

STASIS IN RANCHO LA BREA BLACK VULTURES (*CORAGYPS OCCIDENTALIS*) OVER THE LAST GLACIAL-INTERGLACIAL CYCLE

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Abstract—In textbooks, bird evolution is often modeled on the example of the Galápagos finches, which show rapid responses to climatic change. We studied the sample of Pleistocene black vultures (*Coragyps occidentalis*) from Rancho La Brea to see if they showed size or shape changes in response to the climate changes of the last 35,000 years, including the last complete glacial-interglacial cycle. Although living *Coragyps atratus* shows a slight Bergmann's rule effect, with larger body sizes in colder climates and smaller subspecies in the tropics, the Rancho La Brea *C. occidentalis* showed no statistically significant change over this interval, with no meaningful changes in size or robustness. This was true even during the peak glacial interval at 18,000–20,000 years ago, when the region was covered by coniferous forests and experienced snowy winters. These results are consistent with earlier studies on La Brea condors, golden eagles, bald eagles, turkeys, great horned owls, barn owls, teratorns, and caracaras. In contrast to the Galápagos finches, none of the studied fossil birds from Rancho La Brea respond rapidly to long-term changes in climate in a simple fashion. Instead, they are ecologically flexible and live in a wide range of habitats and climates. The slight increase in body sizes between the youngest Pleistocene sample and the modern *C. atratus* contradicts the assertion that black vultures, like other scavengers at Rancho La Brea, became smaller for dietary reasons as a result of the Pleistocene megafaunal extinctions.

INTRODUCTION

It has been long taught in evolutionary biology that species respond to environmental change, the most notable example being Darwin's Galápagos finches (Weiner, 1995; Grant and Weiner, 1999; Grant and Grant, 2007). In fact, some researchers from Princeton University studied the effects of seed dispersal on the finches and have discovered significant changes in their beaks in as little as a single generation (Weiner, 1995). As a result of the bird's obvious and observable responses to ecological conditions, most scientists consider Darwin's finches to be a classic example of adaptation (Zink, 2002; Weiner, 1995). Adaptation in birds has been observed in response to not only food availability, but climate change as well. From these findings, it would be appropriate to say that the bodies of birds do respond to environmental change.

The rapid evolution of the Galápagos finch, which has allowed it to be observable on human time scales, is a very rare circumstance (Zink, 2002). In fact, most fossil animals show no change over millions of years (Gould, 2002). Darwin wrote that evolution works "silently and insensibly," in his book *On the Origin of Species*: "We see nothing of these slow changes in progress, until the hand of time has marked the lapse of ages" (Weiner, 1995). For a long while, paleontologists have contended with this feature of the fossil record. This phenomenon, known as stasis, is one in which fossil species do not change over extended periods of time, but instead change rapidly in short bursts between long periods of stasis (Eldredge and Gould, 1972; Eldredge, 1999; Gould, 2002). This is true for most fossil species even through periods of environmental change, which according to the simplest concept of adaptation would be expected to coincide with periods of changes in morphology.

The Rancho La Brea (RLB) asphalt seeps in Los Angeles are considered someone of the most important and famous fossil deposits in North America, and are a prominent area of research for Pleistocene animals in the region. The tar pits produce an unusually large and well-preserved sample of fossil birds, with over 85,000 individual bones representing at least 114 extant species and 19 extinct species (Howard, 1962a). The pits not only trapped these birds over several thousands of years, but preserved their delicate skeletal anatomy by allowing natural asphalt to infiltrate their bones, preserving their delicate integrity (Akersten et al., 1983; Coltrain, 2004; Stock and Harris, 1992). Since the various pits have seeped up to the surface actively over different periods of time, they can be identified as corresponding to particular late Pleistocene climate cycles based on radiocarbon dating (Marcus and Berger, 1984; O'Keefe et al., 2009). For the multitude of information that RLB thus presents a wealth of well-dated and well-preserved fossil bird material, it making it a great location in which to

test a hypothesis on morphological adaptations in birds over a timescale of several thousands of years, including through the last glacial maximum from 22–19 ka and the glacial-interglacial cycle deglaciation from 14–10 ka (Coltrain, 2004).

