EVOLUTIONARY PATTERNS IN LATE QUATERNARY CALIFORNIA CONDORS

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ABSTRACT

Pleistocene fossils related to the living California condor (*Gymnogyps californianus*) have been found in several locations in western North America. Different authors have either assigned these to the species *G. amplus* or considered them a chronological subspecies of *G. californianus*. We examined the morphology of the genus *Gymnogyps* from the late Pleistocene to the present, using hundreds of specimens from the asphalt deposits of Rancho La Brea (RLB) and 62 partial modern skeletons. The limb bones (using seven variables on each element) and skulls (using 13 variables) were quantitatively compared using bivariate and multivariate techniques. No significant size or shape change through time was apparent in RLB samples ranging from the late Pleistocene (35,000 radiocarbon years b.p.) to the early Holocene (9000 radiocarbon years b.p.), suggesting evolutionary stasis in the face of the climatic changes of the last glacial-interglacial cycle. Proximal limb elements and skulls showed patterns of variation consistent with a species distinction between the RLB specimens and modern *G. californianus*. This confirms Fisher's (1944) contention that the RLB species is referable to *G. amplus* Miller 1911, and not referable to the modern species. A set of specimens from a 9000-year-old Indian midden in Oregon as well as the presence of *Gymnogyps* in early Holocene Pit 10 at RLB suggest that the modern and ancient *Gymnogyps* may have coexisted with each other as well as with humans, and not died out or become dwarfed with the extinction of the rest of the Pleistocene megafauna, as suggested by some authors.

Introduction

The Rancho La Brea (RLB) fossil asphalt pits of Los Angeles, California, are one of the most important and famous late Pleistocene fossil localities in the world (Akersten *et al.*, 1983; Stock & Harris, 1992). These deposits have been radiocarbon dated from 35 ka to 9 ka, or from the late Pleistocene to the early Holocene (Marcus & Berger, 1984). Fossils from these deposits provide a fairly complete longitudinal picture of the fauna during this period, spanning most of the last glacial interval, and the beginning of the Holocene interglacial period. A recent survey of both modern and RLB fossil golden eagles, *Aquila chrysaetos*, indicates no overall trends in body size over the period from 35 ka to the present (Molina & Prothero, 2008 [in press]). In this study, we measured a set of modern and RLB bones from the California condor, genus *Gymnogyps*, in order to look for morphological trends over time related to the environmental changes due to glacial-interglacial cycles.

There has long been a debate in the literature regarding the validity of the species distinction between *Gymnogyps californianus*, the modern California condor, and *G. amplus*, a Pleistocene species (figure 1A). The type specimen for the latter is a single broken right tarsometatarsus (UCMP 9834) from the Pleistocene of Samwel Cave near Shasta Lake (figure 1B). Fossils from this deposit yield radiocarbon ages between 16 and 20 ka (Feranec *et al.*, 2007). UCMP 9834 was figured and described by Miller (1911) who regarded the robustness of the specimen as an indication of species distinct from the living California condor. However, Miller compared it to only 14 RLB condor tarsometatarsi, since the RLB deposits and their fossils were just beginning to be discovered. The type specimen is of limited diagnostic use, so taxonomic opinion is divided on the identity of the RLB specimens. Based on a number of cranial characters, Fisher (1944, 1947) argued that the RLB condor could be referred to *G. amplus* as a distinct, valid species. But Emslie (1988: 220) argued that the *G. amplus* was not a distinct species, but at best a temporal subspecies of *G. californianus*. This follows the general opinion of many avian paleontologists (Howard, 1947; Wetmore, 1959; Brodkorb, 1964; Jollie, 1976-1977; Rea & Hargrave, 1984). We attempted to resolve this issue by applying statistical techniques to our much larger morphological data set.

Methods

Nearly every available unbroken adult or subadult specimen of the bones listed in table 1 was measured in the collections of the George

Figure 1A. Mounted specimen of the RLB condor in the Page Museum. Photography by D.R. Prothero.

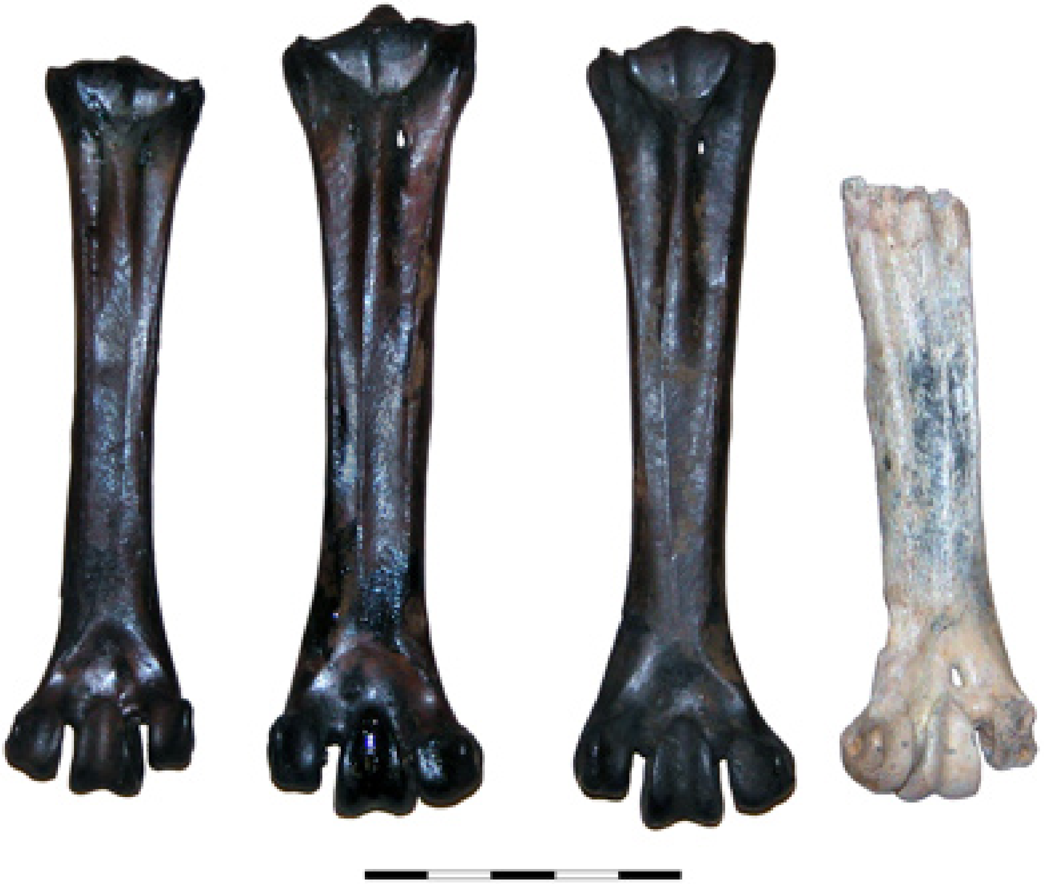


Figure 1B. Type specimen of *G. amplus* (UCMP 9834 on right) compared with the more robust TMT specimens from the RLB collections (LACMHC B2832, B2703, and B3781). Scale bar in cm. Photography by D.R. Prothero. Re-worked by A. 't Hooft Photographic Services.

