentally restricted mammals and birds with small body sizes and home ranges also demonstrate stasis.

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