

## STASIS IN LATE QUATERNARY GOLDEN EAGLES FROM LA BREA TAR PITS OVER THE LAST GLACIAL-INTERGLACIAL CYCLE

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**Abstract**—Late Quaternary fossils from Rancho La Brea span 35,000 years of climate change from the last glacial-interglacial cycle, and a major change in ecology as the larger Pleistocene mammals vanished about 10,000–11,000 years ago. According to conventional Neo-Darwinian evolutionary theory, the effects of this instability should be seen as morphological changes in the most commonly preserved bird, the golden eagle, *Aquila chrysaetos*. Five variables each were measured on over 600 well-preserved tarsometatarsi from the Page Museum at Rancho La Brea, and the same measurements were taken from a sample of 63 extant golden eagles. Change in size and shape over time was evaluated through bivariate comparisons of the tarsometatarsi in the Pleistocene and extant golden eagles, using ANOVA to test for significance of differences. The data show no statistically significant change in size or shape during the Pleistocene (35 Ka to 10 Ka), even though living golden eagles show increased body size in colder climates at higher latitudes (Bergmann's Rule). *Aquila chrysaetos* experienced evolutionary stasis in spite of the change of food resources and the climatic changes of the most recent glacial-interglacial cycle.

### INTRODUCTION

The prevailing model of evolutionary theory views organisms as delicately sensitive and responsive to changes of their environment. As exemplified by the classic studies on Galapagos finches (Weiner, 1995; Grant and Weiner, 1999; Grant and Grant, 2007), bird evolution is commonly portrayed as constant small-scale adaptations of size and morphology in response to climate and other environmental factors. 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.

However, the challenge of the “punctuated equilibrium” model of evolution (Eldredge and Gould, 1972) and the subsequent development of that theory suggests a very different model of evolution. The consensus of hundreds of studies (Jackson and Cheetham, 1999; Jablonski, 2000, 2008; Gould, 2002; Geary, 2009; Hallam, 2009; Princehouse, 2009; Ruse and Sepkoski, 2009) is that most fossil metazoans show evolutionary stasis, rather than gradual evolution, over geologic spans of time. More importantly, many studies (e.g., Coope, 1979; Davis, 1983; Bennett, 1990; Valentine and Jablonski, 1993; Prothero and Heaton, 1996; Prothero, 1999) have demonstrated that most groups of organisms are static in size and morphology despite the environmental pressures of climatic changes. Morphological stasis over millions of years despite strong environmental selection pressures is still an important unresolved issue in evolutionary biology, as even Mayr (1992, 2001) conceded.

This study investigates the effects of the variable climate and ecology of the Quaternary on the North American golden eagle (*Aquila chrysaetos*) beginning in the late Pleistocene and continuing to the present. The Rancho La Brea (RLB) tar pits have produced one of the most plentiful and well-preserved fossil collections representing the late Pleistocene flora and fauna of North America. The unique geologic setting of sands and clays permeated with asphalt produced ideal conditions for preserving over 3 million plant and animal fossils of the late Pleistocene (Akersten et al., 1983; Stock and Harris, 1992; Friscia et al., 2008). The extraordinary preservation of these fossils and the detailed paleoecological reconstruction for the area allows for paleontologic study of the effects of changing climate on the variability in dozens of different species of mammals and birds.

In addition, the majority of the fossils at RLB are well dated by

radiocarbon methods (Marcus and Berger, 1984; O'Keefe et al., 2009). The climatic record from RLB is also excellent and well dated (Warter, 1976; Coltrain et al., 2004; Ward et al., 2005). These ages allow us to examine climatic changes represented by the stratigraphic intervals previously defined by Gardner et al. (1997): the oxygen-isotope stage 3 (OIS 3; 59–24 Ka), last glacial interval (LGI; 24–14 Ka), glacial-interglacial transition (GIT; 14–10 Ka), and Holocene (10–0 Ka). Heusser (1998) detailed the climate change intervals by correlating pollen analysis in nearshore sediment cores from the California Current system to changes in the North Pacific circulation patterns in the ocean and troposphere. Her analysis shows that over the past 59 Ka, southern California has transitioned from oak and chaparral vegetation to pine-juniper-cypress woodlands during OIS 3, peak juniper and closed-cone pine during LGI, a return to dominant oak-chaparral and coastal sagebrush with pulses of alder in the GIT, and the modern environment of increasing oak-chaparral-herbaceous vegetation in the Holocene. In particular, the prevalence of closed-cone pines and junipers in the LGI (comparable to the vegetation of the present-day mountains in southern California) suggests much cooler, even snowy conditions during the winter, which does not happen at RLB elevations today. Stable isotope analysis performed by Coltrain et al. (2004) also notes increases in seasonal aridity in the southern California region during the last interglacial and previous glacial.