Based upon plant fossils from the tar pits along with an even better record of pollen grains in deep-sea cores just off shore (Heusser, 1998), the climate of southern California changed frequently over many thousands of years. At 59 ka, the region was cloaked in oak and chaparral vegetation. As the climate cooled, it changed to a pine, juniper, and cypress woodland, and by 24 ka, to a juniper-ponderosa forest with winter snow. From 14 to 10 ka, during the glacial-interglacial transition, the landscape returned to dominant oak-chaparral and coastal sagebrush, and since then the region has been vegetated by the modern oak-chaparral-herbaceous assemblage (Heusser, 1998).

According to evidence from previous studies of modern birds, we might expect an Allen's rule or Bergmann's rule effect in RLB birds during a climatic cooling cycle. Allen's rule points out that the appendages of endotherms adapt to be smaller and stouter, relative to body size, in cold climates to aid in heat retention. Evidence for Allen's rule is mostly taken from several cases of known geographic clines within species, where average limb robustness is larger in populations found in colder climates (Symonds, 2010). Bergmann's rule is a similar generalization, which holds that body size tends to be larger in populations that live in colder climates, reducing heat loss via a smaller ratio of surface area to volume. In a particular study testing Bergmann's rule, over 70% of the 94 studied bird species had geographic clines that followed Bergmann's rule, indicating it to be generally true for birds (Meiri and Dayan, 2003).

Modern *Coragyps atratus* exhibits a slight Bergmann's rule effect. The largest subspecies, *C. atratus foetens*, lives mostly in the colder climates of the High Andes, while the smallest subspecies, *C. atratus brasiliensis*, is found in the lower elevations of the Brazilian jungle and the Mexican deserts (Blake, 1953). Fisher (1944), Howard (1962b, 1968), Brodkorb (1964), Steadman and Martin (1984), and Steadman et al. (1994) noted that the Pleistocene *C. occidentalis* was a larger and more robust species than modern *C. atratus*. This size difference was the original basis for separating the Pleistocene species from the modern species. None of these previous studies, however, attempted to document the details of the changes in size or robustness through time.

Although these previous studies on modern birds suggest that climate change may catalyze morphological changes in birds, several previous studies at RLB identified no change in mean size or robustness in golden eagles (Molina and Prothero, 2011), California condors (Syverson and Prothero, 2010), great horned owls (Madan et al., 2015), bald eagles, turkeys, or caracaras (Fragomeni and Prothero, 2011), throughout the past 40,000 years of glaciation and deglaciation. The

most generally accepted explanation for these long periods of stasis is that organisms with large geographic ranges tend to be adapted to a wide range of climates and environments, and thus do not respond morphologically to climate change (Eldredge, 1999; Lieberman and Dudgeon, 1996; Eldredge et al., 2005).

In this study, we will attempt to document the presence or absence of morphological change in black vultures over the last glacial-interglacial cycle by examining the extinct Pleistocene black vulture (*Coragyps occidentalis*) sample from RLB and its modern relative, the black vulture (*Coragyps atratus*). Morphological change would be expected in Pleistocene to modern *Coragyps* based on the applicability of Allen's and Bergmann's rules to *C. atratus* and other modern birds.

METHODS

The tarsometatarsus (TMT) was measured since it is the best represented avian skeletal element in the RLB sample. TMTs are the most robust bones in the avian skeleton and thus have lower odds of being broken or deformed, and they have not been found to differ from other skeletal remains in disarticulated samples (Syverson and Prothero, 2010).