C. Page Museum, the Natural History Museum of Los Angeles County, the Santa Barbara Natural History Museum, and the Museum of Paleontology and Museum of Vertebrate Zoology at the University of California, Berkeley. Seven dimensions were measured on limb bones, 11 on crania, and two on maxillae. Although beak features are important on many kinds of birds, there were not enough complete premaxillae in the collections to use in this study. Measurements were made with dial calipers, accurate to the nearest 0.1 mm, following the landmarks and protocols used by Fisher (1944) and Bochenski & Campbell (2006), and then entered into Excel spreadsheets. Statistical analyses were performed using Excel and SYSTAT software.

In this study, we follow the well-established paleontological and morphological species concepts of Eldredge & Cracraft (1980), where fossil morphospecies are defined as the "smallest diagnosable clusters of individual organisms" that can be recognized by morphology. This is consistent with the concept of species as practiced in the systematics of most fossil vertebrates. Some paleornithologists prefer to use subspecies for members of lineages with only small differences in size or proportion. However, as we discuss below, this does not seem to be the case for the two different morphs of *Gymnogyps*.

Abbreviations

LACM, Natural History Museum of Los Angeles County;
LACMHC, Hancock Collection, George C. Page Museum, Natural History Museum of Los Angeles County;
SBNHM, Santa Barbara Natural History Museum;
UCMP, University of California Museum of Paleontology;
UCMVZ, University of California Museum of Vertebrate Zoology;
CMC, carpometacarpus; TBT, tibiotarsus; TMT, tarsometatarsus.

Systematic Palaeontology

Order Ciconiiformes Bonaparte, 1854
Family Vulturidae (Illiger, 1811)
Genus *Gymnogyps* Lesson, 1842

Gymnogyps amplus Miller, 1911

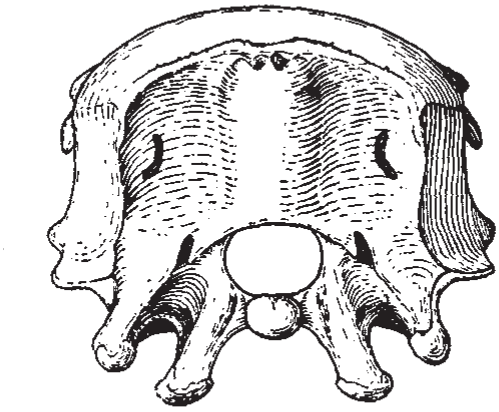
Type specimen – UCMP 9834, a right tarsometatarsus with the proximal end broken (figure 1B), from Samwel Cave, Shasta County, California.

Plesiotypes – LACMHC B2832, B2703, and B3781, cranium, rostrum, and mandible, from La Brea tar pits, Los Angeles County, California (*fide* Fisher, 1944)

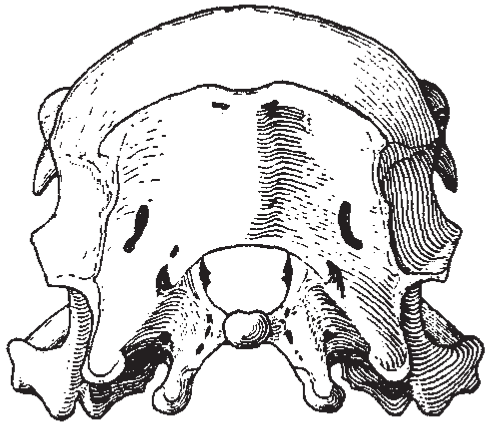
Revised specific diagnosis – Distinguished from *G. californianus* by general larger size and greater robustness, especially in the proximal limb elements (humerus and femur). Distinct columnar swelling above the foramen magnum. Robust, widely spread occipital processes with wide, blunt ends (figure 2). Frontoparietal suture farther forward, much wider occipital, and a larger ratio of occipital width to cranial length than *G. californianus*.

Discussion – Miller (1911: 390) erected the species *G. amplus* based on a broken (proximal end missing) right tarsometatarsus, UCMP 9834 (figure 1B) from the late Pleistocene (16-20 ka, fide Feranec *et al.*, 2007) deposits of Samwel Cave in Shasta County, California. He (*Ibidem*) diagnosed this species as distinct from *G. californianus* (the living California condor) based on its much broader, more robust proportions, and "foot set inward on the shaft so that the median line of the shaft falls outside the center of the foot." Based on 14 specimens of tarsometatarsi that had become available from the recently discovered Rancho La Brea deposits, Miller (1911) regarded the type specimen of *G. amplus* as distinct from the RLB condors, as well as from the living species. As he noted, "in this splendid series [of RLB condor TMTs], there is no individual which approaches in breadth of shank the dimensions displayed in the specimens here described." Miller (1911) regarded the type of *G. amplus* as outside the range of variation of any fossil or living condor described up to that time. On the other hand, he considered the RLB condor specimens to be within the range of variation of living *G. californianus*.

Fisher (1944, 1947) examined a much larger sample of RLB condors, including 107 crania, and numerous other bones, and revised Miller's (1911) taxonomy. He noted that the type specimen of *G. amplus*, UCMP 9834, was no longer distinctively robust, but was similar to some other RLB condor TMTs (figure 1B). Our own measurements confirmed this (figure 3). Although the type of *G. amplus* is one of the most robust specimens of *Gymnogyps* TMTs known, it falls within the range of variation of RLB specimens. Some RLB TMT specimens, such as LACMHC B2832, B2703, and B3781, are comparable in proportions (figure 1B). In addition, the clusters of RLB TMTs overlap with those of *G. californianus*, so the two species cannot be distinguished based on this particular bone.



GYMNOGYPS AMPLUS



GYMNOGYPS CALIFORNIANUS

Figure 2. Posterior views of skulls of *G. amplus* and *G. californianus*, showing the differences in the skull proportions and the shape of the occipital processes (after Fisher, 1944: 284, fig. 6).

For this reason, Fisher (1944) redefined *G. amplus* (based entirely on RLB specimens, including plesiotype skull elements LACMHC B5415, B6513, and B7591) to include a suite of characters that distinguished RLB condors from the living species. He noted that there were many differences in the skull, mostly related to greater size and robustness. He observed that the frontoparietal suture was farther forward in the RLB condor skulls, and that there was a columnar swelling above the foramen magnum. The RLB skulls also had a deeper temporal fossa and temporal muscle attachment. In addition to these and some other less striking differences, the most obvious distinction occurred in the robustness and spread of the occipital process, which are terminated with a wide, blunt end. This is a uniquely derived character for *G. amplus,* in contrast to the shorter, more pointed occipital processes of *G. californianus* (figure 2) and all other condors, which do not flare as widely. Our own measurements of these processes (see below) confirm how distinct they are in shape and size. As noted by Fisher (1944: 290), the RLB skulls had a much wider occipital width, and a larger ratio of occipital width to cranial length, which did not overlap with that of the living species. Fisher's (1944) paper was chiefly focused on skulls, but he commented (*Ibidem,* 290) "it is hoped that the entire skeleton of the Pleistocene species may be studied statistically since large series of most bony elements are available. At that time it may be possible to add substantially to the differentiation between the two species." Fisher (1947) later examined and measured most of the postcranial elements in the RLB sample, but failed to find any distinctions between *G. amplus* and *G. californianus* in his measurements. Finally, Miller (1957) reexamined his type specimen of *G. amplus* and again argued that it was more robust than any RLB condor TMT.