The rapidity of these changes and the underlying environmental instability since the last glacial interval pose the question of how such climate change would affect the local fauna. Modern evolutionary theory suggests that drastic changes in climate would, over time, be recorded in the size and morphology of a species. The golden eagle, *Aquila chrysaetos*, is the most abundant species of bird found at RLB (Howard, 1930, 1962) and so is a natural choice for such a study (Fig. 1). Although large eagles are relatively rare birds today, the tar seeps must have been frequently baited with mammals and turkeys (Bochenski and Campbell, 2006) and trapped a disproportionate number of eagles as a result (especially their lower leg bones). The Falconiformes represent about 60% of the avifauna in RLB deposits, with Accipitridae making up 68.8% of Falconiformes. Based on a census of the most common bones, *A. chrysaetos* is represented by a MNI (minimum number individuals) of 960 (Howard, 1930, 1962; Marcus and Berger, 1984). Previous studies on RLB *A. chrysaetos* are confined mostly to a short paper by Miller (1911) and work by Howard. She compared several elements of the Pleistocene *Aquila* to the modern species (Howard, 1930, 1932, 1947a, b).

In this study, we will test the hypothesis that golden eagles change in size or shape (especially becoming larger in cold glacial times following Bergmann's Rule) during the last 35,000 years of climate change at Rancho La Brea.

## MATERIALS AND METHODS

**Sampling and Measurement:** The most common and best-preserved element of *Aquila chrysaetos* was the right tarsometatarsus (TMT), the main lower leg bone (Fig. 1). Although nearly every other bone of the eagle skeleton is also represented in the Page Museum collections, most are not common enough in well-dated pits to give statistically useful samples at enough different temporal levels. We measured a total of 753 TMTs including over 690 Pleistocene specimens at the Page Museum, and 63 Recent specimens from the Natural History Museum of Los Angeles County (LACM), the Santa Barbara Natural History Museum (SBNHM), and the University of California Museum of Vertebrate Zoology (UCMVZ). Total number of specimens of each age are summarized in Table 1.

Measurements were taken using a handheld dial caliper with 0.01 mm accuracy. Five variables were measured on the tarsometatarsi: the total length, the proximal width, the midshaft width and depth, and the distal width. Measurement landmarks and protocols were adapted from Bochenski and Campbell (2006) who analyzed the osteology of the La Brea turkey, *Meleagris californica*.

All available adult *Aquila* right TMT elements were included in the study, with the exception of those that were not catalogued, or those that were juveniles or too damaged to produce accurate data. Most of the bones were very well preserved, since the TMT is one of the most robust bones in the bird skeleton. Only about 50-80 whole specimens were not catalogued and about 100-150 specimens were too damaged to measure.

**Statistical Analysis:** After the measurements were taken, we then searched the Page Museum records for the pit number, and determined the radiocarbon age of the pit sample using Marcus and Berger (1984) and O'Keefe et al. (2009). A large number of specimens from Pit 16 and most specimens from Pits 1, 67, and 91 were excluded from the data set after the measurements were completed, because these pits yielded mixed or highly variable radiocarbon ages, or the ages of the individual specimens from these pits are uncertain. This reduced to the total number of specimens to about 200, but most pits had at least 10-20 specimens, enough to give a statistical sample.

The 63 Recent specimens were measured along the same five dimensions. Brown (1968) and Johnsgard (1990) note that in *Aquila chrysaetos*, as in most Falconiformes, the females are slightly larger than the males. Bivariate plots of male and female measurements in the extant samples were made to rule out any influence of possible sexual dimorphism on the data range (Fig. 2). Most of the recent eagle specimens did not have the sex recorded, so only 23 of the original 63 specimens could be used. As can be seen from the plot, the differences between male and female specimens are minimal, and not statistically significant, since the two sexes completely overlap. The largest specimens tend to be female and the smallest specimens tend to be male, but there are numerous small females and large males. Bivariate plots of all dimensions of the TMT (length, proximal width, mid-shaft width, mid-shaft depth, and distal width) of the male and female extant *Aquila* show a large overlap in values. Thus, individual fossil specimens cannot be confidently assigned to one gender or the other. Because our study involves large samples of the entire population over time, we do not expect differences due to sexual dimorphism to be important in any case.

After we recorded the measurements, frequency distribution plots were created to determine the normality of the samples. We generated cumulative probability plots and used F statistics to determine if samples were normally distributed. After we determined that the samples were parametric, the mean, standard deviation, and coefficient of variation were computed to give a sense of central tendencies and variability of the