TMT specimens that were identified as adult *C. occidentalis* (based on fusion of the epiphyses) were measured with metric dial calipers, in three dimensions (Fig. 1): maximum shaft length between the foramen beneath each epiphysis; mid-shaft transverse width; and mid-shaft anteroposterior thickness of the TMT. Avian specimens at RLB from different pits are mixed together, so we searched the RLB bird database for each individual specimen to identify the pit they were found in. We excluded data from Pit 16, which has widely scattered radiocarbon ages that prevent it from being useful for this project (Marcus and Berger, 1984; O'Keefe et al., 2009). Modern black vulture (*C. atratus*) TMTs were also measured at the Museum of Vertebrate Zoology at the University of California, Berkeley (UCMVZ), and at the Department of Ornithology, American Museum of Natural History in New York (AMNH).

These measurements were used to calculate two derived values, the

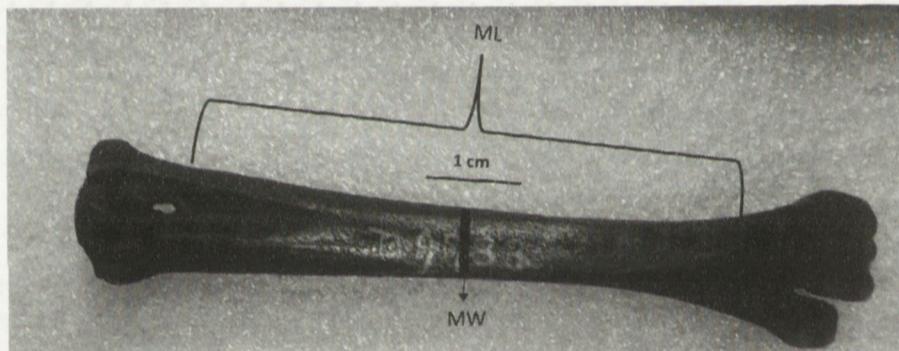


FIGURE 1. Location of measurements on a typical TMT of *Coragyps atratus*.

midshaft area (width times depth) and a robustness index (area divided by length). Age groups were evaluated for significant differences from the overall sample mean using the non-parametric Kruskal-Wallis test with pooled variance, as the distributions of several variables were non-normal (left-skewed).

RESULTS

Simple plots of specimens and sample means through time (Table 1; Figures 2, 3) show that neither size nor robustness changes between any Pleistocene samples. In particular, there is no increase in size or robustness from 35 ka to the glacial maximum at 20–18 ka, as would be expected from Allen's rule or Bergmann's rule. The only obvious change is the distinction between the two species, modern *C. atratus* being slightly larger and more robust than Pleistocene *C. occidentalis*. This is the opposite what previous authors such as Fisher (1944), Howard (1962b, 1968), Brodkorb (1964), Steadman and Martin (1984), and Steadman et al. (1994) have suggested about *C. atratus* being smaller, although the modern sample is very large and variable, and not dramatically different from the Pleistocene samples.

Statistical analysis of sample differences (Table 2) confirms that the modern specimens are significantly different from the Pleistocene samples along all measurements except depth, validating the distinction between *C. occidentalis* and *C. atratus*. However, when the 0 ka (modern) specimens were excluded and only the *C. occidentalis* specimens considered, no age interval was significantly different at $p=0.05$. Although there were too few time intervals sampled for a

TABLE 1. Basic statistics of *Coragyps* TMTs. (SD=standard deviation; CV=coefficient of variation)

Character	Age (ka)	N	Mean	SD	CV
Length (diaphysis)	0	45	58.9	0.1	0.1
	14	91	56.8	2.2	3.9
	18	61	56.2	2.9	5.3
	21	12	57.4	1.1	1.9
	35	9	56.6	2.1	3.7
Midshaft depth (antero-posterior)	0	45	7.6	0.6	7.8
	14	91	7.3	0.5	7.9
	18	61	7.5	0.5	7.2
	21	12	7.3	0.5	7.4
	35	9	7.7	0.7	8.7
Midshaft transverse width	0	45	6.1	0.1	1.2
	14	91	5.6	0.4	7.9
	18	61	5.6	0.5	8.0
	21	12	5.6	0.4	7.0
	35	9	5.6	0.5	9.1

TABLE 2. Kruskal-Wallis tests of sample difference on all *Coragyps* TMT parameters. Note that when modern (0 ka = *C. atratus*) specimens are excluded and the analysis is confined to fossil *C. occidentalis*, no sample is significantly different from the rest.