Since Fisher's (1944, 1947) and Miller's (1911) papers, however, most avian paleontologists have regarded *G. amplus* as a larger, more robust temporal subspecies of *G. californianus* (Howard, 1930, 1947; Wetmore, 1959; Brodkorb, 1964; Jollie, 1976-1977; Rea & Hargrave, 1984). Emslie (1988: 220) restudied the problem, and argued that the differences were simply due to the larger size of the RLB specimens, and thus the RLB specimens were not a distinct species. Emslie commented that many of the qualitative differences noted by Fisher (1944) could be seen in *G. californianus,* and thus the two species could only be distinguished by size. In this regard, Emslie (1988: tables 2, 3, and 4) argued that the RLB and modern species overlap in most dimensions, so the distinction is not valid. However, he measured only 32 CMCs and TMTs of RLB condors, and expressed his results as means and ranges of variation, without publishing any bivariate plots that would clearly show whether the two clusters of morphology could be distinguished.

In our own measurements, it is apparent that RLB and modern condors do overlap in most measurements of the TMT (figure 3) and other distal limb elements, such as the tibiotarsus. Skull dimensions and proximal limb elements, however, showed patterns of variation consistent with a species distinction between the RLB specimens and modern *G. californianus.* In figure 4A, all cross-sectional areas of the femur display noticeable segregation between the

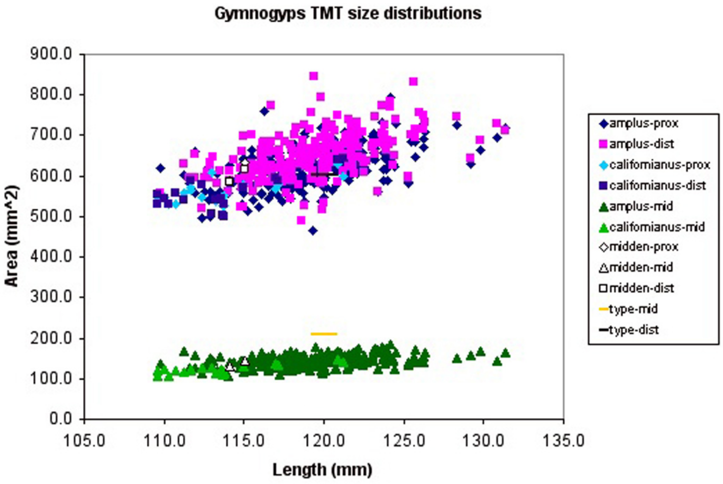


Figure 3. Plot of TMT dimensions from modern and RLB *Gymnogyps*. Note that the TMT samples do not discriminate the RLB specimens from the modern specimens as well as do the proximal limb elements, such as femora and humeri.

RLB and modern specimens; the same is true to slightly lesser extent in the humeri (figure 4B). This is marked even more strongly in several skull dimensions (figures 5A, B & C), specifically the ratio of skull length to temporal width (figure 5A), ratio of skull length to height of the cranial vault, ratio of the width between the occipital processes versus that between the opisthotic protrusions (figure 5B), and the relative length of the occipital processes (figure 5C). This last feature was noted by Fisher (1944) as one of the distinctions between the RLB specimens (*G. amplus, fide* Fisher) and *G. californianus.*

These data distinctions are apparent not only in bivariate plots such as those in figures 4 and 5, but also in statistical analysis of the dataset. Each measurement of extant *G. californianus* was compared to the comparable measurement of RLB specimens (table 2). Nearly all samples had significantly equal variances, as established by the F-test, and were normally distributed. Thus, we performed t-tests on the samples assuming equal variances. In nearly every dimension, the RLB specimens were significantly larger than the comparable modern condor specimens (at the 95% confidence level). We also performed a one-way ANOVA of the separate samples from RLB localities, and found there were no significant differences between Pleistocene samples (table 4), but when the modern specimens were added the differences were significant. Thus, the distinction is not only established by visual inspection and bivariate plots, but also by statistical analysis.

Surprisingly, Fisher (1947) did not find these distinctions in his data set of postcranial bones. This may be due to the fact that he measured a smaller number of specimens (typically only a dozen). He also displayed his results as simple tables of means and standard deviations. In data such as those in figures 4A and 4B, there is a slight overlap in individual variables between humeri and femora of *G. amplus* and *G. californianus*, but it is clear from visual inspection of bivariate plots and from statistical analysis (table 2) that the clusters are distinct, with only a few outlying points that fall inside the cluster of the other species. Indeed, if one looks closely at the data in Fisher's (1947: table 2) humerus sample or his femur sample (Fisher, 1947: table 11), it is clear that the means are strikingly different between *G. amplus* and *G. californianus.* If we had his original data available and could analyze them ourselves, they would prove to be statistically non-overlapping. But Fisher did not notice these differences because the distal limb elements do not show the distinction between species as well as the proximal elements do. Thus, it appears that Fisher (1947) did not use the appropriate methods for discriminating two populations that are subtly separated in proportions.

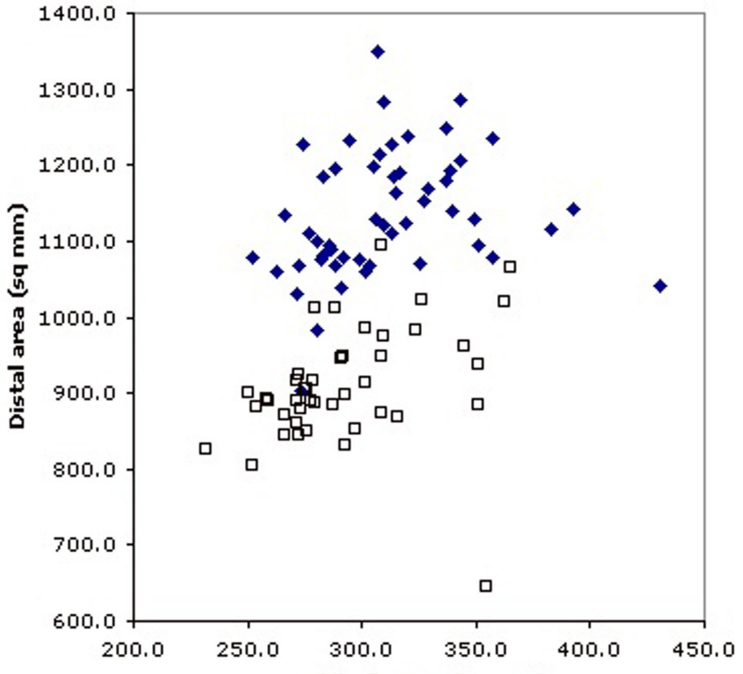


Figure 4A. Plot of cross-sectional area of distal femur (ordinate) versus midshaft area (abscissa), showing the clear separation between modern condor femora (open squares) and RLB condors (blue diamonds). All measurements in mm.