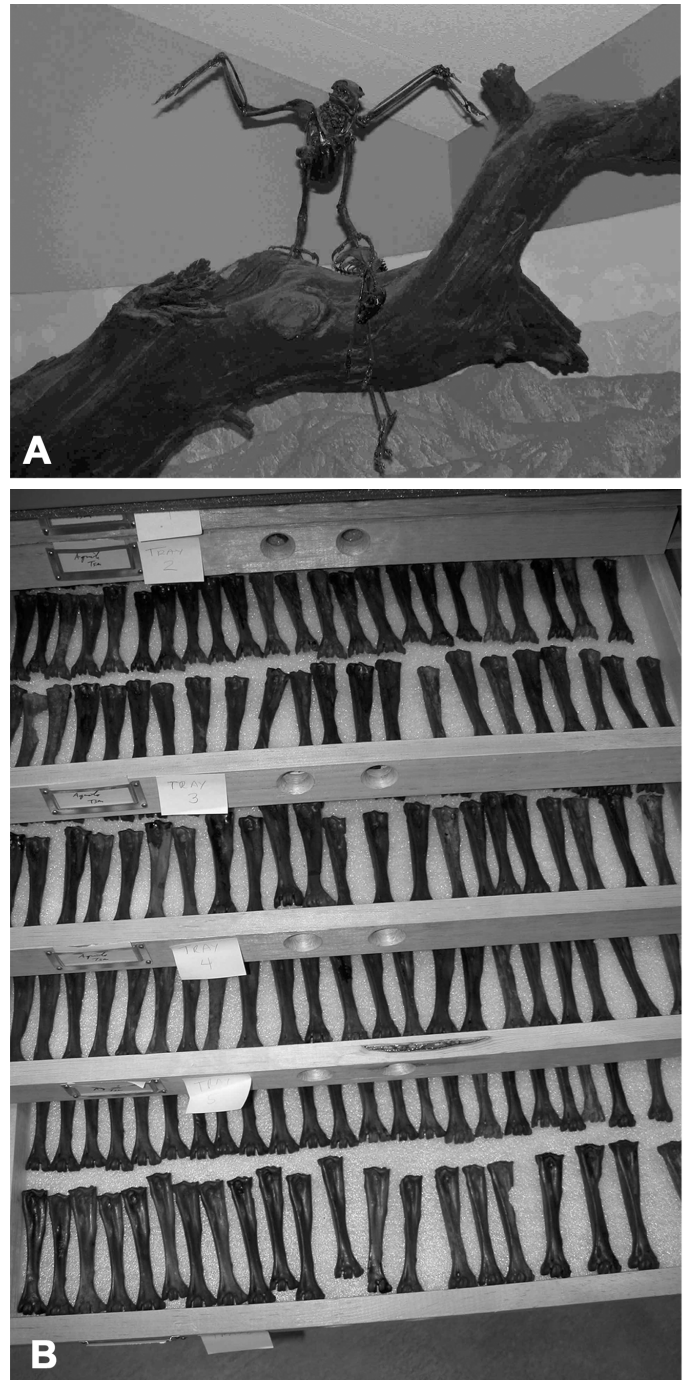


FIGURE 1. A, Mounted specimen of *Aquila chrysaetos* in the Page Museum. B, Photograph of representative drawers of the *Aquila* sample in the Page Museum, showing just a few of the many drawers, each containing over a hundred bones.

samples (Table 1). ANOVA was then performed, testing for heterogeneity among the means of samples of different ages (Table 2).

## RESULTS

Using the F-test, we found that all the samples were normally distributed, and determined that the samples had statistically equal variances as well. Of the well-dated samples, mean values for each dimension are listed in Table 1 along with the corresponding standard deviation, and the radiocarbon age of each sample. Standard deviations are similar for all age groups. Coefficients of variation range from 1.672-11.34 across all

TABLE 1. Mean and standard deviation (in parentheses following mean) for each measurement grouped by radiocarbon age of the pit sample. **Abbreviations:** L = length; n = number of specimens; PW = proximal width; MW = midshaft width; MD = midshaft depth; DW = distal width. All measurements in mm.

Age (ka)	n	L	PW	MW	MD	DW
0	63	101.75 (3.5)	22.57(1.4)	12.90(1.2)	11.16(0.7)	24.76 (1.5)
9	20	98.05 (2.7)	21.29(1.4)	11.0 (0.7)	9.71(1.1)	23.43 (1.9)
12	43	97.56 (2.2)	21.22(1.4)	11.0 (0.7)	9.89(0.7)	23.94 (1.2)
14	98	98.10 (2.5)	21.05(1.2)	10.95(1.0)	9.77(0.9)	23.26 (1.2)
15	16	97.38 (1.6)	21.31(1.2)	10.94(0.9)	10.06(0.7)	23.50 (1.1)
23	36	99.14 (2.6)	21.54(1.4)	11.19(0.8)	9.97(0.7)	23.84 (1.3)
28	1	95.00 (0)	20.00 (0)	11.00(0)	10.00(0)	23.00 (0)
35	11	99.33 (3.1)	21.08(1.2)	11.0 (0.9)	9.92(0.9)	23.58 (1.5)

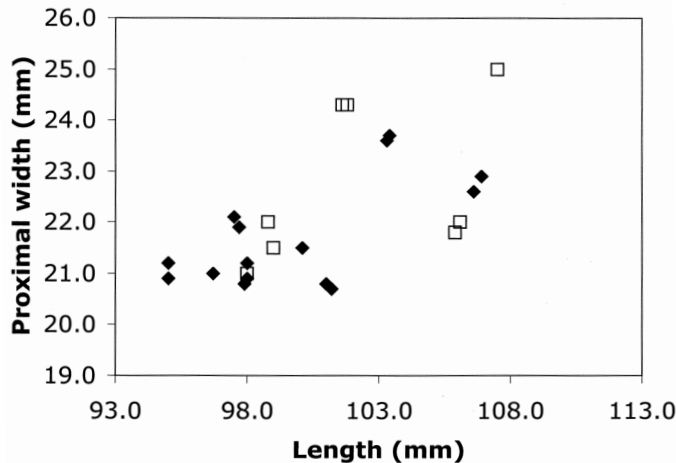


FIGURE 2. Plot showing the length and proximal width of Recent male and female golden eagle TMTs. Males are indicated with solid diamonds; females with open squares. Although the largest individuals are female and the smallest ones are males, the two sexes overlap completely, so there is no way to reliably estimate the sex of fossil specimens.

dimensions, but most fall in the range of 5-6, which is within the range of a single species for most vertebrate populations (Kurtén, 1953; Simpson et al., 1960; Yablokov, 1974; Plavcan and Cope, 2001).