Parameter	Including 0 ka (<i>C. atratus</i>) specimens			Excluding 0 ka (<i>C. atratus</i>) specimens		
	χ^2	df	P-value	χ^2	df	P-value
Length	24.14	4	7.50E-05	4.59	3	2.04E-01
Width	5.95	4	2.03E-01	6.71	3	8.18E-02
Depth	12.87	4	1.19E-02	0.96	3	8.12E-01
Area	9.27	4	5.46E-02	4.20	3	2.41E-01
Robustness	7.10	4	1.31E-01	6.19	3	1.03E-01

formal time-series test of evolutionary hypotheses, it is apparent that the size and robustness of the Pleistocene black vulture population at RLB did not change over time.

DISCUSSION

This sample of Pleistocene black vultures agrees with previous results from RLB in several respects. Despite the substantial climatic changes which occurred in the Los Angeles Basin over the Pleistocene and the documented applicability of Bergmann's and Allen's rules to modern *Coragyps*, neither of these ecological effects are in evidence in the Los Angeles Basin population during the last glacial-interglacial cycle. Instead, the size and robustness of TMTs sampled at 35 ka (decreasing temperatures with coniferous forests), 21 and 18 ka (last glacial maximum with substantial winter snow), and 14 ka (deglaciation) are statistically indistinguishable. This indicates that neither morphological evolution nor a southward geographic range shift occurred.

The increased size and robustness of modern black vultures with respect to the Pleistocene populations is inconsistent with results from other scavenging species. Both the California condor *Gymnogyps amplus/californianus* (Syverson and Prothero, 2010) and the coyote *Canis latrans* (Meachen and Samuels, 2012) demonstrate a shift toward smaller body size at RLB and other California tar-pit deposits during the interval from 14 ka to the present. In the former, the larger Pleistocene and smaller modern species are both present at 9 ka; in the latter, where no species distinction is recognized, the shift from larger to smaller body size is constrained at RLB to between 12 and 9 ka.

Since these changes all occur in scavenging species over a period during which climate change was not prominent, but during which the Pleistocene megafaunal extinctions were occurring in this part of North