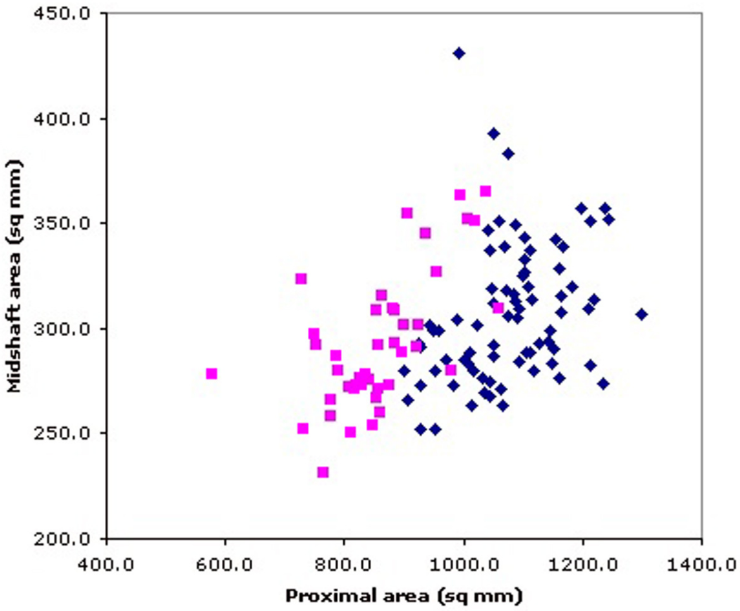


Figure 4B. Plot of cross-sectional area of proximal femur versus midshaft area, showing separation between modern condors (magenta squares) and RLB condors (blue diamonds). All measurements in mm.

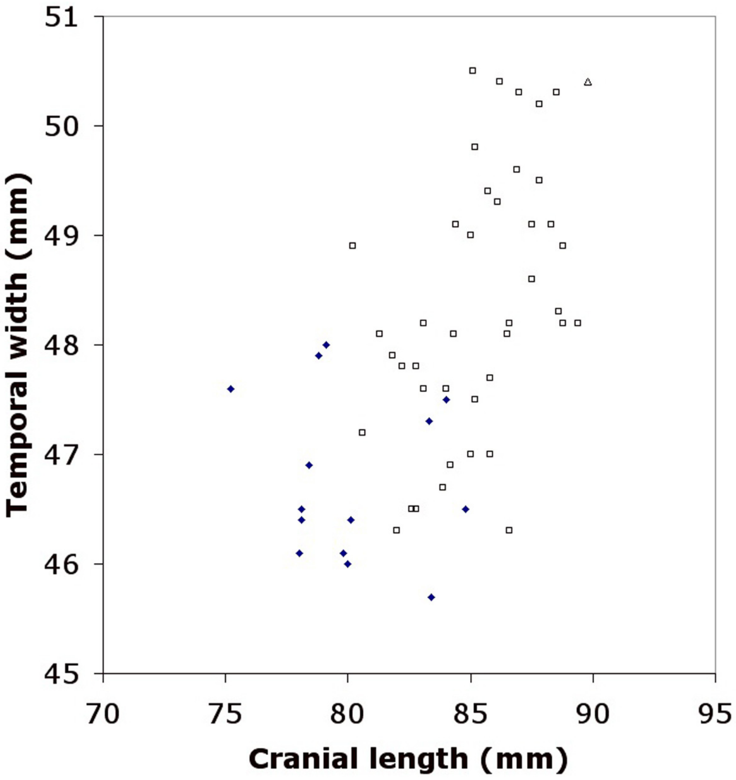


Figure 5. Bivariate plots of skull dimensions, showing the distinction between modern condors (blue diamonds) and RLB specimens (open squares or triangles).

A) Cranial length vs. temporal width. All measurements in mm.

As noted above, paleornithologists have long considered *G. amplus* to be only a larger subspecies of *G. californianus*. However, there are several good lines of evidence against this position: 1) the samples of RLB *G. amplus* are statistically distinct from *G. californianus* in many variables; 2) *G. amplus* possesses a suite of derived characters (especially the enlarged occipital processes, found in no other condor) that are not simply matters of size and scaling, but distinctive derived meristic characters that consistently distinguish the two species; 3) as discussed below, recent evidence suggests that *G. amplus* persisted into the Holocene and probably overlapped with *G. californianus*. If the two species coexisted by a splitting and speciation event, then it would be inappropriate to label one of them as a subspecies of the other.

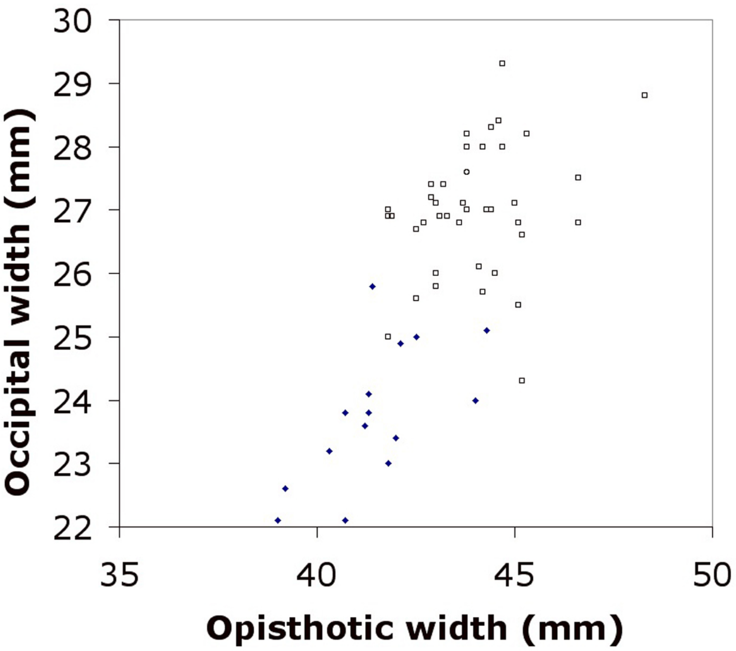


Figure 5. Bivariate plots of skull dimensions, showing the distinction between modern condors (blue diamonds) and RLB specimens (open squares or triangles).

B) Occipital width vs. opisthotic width All measurements in mm.

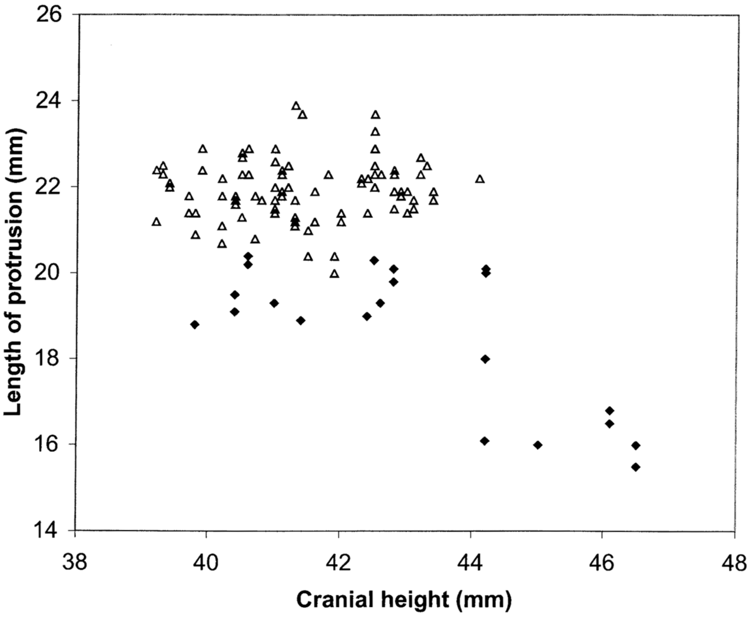


Figure 5. Bivariate plots of skull dimensions, showing the distinction between modern condors (blue diamonds) and RLB specimens (open squares or triangles).