The samples meet all the conditions required for analysis of variance (ANOVA), because the variables are independent, normally distributed, and have equal variances. We conducted a one-way ANOVA, comparing dimensions of each bone from all the pits to see if there were significant differences in the mean (null hypothesis is that the means are not significantly different). If just the RLB samples are compared, then the  $F$  value was always smaller than the  $F$ -critical value, and the null hypothesis was accepted (Table 2). In other words, among the RLB samples none of the sample means are significantly different from the others. The  $p$  values, however, are often larger than the cutoff value of 0.05, so they are not significant at the 95% confidence level.

However, if the Recent specimens are added to the total sample, then each value of  $F$  is greater than  $F$ -critical (Table 2), suggesting that the modern golden eagle TMTs are significantly different from the means of the RLB specimens. In addition,  $p$  values are all much less than 0.05, indicating that this result is significant at the 95% confidence level. This is consistent with the fact that the means of most of the modern samples (Fig. 3A-B) are slightly larger than the trend of the means of RLB samples.

We evaluated shape by using a ratio of the TMT length to the midshaft width to determine if the bones became more or less robust through time. We also conducted a one-way ANOVA analysis of the change in this ratio through time. First, the ANOVA of the RLB samples showed that there were no significant differences among the ratios within the sequence (Table 3, Fig. 4). Adding the modern sample to the total data set did not change the result, so the ratio of TMT length/width is not significantly different between extant eagles and the RLB samples either.

TABLE 2. Single-factor ANOVA results comparing temporally sequential samples of *Aquila* TMTs to determine whether the different pit samples have significantly different means (null hypothesis = no difference in mean).  $df$  = degrees of freedom (6 for Pleistocene only, 7 for Pleistocene plus Holocene samples).  $P$  level = 0.05. RLB only = Pleistocene samples; Plus modern = Pleistocene plus Recent specimens.

	$F$	$F_{critical}$	$P$
<b>LENGTH</b>			
RLB only	0.740	2.320	0.595
Plus modern	3.480	2.174	0.003
<b>PROXIMAL WIDTH</b>			
RLB only	0.979	2.320	0.435
Plus modern	5.023	2.174	0.000
<b>MIDSHAFT WIDTH</b>			
RLB only	0.587	2.320	0.709
Plus modern	4.565	2.174	0.000
<b>MIDSHAFT DEPTH</b>			
RLB only	0.962	2.320	0.445
Plus modern	8.286	2.174	0.000
<b>DISTAL DEPTH</b>			
RLB only	0.643	2.320	0.667
Plus modern	3.845	2.174	0.002

## DISCUSSION

Our analysis of data has revealed no statistically significant changes in size or shape between 35 Ka and 10 Ka, suggesting morphological stasis of *Aquila chrysaetos* during the late Pleistocene. As shown by ANOVA, there are no significant differences in the means between samples dated at 32 Ka right up to 10 Ka. However, the Holocene samples are significantly different from those of the late Pleistocene. Howard (1947b) claimed (based on visual inspection of a few samples lumped from many pits without any radiocarbon-dated age sequence or adequate quantitative analysis of enough specimens) that the leg bones of modern *Aquila* are on average smaller than those from RLB. Our modern samples were slightly larger, even if this was barely statistically significant in the ANOVA.

Howard (1947b) also claimed that the skulls of RLB *Aquila* were more robust and had sturdier maxillae and mandibles, suggesting that they ate larger prey during the Pleistocene. We did observe some tendency toward robustness among the RLB skulls, although the differences were very slight when compared to modern *Aquila chrysaetos* skulls. We found no easy way to measure or quantify this difference that would show whether it was statistically significant. We looked at a number of skulls, but found that the degree of robustness overlapped completely between RLB and modern specimens. In addition, the sample of well-preserved RLB and recent skulls is very small, so it would be hard to calculate significance on a pit-by-pit basis. The hypothesis that the RLB *Aquila* skulls are more robust than modern golden eagle skulls cannot be rigorously evaluated at this time.