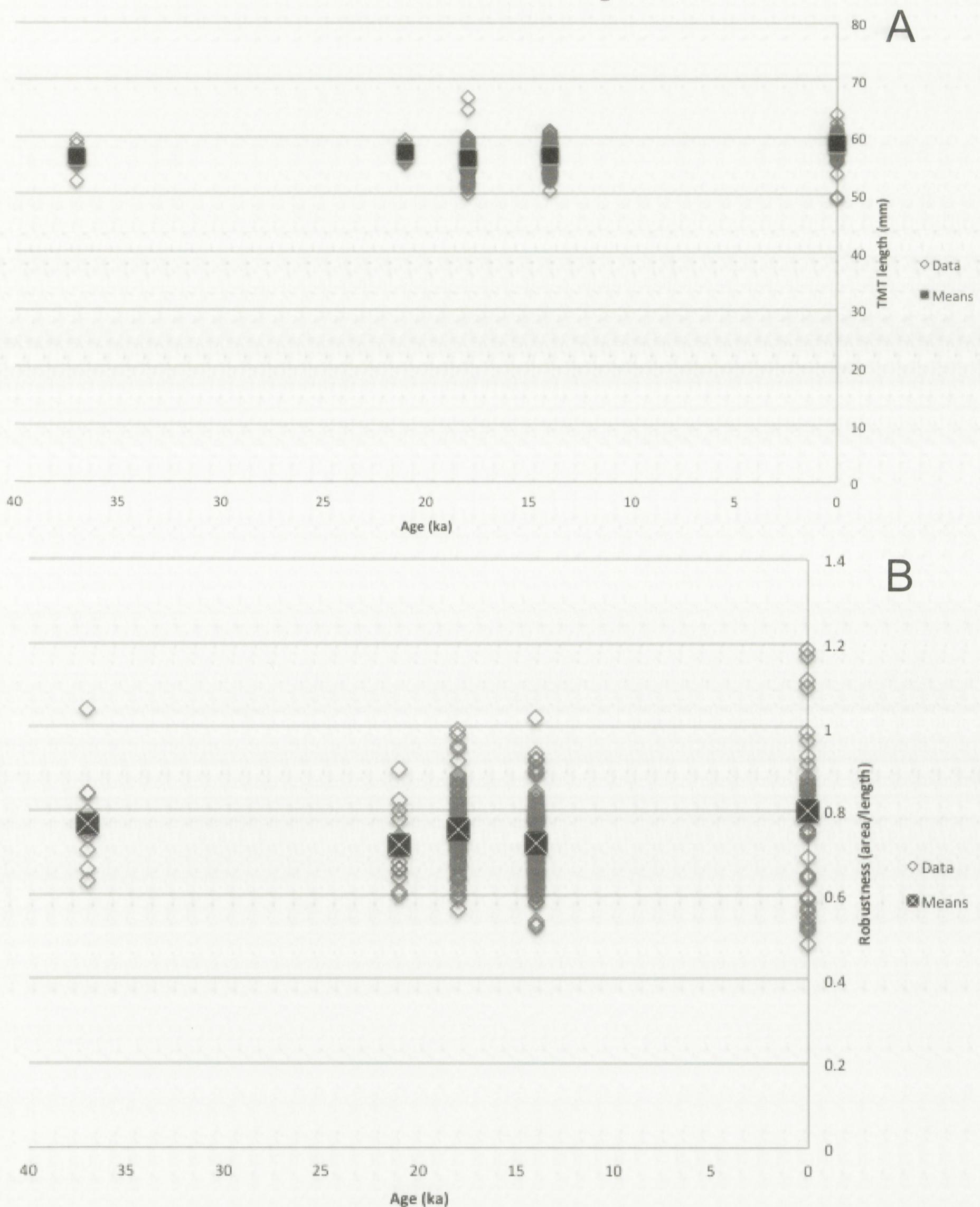


FIGURE 2. Plots of the measured and calculated dimensions of *Coragyps occidentalis* and *Coragyps atratus* TMTs versus age. Age in ka is across the x-axis. Open diamonds = individual specimens; solid squares = mean for each pit; (± 1 SE). **A.** TMT length. **B.** robustness (cross-sectional area/length).