C) Length of occipital processes vs. cranial height. All measurements in mm.

There is also the possibility that *Gymnogyps* populations were simply highly variable, and that the larger RLB species is within the range of variation of a single species. However, it is clear from the analysis just discussed that many variables of the two samples (RLB vs. modern) are statistically distinct and non-overlapping, so they do not appear to be part of a single continuous distribution. In addition, the coefficients of variation (table 5) of the combined RLB plus modern population are much too large to belong to a single species, since many of the CV values are over 10, while the individual RLB and modern samples generally have CV values that are within the range for a single modern population (Kurtén 1953; Simpson *et al.* 1960; Yablokov, 1974).

Sexual Dimorphism

In analyzing size changes through time of any fossil species, it is important to account for possible differences in size due to sexual dimorphism. Living *G. californianus* shows only the slightest sexual dimorphism, with males averaging slightly larger than females (Koford, 1953; Snyder & Snyder, 2000, 2005). To confirm this, we examined the distribution of sexed specimens in the samples of living condors. Although we measured every available specimen in the UCMVZ, SBNHM, and LACM collections, and had as many as 62 femora and 29 humeri in our sample (table 1), only a handful of the bones had the gender of the bird recorded. Nonetheless, the size of the sexes overlaps in our largest sample of sexed bones (7 males, 2 females), as shown in figure 6. The largest specimens were indeed males, but their cloud of variation encompassed the females, and some of the smallest were also males (not surprising, considering there were three times as many male specimens). The two genders have slightly different distributions, with the males averaging slightly smaller and more robust, although the sample size is too small to argue that there is significant size dimorphism. Using a t-test, the differences were not significant for humerus length, width, or any other dimension. Thus, there is no reason to expect that sexual size dimorphism is a factor when discussing size changes through time.

Discussion

Morphological Stasis Through Time

The late Pleistocene was a time of dramatic global climatic change. From the peak interglacial at 125 ka, the planet went through a steady decline into the early Wisconsinan glacial stage, also known as oxygen isotope stage 3 in the marine record. The last glacial maximum spans the interval from 24-14 ka, with the peak cooling at 20 ka. Between 14-10 ka, the planet then went through a glacial-interglacial transition, with a rapid pulse of warming and cooling during the Younger Dryas event between 12.8 ka and 11.5 ka, which marked the transition into the Holocene interglacial (the last 10,000 years).

Although southern California did not experience the climatic extremes of icecaps or tundra vegetation, nevertheless the climatic changes in the region were dramatic. Analysis of wood specimens (Ward *et al.*, 2005) demonstrated that C3 plant primary productivity was greatly reduced during the last glacial maximum. Analyses of plant fossils (Warter, 1976) and mollusks (Lamb, 1989) show that the Pleistocene climate was cooler, milder and wetter than today. Stable isotope biogeochemistry on bones (Coltrain *et al.*, 2004) suggest a drying trend during the last glacial maximum, followed by dramatic changes in carbon and nitrogen isotopes as the Holocene approached.

Heusser (1998) analyzed the pollen preserved in deep-sea cores offshore from southern California, and was able to obtain a more detailed record of climatic and vegetational change. Between 40 and 24 ka, southern California made the transition from oak and chaparral vegetation to pine-juniper-cypress woodlands. At the glacial maximum (24-14 ka), the RLB region was covered in junipers and closed-cone pines such as piñon and ponderosa, with mean an-

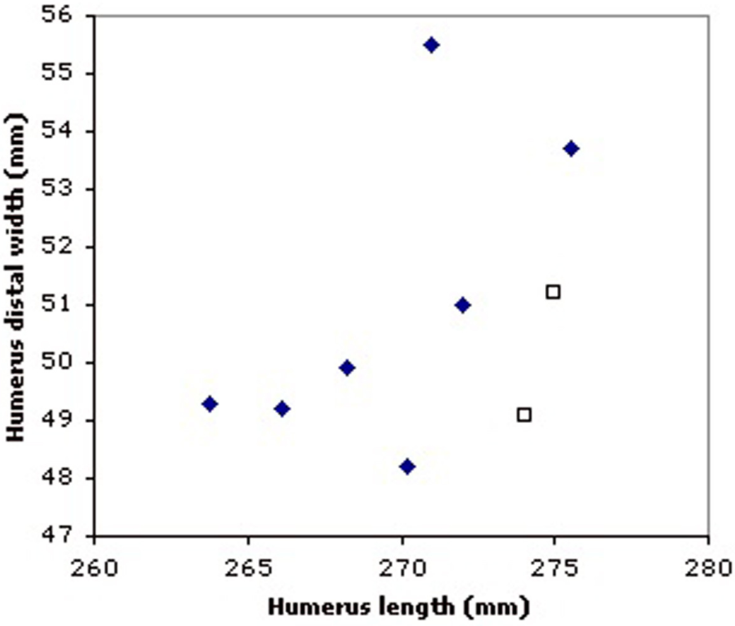


Figure 6. Modern condor bones do not show marked sexual size dimorphism. Here, the humerus length is plotted against the humerus distal width for sexed specimens of *G. californianus.* The two female humeri (open boxes) fall within the range of the scatter of male humeri (blue diamonds), and are not significantly different as evaluated by a t-test.

nual temperatures of only 4°C (40°F), compared to 17°C (63°F) today. There was a brief return to oak-chaparral at 15 ka. During the glacial-interglacial transition (14-10 ka), the oak-chaparral was mixed with alders. Since 10 ka, the region has been dominated by the modern oak woodland-chaparral vegetation.

Given these dramatic changes in climate and vegetation over the past 40,000 years, one would expect to see significant changes in size and/or shape in the condor population that soared above and scavenged from this landscape. At the very least, the cooling trend would tend to favor larger-bodied condors (following Bergmann's rule), as would the abundance of large animals to scavenge. However, in the RLB specimens we measured, no significant (tables 3 & 4) size or shape change through time was apparent in any element for samples ranging from 35,000-9,000 ka, suggesting evolutionary stasis in the face of the climatic changes of the last glacial-interglacial cycle (figure 7). A series of pairwise t-tests between temporally sequential samples yielded no significant differences between RLB samples; the only statistically significant difference was between the youngest RLB samples (typically 12 ka) and the recent sample. Similarly, a one-way ANOVA showed no significant differences among the RLB samples (table 4), but when the modern sample was added, the differences between samples were significant. This is consistent with the recent study showing a similar lack of change in golden eagles from the RLB asphalts (Molina & Prothero, 2008 [in press]), or the lack of notable size changes in the RLB turkey (Bochenski & Campbell, 2006).