This stasis in size and shape of limb bones among RLB eagles is surprising, considering how much cooler, snowier and forested the region became during the LGI. Golden eagles have considerable clinal variation,

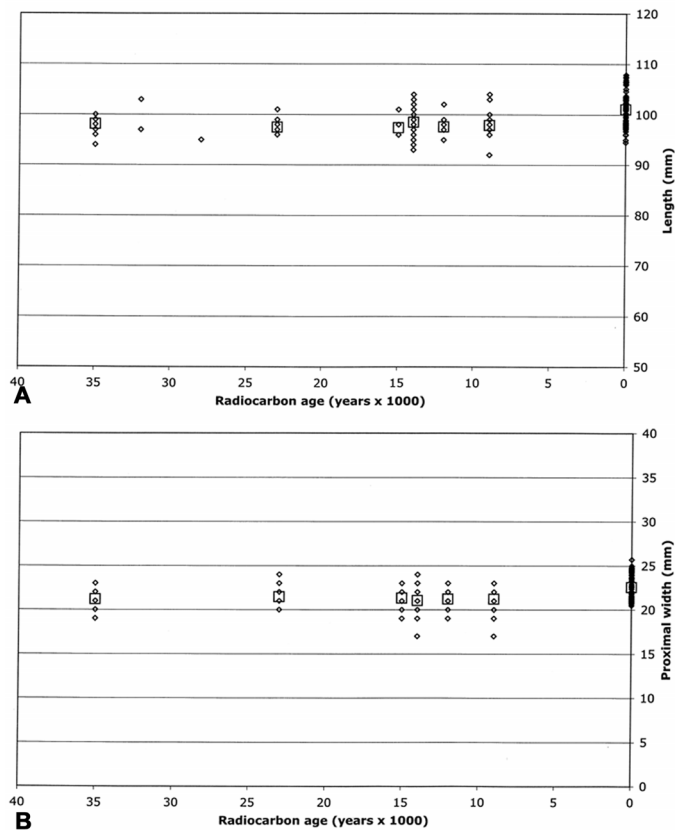


FIGURE 3. Plots of dimensions of golden eagle TMTs against the age of the pit sample. Open diamonds indicate individual specimens; large open squares are the means for each time interval. **A**, Length. **B**, Proximal width.

TABLE 3. Single-factor ANOVA results comparing temporally sequential samples of the ratio of TMT length to midshaft depth to determine whether the different pit samples have significantly different ratios of robustness (null hypothesis = no difference in mean). df = degrees of freedom. *P* level = 0.05. RLB only = Pleistocene samples; Plus modern = Pleistocene plus Recent specimens.

	df	<i>F</i> value	<i>F</i> critical	<i>P</i> value
RLB only	5	0.723	2.336	0.608
Plus modern	6	0.967	1.172	0.450

following Bergmann's rule of larger more robust body sizes in higher latitudes and colder climates (Brown, 1968; Johnsgard, 1990). The subspecies *Aquila chrysaetos canadensis* is found in northern Canada and Alaska and weighs up to 9 kg (normal temperate latitude subspecies weigh 2.5-7 kg) with body lengths of 102 cm (temperate species are 65-95 cm in length) (Brown, 1968; Johnsgard, 1990). Likewise, the subspecies *Aquila chrysaetos daphanea*, which is found in Siberia, northern China, Manchuria, and Kazakhstan, is the largest subspecies in the Old World. Because the climatic data show that the RLB area had a closed-cone coniferous forest with seasonal snowfall during the LGI, one would expect eagles of larger body size during that time, or maybe the migration of the cline southward to bring larger, cold-adapted populations into the region. Indeed, large, cold-adapted eagles such as *Aquila chrysaetos bonifaci* have been reported from the middle Pleistocene of France, and the late Pleistocene *Aquila chrysaetos simurgh* from Crete was even

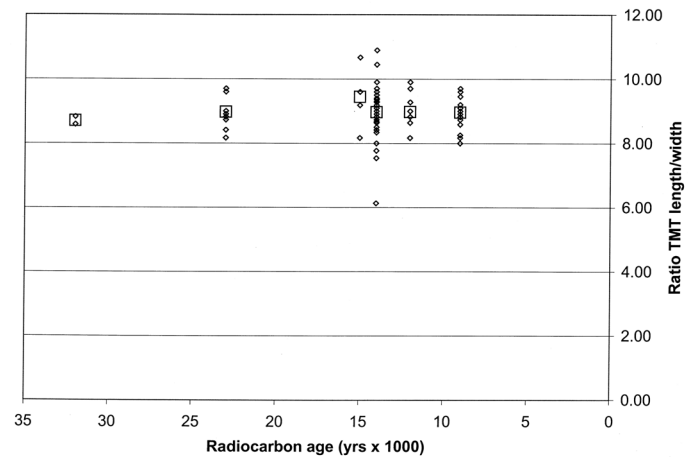


FIGURE 4. Plot of ratios of TMT length to midshaft depth against the age of the pit sample. Large open squares indicate mean of temporal sample; solid diamonds are individual data points.

larger (Sanchez Marco, 2004). Instead, at RLB there was no apparent response to the increase in cold weather, boreal forests, and snowier conditions.

Stasis seems to be a widespread phenomenon among Pleistocene large mammals as well, even though they lived in a time of rapid climatic change and rapidly changing vegetation and habitats (Barnosky, 1994, 2001, 2005; Lister, 2004). As part of this study, a group of us (Prothero et al., 2009) have undertaken a program of measuring all of the common and well-dated mammals and birds from RLB, and subjecting these data to rigorous statistical analysis, using only samples from well-dated pits. Preliminary results indicated that all the common large mammal species (horses, bison, camels, ground sloths, dire wolves, saber-toothed cats, and American lions) show complete stasis through the entire late Pleistocene until they vanished at the end of the Pleistocene. Among birds, a similar degree of stasis is seen in turkeys (*Meleagris californica*), bald eagles (*Haliaeetus leucocephalus*), and caracaras (*Caracara plancus prelutosus*) (Fragomeni and Prothero, this volume).