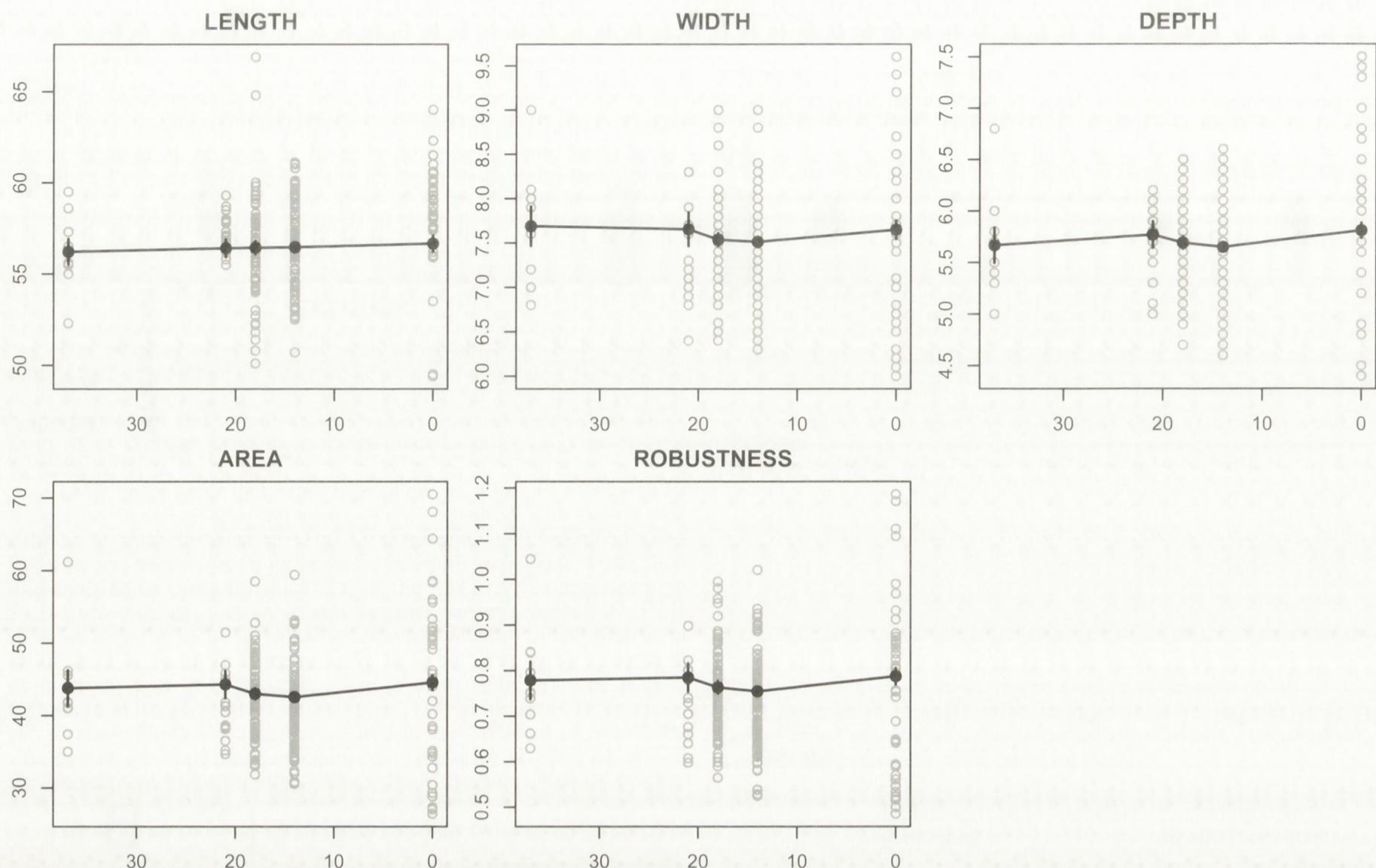


Figure 3. Plot of all five variables against time. Age in ka is across the x-axis. Open circles = individual specimens; error bars indicate variance (± 1 SE).

America, the evidence presented here for *Coragyps* contradicts the interpretation that decreased availability of large terrestrial prey post-extinction led to decreased body sizes in predators and scavengers. This is consistent with the observations of Syverson and Prothero (2010), who found that the shift in smaller body size among modern California condors did not happen at the beginning of the Holocene after the extinction of the megafauna, but within the Holocene.

CONCLUSIONS

Like other Pleistocene birds from RLB, such as great horned owls (Madan et al., 2015), golden eagles (Molina and Prothero, 2011), California condors (Syverson and Prothero, 2010), bald Eagles, turkeys, and caracaras (Fragomeni and Prothero, 2011), no significant changes were discovered in size or shape of black vultures (*Coragyps occidentalis/atratus*) through the last glacial cycle at RLB. The phenomenon of stasis is apparent not only in these bird species, but also in many other mammal species in the RLB record over the last 35,000 years (Prothero et al., 2012; Prothero and Raymond, 2008, 2011; DeSantis et al., 2011; Raymond and Prothero, 2011; Madan et al., 2011). However, the slight increase in body sizes between the last Pleistocene sample and the modern sample contradicts the interpretation that black vultures, like other scavengers at RLB, became smaller for dietary reasons as a result of the Pleistocene megafaunal extinctions.

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