Such stasis in the face of climatic changes, especially significant drying and vegetational change, are in stark contrast to the highly influential model of island bird evolution as exemplified by the Galapagos finch (Weiner, 1995; Grant & Weiner, 1999; Grant & Grant, 2007). If such disparate birds as turkeys, eagles, and condors show stasis despite the dramatic climatic changes of the past 40,000 years, perhaps the Galapagos finch model of immediate response to climate change is only appropriate for small island populations, and may not be generally

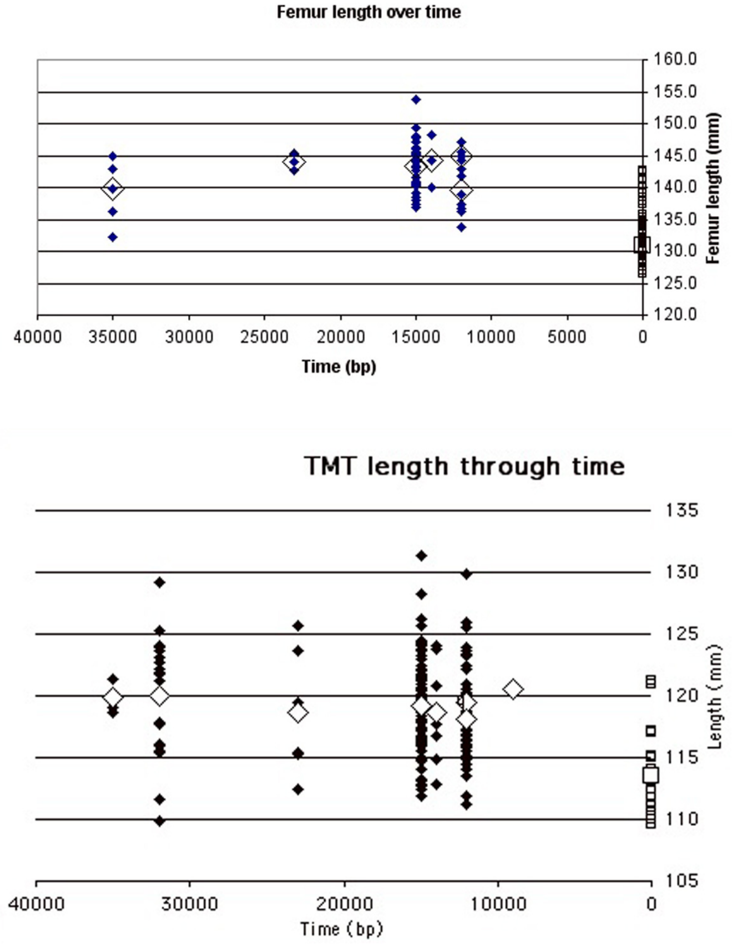


Figure 7. Size trends through time in RLB and modern condors.

A) Femur length over time.

B) TMT length through time.

Solid diamonds = individual RLB condor specimens; large open diamond = mean for time interval; small open squares = modern condor data points; large open square = mean for modern condors.

In each dated sample from a RLB pit, the mean is statistically indistinguishable from the previous and subsequent sample, as determined by t-tests and ANOVA. This is despite the fact that the climate changed dramatically over the 40,000 years represented by these samples, from the glacial conditions beginning around 40 ka, and peaking at 20 ka to the beginning of the Holocene interglacial at 10 ka.

applicable to large continental populations of birds, or to mammals, either (Prothero & Heaton, 1996; Prothero, 1999; Barnosky, 2005; Prothero *et al.*, 2009). The widespread stasis of many different groups of animals in response to climatic and vegetational change suggests that we may need to rethink just how sensitive organisms are to climate, and reassess the importance of climate in driving evolution.

Potential Temporal Overlap with Humans

There is a partial skeleton tagged as *G. californianus* (UCMVZ 13377) which bears a written note indicating that it was not a museum-prepared skeleton like all the others in the collection, but instead was found in a midden at an archaeological dig at The Dalles, Oregon, associated with ancient Native Americans. As there are three humeri present, this box clearly holds the remains of more than one animal. For the purposes of the present study, however, the interesting aspect of the specimen lies in its measurements. The skull of UCMVZ 13377 falls well outside the range of sizes observed for *G. californianus*, and indeed at the large end of the spectrum of RLB specimens.

There is no reason to assume these fossils are from a single individual, and indeed the assemblage of bones certainly contains at least one element from a second condor, if not more. However, since the bird to which skull UCMVZ 13377 belonged presumably lived (and died) at the same time as the people depositing the midden, this unique specimen indicates likely coexistence of the late Pleistocene California condor with humans.

An Indian midden, known as Five Mile Rapids, not far from The Dalles (Simons, 1983), yields condor bones that were mostly referred to *G. californianus* by Miller (1957), although his concept of *G. amplus* is different from that of Fisher (1944, 1947) or as used in this paper. This midden ranges in age from 9785 ± 220 radiocarbon years at the base to 7875 ± 100 radiocarbon years at the top (Simons, 1983). We are not sure whether the UCMVZ specimens mentioned above are from this midden, since the locality information is vague on the specimens, but it seems very unlikely that there are two such major condor-bearing Indian midden localities next to The Dalles. We surmise that the collections made for the UCMVZ were made before the locality was formally described as the Five Mile Rapids midden. If so, then Miller's identification of these condors as *G. californianus* should be amended to *G. amplus.* In addition, Simons (1983) mentions a number of other Holocene middens that appear to preserve *G. californianus* as well, suggesting that *G. amplus* and *G. californianus* overlapped during at least some of the Holocene.

The idea that large Pleistocene condors survived into the early Holocene is consistent with another specimen of *Gymnogyps* amplus (LACM G2465, a very robust TMT) found in Pit 10 at Rancho La Brea. It is the only condor specimen in Pit 10, and there are none that suggest the less robust modern species. Pit 10 was the location where 'La Brea Woman', the only human fossil found in the RLB deposits, was unearthed; it is also the youngest of the RLB excavations so far, with a Holocene radiocarbon age of 9,000 years.

If both of these occurrences of *G. amplus* in the early Holocene are valid, this has implications for studies that argue that that large condors vanished, or became dwarfed, in response to the Holocene changes in climate and the loss of their megafaunal prey. For example, Emslie (1987) showed that condors vanished from the Grand Canyon region in synchrony with the loss of the megafauna about 10 ka. However, these occurrences in California and Oregon show that a similar extinction did not occur in on the Pacific Coast. Chamberlain *et al.* (2005) and Fox-Dobbs *et al.* (2006) looked at the isotopic values of a number of large Pleistocene vultures, and concluded that *Gymnogyps* survived into the Holocene when their megafaunal prey vanished by shifting to a diet of marine food items, especially marine mammal carcasses. The isotopic evidence for diet is strong, but our data show that the dwarfing of *G. amplus* to give rise to *G. californianus* did not occur immediately upon the extinction of the Pleistocene megafauna, but apparently took place some time in the early Holocene, later than 9000 years ago, and possibly as recently as 7000 years ago. From these data, it is clear that the size reduction did not happen immediately after the megafaunal extinction. The location and timing of the speciation event, however, would be difficult to determine without a larger set of Holocene samples.