By contrast, the RLB condor, *Gymnogyps amplus*, is static through the entire late Pleistocene, but then becomes significantly smaller as it evolved to become the living California condor, *G. californicus* (Syverson and Prothero, 2010). Yet there is no evidence that the Holocene eagles became smaller when the megafauna disappeared, as Howard (1947b) argued. If anything, they became slightly larger sometime during the Holocene (since the early Holocene samples at 9 Ka are the same size as Pleistocene samples, and slightly smaller than the Recent specimens). This suggests that golden eagles did not respond to the major difference in ecology and prey species as the Pleistocene ended and the large mammals vanished, as has been proposed for the condors of the late Pleistocene-Holocene.

A number of different attempts have been made to explain such stasis in the face of major climatic and ecological change. Clearly, neontological concepts such as "stabilizing selection" (Estes and Arnold, 2007) are not applicable, because paleontological stasis operates on thousand-year to million-year time scales, and also the environment is changing, not stabilizing (Lieberman and Dudgeon, 1996). Many biologists have suggested that long-term stasis might be due to developmental constraints and canalization (Eldredge and Gould, 1972), but the reality is that recent organisms (such as domesticated dogs) are capable of a great deal of variability and do not seem fully constrained by canalization in development (Gould, 2002; Eldredge et al., 2005). Bennett (1990, 1997) argued that Pleistocene species might be more stable because the climate changes of the glacial-interglacial cycles were too rapid for long-term adaptation, but these glacial-interglacial cycles take tens of thousands of years to cycle, well beyond normal biological time scales. In

addition, this is not consistent with the idea from the Galapagos finch studies that birds can change in a matter of years and decades in response to small-scale climatic change.

A currently popular mechanism is the idea that widespread organisms are broken into many geographic subpopulations with a wide range of ecological tolerances, so that no matter how severe the local environmental changes are, there are places that are suitable (Eldredge, 1989; Lieberman et al., 1995; Lieberman and Dudgeon, 1996; Eldredge et al., 2005). This may be applicable to the golden eagle, which is distributed all over Holarctica with significant geographic variation (Brown, 1968; Johnsgard, 1990). However, environments changed all over Holarctica during glacial advances and interglacial retreats, so it is hard to argue that there were large areas of refugia that were unchanged during the Pleistocene and Holocene. In addition, there was a striking change in the ecosystem when the megamammals vanished in the end of the Pleistocene, yet the late Pleistocene RLB specimens are statistically indistinguishable from the early Holocene (9 Ka) specimens. If there was any change in golden eagles in the western U.S. at all, it came during the Holocene (between 9 Ka and present), judging from our data (Fig. 3A-B).

This is similar to what was noted by Syverson and Prothero (2010). In that study, the large RLB condors (*Gymnogyps amplus*) also did not immediately shrink in size in the early Holocene when the megamammal prey and carrion vanished, but may have lasted well into the Holocene, or even overlapped in time with modern California condors.

Finally, the idea that animals had broad geographic ranges with many suitable subhabitats that buffered them against environmental change does not work for smaller vertebrates, many of which show just as prolonged episodes of stasis during major climatic change as do the larger vertebrates (e.g., Prothero and Heaton, 1996; Barnosky, 2005; Blois et al., 2010, and studies cited therein).

## CONCLUSION

Although previous authors have suggested that the RLB golden eagles were slightly larger and more robust than modern *Aquila chrysaetos*, this conclusion is not borne out by a rigorous statistical analysis of well-dated samples from sequential pits through the entire span of the RLB sequence. The RLB eagle skulls may have been more robust and strongly built than modern golden eagles, but this is impossible to evaluate since the differences are subtle, hard to quantify, and the sample sizes are too small to rigorously test this hypothesis. In contrast to the size reduction in the La Brea condor, there is no similar size reduction in eagles when Holocene climate began and the megafaunal influence on the ecosystem vanished. Thus, the golden eagles are good examples of a species that is completely static despite major changes in climate, ecology and prey species between 35 Ka and 9 Ka. Such stasis might be explained by the idea that golden eagles are very generalized predators that live over a wide range of habitats on a worldwide scale, and are not responsive to small-scale local changes in environment. This may be true, but it is surprising, since golden eagles demonstrate a tendency toward larger-sized subspecies in high latitudes. In addition, it is very interesting that (unlike the condors) the eagle showed no apparent response to the global changes of climate at the end of the Pleistocene, nor to the major change in the ecosystem when the Pleistocene megamammals vanished.