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Cited Literature

Akersten, W.A., C.A. Shaw, & G.T. Jefferson. 1983. Rancho La Brea: status and future. – Paleobiology 9: 211-217.

Barnosky, A.D. 2005. Effect of Quaternary climate change on speciation in mammals. – Journal of Mammalian Evolution 12: 247-264.

Bochenski, Z.M., & K.E. Campbell Jr. 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, 509: 1–92.

Brodkorb, P. 1964. Catalogue of fossil birds: Part 2 (Anseriformes through Galliformes). – Bulletin of the Florida State Museum, Biological Sciences 8: 195-335.

Chamberlain, C.P., J.R. Waldbauer, K. Fox-Dobbs, S.D. Newsome, P.L. Koch, D.R. Smith, M.E. Church, S.D. Chamberlain, K.J. Sorenson & R. Risenbrough. 2005. Pleistocene to recent dietary shifts in California condors. – Proceedings of the National Academy of Sciences 102: 16707-16711.

Coltrain, J.B., J.M. Harris, T.E. Cerling, J.R. Ehleringer, M. Dearing, J. Ward & J. Allen. 2004. Rancho La Brea stable isotope biogeochemistry and its implications for the palaeoecology of the late Pleistocene, coastal southern California. – Palaeogeography, Palaeoclimatology, Palaeoecology, 205: 199-219.

Eldredge, N. & J. Cracraft. 1980. Phylogenetic Patterns and the Evolutionary Process. – New York, Columbia University Press.

Emslie, S.D. 1987. Age and diet of fossil California condors in Grand Canyon, Arizona. – Science 237: 768-770.

Emslie, S.D. 1988. The fossil history and phylogenetic relationships of condors (Ciconiiformes: Vulturidae) in the New World. – Journal of Vertebrate Paleontology 8: 212-228.

Feranec, R.S., E.A. Hadly, J.L. Blois, A.D. Barnosky & A. Payton. 2007. Radiocarbon dates from the Pleistocene fossil deposits of Samwel Cave, Shasta County, California, USA. – Radiocarbon 49: 117-121.

Fisher, H.I. 1944. The skulls of cathartid vultures. – Condor 46: 272-296.

Fisher, H.I. 1947. The skeletons of recent and fossil *Gymnogyps*. – Pacific Science 1: 227-236.

Fox-Dobbs, K., T.A. Stidham, G.J. Bowen, S.D. Emslie & P.L. Koch. 2006. Dietary controls on extinction versus survival among avian megafauna in the late Pleistocene. – Geology 34: 685-688.

Grant, P.R., & J. Weiner. 1999. The ecology and evolution of Darwin's Finches. – Princeton, NJ, Princeton University Press.

Grant, P.R., & B.R. Grant 2007. How and why species multiply: the radiation of Darwin's finches. – Princeton, NJ, Princeton University Press.

Heusser, L. 1998. Direction correlaton of millennial-scale changes in western North American vegetation and climate with changes in the California Current system over the past 60 kyr. – Paleoceanography 13: 252-262.

Howard, H. 1930. A census of the Pleistocene birds of Rancho La Brea from the collections of the Los Angeles Museum. – The Condor 32: 81-88.

Howard, H. 1947. A preliminary survey of trends in avian evolution from Pleistocene to recent time. – The Condor 49:10-13.

Jollie, M. 1976-1977. A contribution to the morphology and phylogeny of the Falconiformes. – Evolutionary Theory 1:285-298, 2:115-300, 3: 1-142.

Koford, C.B. 1953. The California condor. – National Audubon Society Research Report 4: 1-154.

Kurtén, B. 1953. On variation and population dynamics of fossil and recent mammal populations. – Acta Zoologica Fennica 76: 1-122.

Lamb, R.V. 1989. The nonmarine mollusks of Pit 91, Rancho La Brea, southern California, and their paleoecologic and biogeographic implications. – Unpublished master's thesis, California State University Northridge, Northridge, CA: 1-365.

Marcus, L.F. & R. Berger. 1984. The significance of radiocarbon dates for Rancho La Brea. In:

Martin, P.S. & R.G. Klein. Eds. 1984. Quaternary extinctions: a prehistoric revolution. – Chicago, University of Chicago Press: 159-188.

Miller, L. 1911. Avivfauna from the Pleistocene cave deposits of California. – University of California Publication, Bulletin of the Department of Geological Sciences 6: 385-400.

Miller, L. 1957. Bird remains from Oregon Indian middens. – The Condor 59:59-63.

Molina, S. & D.R. Prothero. 2008. Evolutionary stasis in golden eagles over the last glacial-interglacial cycle (35,000 years ago to present). – Geological Society of America Abstracts with Programs 40, 6: 142.

Prothero, D.R. 1999. Does climatic change drive mammalian evolution? – GSA Today 9, 9: 1-5.

Prothero, D.R. & T.H. Heaton. 1996. Faunal stability during the early Oligocene climatic crash. – Palaeogeography, Palaeoclimatology, Palaeoecology 127: 239-256.

Prothero, D.R., K.R. Raymond, V. Syverson & S. Molina. 2009. Stasis in late Pleistocene birds and mammals from La Brea tar pits over the last glacial-interglacial cycle. – Cincinnati Museum Center Scientific Contributions 3: 291-292.

Rea, A.M. & L.L. Hargrave. 1984. The bird bones from Stanton's Cave. In: Euler, R.C. Ed. 1984. The archeology, geology and paleobiology of Stanton's Cave. – Grand Canyon Natural History Association Monograph 6: 1-141.

Simons, D.D. 1983. Interactions between California condors and humans in prehistoric Far Western North America. In: Wilbur, S.R. & J.A. Jackson. Eds. 1983. Vulture biology and management. – University of California Press, Berkeley, CA: 470-494.

Simpson, G.G., A. Roe & R.C. Lewontin. 1960. Quantitative zoology. – New York, Harcourt Brace and World.

Snyder, N.F.R. & H. Snyder. 2000. The California condor: a saga of natural history and conservation. – Princeton, Princeton University Press.

Snyder, N.F.R. & H. Snyder. 2005. Introduction to the California condor. – Berkeley, University of California Press.

Stock, C. & J.M. Harris. 1992. Rancho La Brea: a record of Pleistocene life in California. – Science Series no. 37, Natural History Museum of Los Angeles County, Los Angeles.

Ward, J.W., J.M. Harris, T.E. Cerling, A. Wiedenhoeft, M.J. Lott, M. Dearing, J.B. Coltrain & J.R. Ehleringer. 2005. Carbon starvation in glacial trees recovered from the La Brea tar pits, southern California. – Proceedings of the National Academy of Sciences 102:690-694.

Warter, J.K. 1976. Late Pleistocene plant communities – evidence from Rancho La Brea tar pits. Symposium Proceedings on the Plant Communities of Southern California, v. 2. – Native Plant Society Special Publication, Pasadena, CA: 32-39.

Weiner, J. 1995. The beak of the finch: a story of evolution in our own time. – New York, Vintage.

Wetmore, A. 1959. Birds of the Pleistocene in North America. – Smithsonian Miscellaneous Collections 138: 1-24.