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## REFERENCES

- Akersten, W.A., Shaw, C.A. and Jefferson, G.T., 1983, Rancho La Brea: status and future: *Paleobiology*, v. 9, p. 211-217.
- Barnosky, A.D., 1994, Defining climate's role in ecosystem evolution: clues from late Quaternary mammals: *Historical Biology*, v. 18, p. 173-190.
- Barnosky, A.D., 2001, Distinguishing the effects of the Red Queen and Court Jester on Miocene mammal evolution in the northern Rocky Mountains: *Journal of Vertebrate Paleontology*, v. 21, p. 172-185.
- Barnosky, A.D., 2005, Effects of Quaternary climatic change on speciation of mammals: *Journal of Mammalian Evolution*, v. 12, p. 247-264.
- Bennett, K.D., 1990, Milankovitch cycles and their effects on species in ecological and evolutionary time: *Paleobiology*, v. 16, p. 11-21.
- Bennett, K.D., 1997, *Evolution and ecology: the pace of life*: Cambridge, Cambridge University Press, 260 p.
- Blois, J.L., McGuire, J.L. and Hadly, E.A., 2010, Small mammal diversity loss in response to late Pleistocene climatic change: *Nature*, v. 465, p. 771-775.
- Bochenski, Z.M. and Campbell, Jr., K.E., 2006, The extinct California turkey, *Meleagris californica*, from Rancho La Brea: comparative osteology and systematics: *Contributions in Science, Natural History Museum of Los Angeles County*, v. 509, p. 1-92.
- Brown, L., 1968, *Eagles, hawks, and falcons of the world*: New York, McGraw-Hill, 945 p.
- Coltrain, J.B., Harris, J.M., Cerling, T.E., Ehleringer, J.R., Dearing, M., Ward, J. and Allen, J., 2004, Rancho La Brea stable isotope biogeochemistry and its implications for the palaeoecology of the late Pleistocene, coastal southern California: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 205, p. 199-219.
- Coope, G.R., 1979, Late Cenozoic fossil *Coleoptera*: evolution, biogeography, and ecology: *Annual Reviews of Ecology and Systematics*, v. 10, p. 247-267.
- Davis, M., 1983, Quaternary history of deciduous forests of eastern North America and Europe: *Annals of the Missouri Botanical Garden*, v. 20, p. 550-563.
- Eldredge, N., 1999, *The pattern of evolution*: New York, W.H. Freeman, 219 p.
- Eldredge, N. and Gould, S.J., 1972, Punctuated equilibria: an alternative to phyletic gradualism; in Schopf, T.J.M., ed., *Models in paleobiology*: San Francisco, Freeman, p. 82-115.
- Eldredge, N., Thompson, J.N., Brakefield, P.M., Gavrilits, S., Jablonski, D., Jackson, J.B.C., Lenski, R.E., Lieberman, B.S., McPeck, M.A. and Miller III, W., 2005, The dynamics of evolutionary stasis: *Paleobiology*, v. 31, p. 133-145.
- Estes, S. and Arnold, S.J., 2007, Resolving the paradox of stasis: models with stabilizing selection explain evolutionary divergence on all timescales: *American Naturalist*, v. 169, p. 227-244.
- Frischia, A.R., Van Valkenburgh, B., Spencer, L., and Harris, J.M., 2008, Chronology and spatial distribution of large mammal bones in Pit 91, Rancho La Brea: *Palaio*, v. 23, p. 35-42.
- Gardner, J.V., Dean, W.E. and Dartnell, P., 1997, Biogenic sedimentation beneath the California Current system for the past 30 kyr and its paleoceanographic significance: *Paleoceanography*, v. 12, p. 207-225.
- Geary, D.H., 2009, The legacy of punctuated equilibrium; in Allmon, W.D., Kelley, P.H. and Ross, R.M., eds., *Stephen Jay Gould: reflections on his view of life*: Oxford, Oxford University Press, p. 127-147.

- Gould, S.J., 2002, *The structure of evolutionary theory*: Cambridge, Harvard University Press, 1464 p.
- Grant, P.R. and Weiner, J., 1999, *The ecology and evolution of Darwin's finches*: Princeton, Princeton University Press, 512 p.
- Grant, P.R. and Grant, B.R., 2007, *How and why species multiply: the radiation of Darwin's finches*: Princeton, Princeton University Press, 256 p.
- Hallam, A., 2009, The problem of punctuational speciation and trends in the fossil record; in Sepkoski, D. and Ruse, M., eds., *The paleobiological revolution*: Chicago, University of Chicago Press, p. 423-432.
- Heusser, L., 1998, Direct correlation of millennial-scale changes in western North American vegetation and climate with changes in the California Current system over the past 60 kyr: *Paleoceanography*, v. 13, p. 252-262.
- Howard, H., 1930, A census of the Pleistocene birds of Rancho La Brea from the collections of the Los Angeles County Museum: *The Condor*, v. 32, p. 81-88.
- Howard, H., 1932, Eagles and eagle-like vultures of the Pleistocene of Rancho La Brea: *Carnegie Institute of Washington, Publication 429*, p. 1-82.
- Howard, H., 1947a, A preliminary survey of trends in avian evolution from Pleistocene to recent time: *The Condor*, v. 49, p. 10-13.
- Howard, H., 1947b, An ancestral Golden Eagle raises a question in taxonomy: *The Auk*, v. 64, p. 287-291.
- Howard, H., 1962, A comparison of avian assemblages from individual pits at Rancho La Brea, California: *Contributions in Science, Natural History Museum of Los Angeles County*, v. 58, p. 1-24.
- Jablonski, D., 2000, Micro- and macroevolution: scale and hierarchy in evolutionary biology and paleobiology: *Paleobiology*, v. 26, p. 15-52.
- Jablonski, D., 2008, Species selection: theory and data: *Annual Review of Ecology, Evolution, and Systematics*, v. 39, p. 501-524.
- Jackson, J.B.C. and Cheetham, A.H., 1999, Tempo and mode of speciation in the sea: *Trends in Ecology and Evolution*, v. 14, p. 72-77.
- Johnsgard, P.A., 1990, *Hawks, eagles, and falcons of North America*: Washington, D.C., Smithsonian Institution Press, 408 p.
- Kurtén, B., 1953, On variation and population dynamics of fossil and recent mammal populations: *Acta Zoologica Fennica*, v. 76, p. 1-122.
- Lieberman, B.S. and Dudgeon, S., 1996, An evaluation of stabilizing selection as a mechanism for stasis: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 127, p. 229-238.
- Lieberman, B.S., Brett, C.E. and Eldredge, N., 1995, A study of stasis and change in two species lineages from the Middle Devonian of New York State: *Paleobiology*, v. 21, p. 15-27.
- Marcus, L.F. and Berger, R., 1984, The significance of radiocarbon dates for Rancho La Brea; in Martin, P.S. and Klein, R.G., eds., *Quaternary extinctions: a prehistoric revolution*: Chicago, University of Chicago Press, p. 159-188.
- Mayr, E., 1992, Speciation evolution or punctuated equilibria; in Somit, A. and Peterson, S.A. eds., *The dynamics of evolution: the punctuated equilibrium debate in the natural and social sciences*: Ithaca, Cornell University Press, p. 21-53.
- Mayr, E., 2001, *What evolution is*: New York, Basic Books, 192 p.
- Miller, L.H., 1911, A series of eagle tarsi from the Pleistocene of Rancho La Brea: *University of California Publications, Bulletin of the Department of Geology*, v. 6, p. 305-316.
- O'Keefe, F.R., Fet, E.V. and Harris, J.M., 2009, Compilation, calibration, and synthesis of faunal and floral radiocarbon dates, Rancho la Brea, California: *Contributions in Science, Natural History Museum of Los Angeles County*, v. 518, p. 1-16.
- Plavcan, J.M. and Cope, D.A., 2001, Metric variation and species recognition in the fossil record: *Evolutionary Anthropology*, v. 10, p. 204-222.
- Princehouse, P., 2009, Punctuated equilibrium and speciation: what does it mean to be a Darwinian?; in Sepkoski, D. and Ruse, M., eds., *The paleobiological revolution*: Chicago, University of Chicago Press, p. 149-175.
- Prothero, D.R., 1999, Does climatic change drive mammalian evolution?: *GSA Today*, v. 9, p. 1-5.
- Prothero, D.R. and Heaton, T.H., 1996, Faunal stability during the early Oligocene climatic crash: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 127, p. 239-256.
- Prothero, D.R., Raymond, K.R., Syverson, V.J. and Molina, S., 2009, Stasis in late Pleistocene birds and mammals from La Brea tar pits over the last glacial-interglacial cycle: *Cincinnati Museum Center Scientific Contributions*, v. 3, p. 291-292.
- Sanchez Marco, A., 2004, Avian zoogeographical patterns during the Quaternary in the Mediterranean region and paleoclimatic interpretation: *Ardeola*, v. 51, p. 91-132.
- Sepkoski, D. and Ruse, M., eds., 2009, *The paleobiological revolution*: Chicago, University of Chicago Press, 584 p.
- Simpson, G.G., Roe, A. and Lewontin, R.C., 1960, *Quantitative zoology*: New York, Harcourt Brace and World, 440 p.
- Stock, C. and Harris, J.M., 1992, Rancho La Brea: a record of Pleistocene life in California: *Natural History Museum of Los Angeles County, Science Series*, v. 37, p. 1-113.
- Syverson, V.J. and Prothero, D.R., 2010, Evolutionary patterns in late Quaternary California condors: *PalArch Journal of Vertebrate Paleontology*, v. 7, p. 1-18.
- Valentine, J.W. and Jablonski, D., 1993, Fossil communities: compositional variation at many time scales; in Ricklefs, R.E. and Schluter, D., eds., *Species diversity in ecological communities*: Chicago, University of Chicago Press, p. 341-349.
- Ward, J.W., Harris, J.M., Cerling, T.E., Wiedenhoef, A., Lott, M.J., Dearing, M., Coltrain, J.B. and Ehleringer, J.R., 2005, Carbon starvation in glacial trees recovered from the La Brea tar pits, southern California: *Proceedings of the National Academy of Sciences*, v. 102, p. 690-694.
- Warter, J.K., 1976, Late Pleistocene plant communities - evidence from Rancho La Brea tar pits: *symposium proceedings on the plant communities of southern California*: Native Plant Society, Special Publication 2, p. 32-39.
- Weiner, J., 1995, *The beak of the finch: a story of evolution in our own time*: New York, Vintage, 352 p.
- Yablokov, A.V., 1974, *Variability in mammals*: New Delhi, Amerind Press, 366 p.