Yablokov, A.V. 1974. Variability in mammals. – New Delhi, Amerind Press.

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Element	RLB specimens	Modern specimens	Dalles Indian midden sp. Samwel Cave	Samwel Cave
Crania	53	16	1	
Maxillae	49	13	1	
Humeri	42	29	3	
Radii	2	24	1	
Ulnae	25	25		
Carpometacarpi	95	21	2	
Femora	75	62	2	
Tibiotarsi	64	20	2	
Tarsometatarsi	238	20	2	1 (holotype)

Table 1. Sample sizes of condor specimens used in the present study.

Measurement	Mean	Var	Mean	Var	DF	T-stat	T critical values	P value
SKULL								
Cranial height	42.2	6.2	42.8	4.5	23	-0.9	1.71-2.06	0.393
Cranial length	*85.5*	*5.3*	*80.0*	*7.7*	*18*	*6.7*	*1.73-2.10*	*<0.001*
Temporal width	*48.1*	*2.5*	*47.0*	*1.2*	*33*	*3.0*	*1.69-2.03*	*0.002*
Occipital width	*26.9*	*1.3*	*23.7*	*1.2*	*24*	*9.8*	*1.71-2.06*	*<0.001*
Opisthotic width	*43.8*	*2.0*	*41.4*	*2.1*	*23*	*5.6*	*1.71-2.07 <*	*0.001*
Occ. Proc. length	19.4	40.8	18.7	2.8	66	0.7	1.66-2.00	0.496
Occ. Proc. width	*3.9*	*0.2*	*3.3*	*0.1*	*31*	*5.5*	*1.70-2.04*	*<0.001*
HUMERUS								
length	*276.1*	*48.9*	*269.0*	*31.1*	*67*	*4.7*	*1.66-1.99*	*<0.001*
proximal width	*53.3*	*3.7*	*50.6*	*4.2*	*58*	*5.6*	*1.67-2.00*	*<0.001*
proximal depth	19.0	0.6	18.8	8.7	31	0.3	1.70-2.04	0.725
midshaft width	*21.9*	*1.5*	*20.4*	*0.8*	*69*	*6.3*	*1.67-1.99*	*<0.001*
midshaft depth	*18.3*	*1.0*	*17.3*	*1.5*	*52*	*3.4*	*1.67-2.00*	*0.001*
distal width	*49.7*	*3.3*	*47.6*	*2.3*	*67*	*5.2*	*1.67-2.00*	*<0.001*
distal depth	25.6	1.9	25.9	1.8	61	-0.8	1.67-2.00	0.416
proximal area	1015.1	4625.2	956.1	34286.6	33	1.7	1.69-2.03	0.111
midshaft area	*401.3*	*1413.0*	*353.6*	*1400.4*	*61*	*5.3*	*1.67-1.99*	*<0.001*
distal area	1275.5	11086.1	1235.0	9631.2	63	1.6	1.67-1.99	0.103
FEMUR								
length	*143.3*	*15.5*	*133.2*	*16.3*	*84*	*11.6*	*1.66-1.99*	*<0.001*
proximal width	*35.1*	*2.7*	*31.9*	*7.7*	*60*	*6.8*	*1.67-2.00*	*<0.001*
proximal depth	*30.6*	*3.9*	*26.9*	*6.3*	*75*	*8.4*	*1.67-1.99*	*<0.001*
midshaft width	*18.6*	*2.2*	*17.7*	*2.7*	*81*	*3.0*	*1.66-1.99*	*<0.003*
midshaft depth	16.4	0.7	16.3	1.0	76	0.9	1.66-1.99	0.353
distal width	*36.9*	*1.9*	*34.2*	*1.7*	*94*	*10.8*	*1.66-1.99*	*<0.001*
distal depth	*30.6*	*1.9*	*26.7*	*2.9*	*76*	*12.9*	*1.66-1.99*	*<0.001*
proximal area	*1076.1*	*8324.7*	*855.8*	*7972.0*	*89*	*12.7*	*1.66-1.99*	*<0.001*
midshaft area	*306.7*	*1114.4*	*287.8*	*1363.5*	*82*	*2.7*	*1.66-1.99*	*<0.003*
distal area	*1129.0*	*7020.5*	*908.5*	*5511.5*	*97*	*14.7*	*1.66-1.99*	*<0.001*

Table 2. T-tests of significance of differences at the 95% confidence level (alpha = 0.05) between *G. amplus* (mean and variance in first pair of columns) and *G. californianus* (mean and variance in second pair of columns). All samples had significantly equal variances (as established by an F- test), so t-test for equal variances was used. DF = degrees of freedom. Dimensions that were statistically different at the 95% confidence level (t-stat greater than t-critical range) are in *Italic*. As can be seen, most of the dimensions of the skull and proximal limb elements meet this criterion.

Sample Comparison	Mean	Var	Mean	Var	DF	T-stat	T critical values	P value
HUMERI								
15 ka vs. 12 ka	276.2	57.0	274.0	61.0	13	0.66	1.77-2.16	0.523
12 ka vs. modern	274.0	61.0	269.0	31.1	9	1.69	1.83-2.26	0.125
CARPOMETACARPI								
35 ka vs. 23 ka	131.9	43.2	137.1	8.4	1	-1.00	6.31-12.7	0.499
23 ka vs. 15 ka	137.1	8.4	135.8	14.1	1	0.59	6.31-12.7	0.676
15 ka vs. 14 ka	135.8	14.2	133.7	36.1	3	0.69	2.35-3.18	0.539
14 ka vs. 12 ka	133.7	36.1	134.8	12.1	3	-0.34	2.35-3.18	0.753
12 ka vs. modern	*134.8*	*12.1*	*131.9*	*13.3*	*46*	*2.77*	*1.67-2.01*	*0.007*
FEMORA								
35 ka vs. 23 ka	139.8	28.7	144.0	3.9	5	-1.52	2.02-2.57	0.189
23 ka vs. 15 ka	144.0	3.9	143.4	16.8	2	0.37	2.92-4.30	0.742
15 ka vs. 14 ka	143.4	16.8	144.2	34.4	1	-0.18	6.31-12.70	0.887
14 ka vs. 12 ka	145.6	15.1	141.1	18.2	1	1.49	6.31-12.70	0.375
12 ka vs. modern	*141.1*	*18.2*	*134.8*	*216.0*	*70*	*2.92*	*1.66-1.99*	*0.002*
TIBIOTARSI								
23 ka vs. 15 ka	218.5	2.1	223.7	39.1	10	-4.10	1.81-2.22	0.002
15 ka vs. 12 ka	223.7	39.1	223.9	61.3	17	-0.10	1.73-2.11	0.921
12 ka vs. modern	*223.9*	*61.3*	*211.1*	*32.5*	*20*	*5.16*	*1.72-2.09*	*<0.01*
TARSOMETATARSI								
35 ka vs. 32 ka	119.8	1.34	119.9	22.1	21	-0.04	1.72-2.08	0.966
32 ka vs. 23 ka	119.9	21.17	118.7	27.3	7	0.54	1.89-2.36	0.601
23 ka vs. 15 ka	118.7	27.3	119.2	12.6	5	-0.26	2.01-2.57	0.807
15 ka vs. 14 ka	119.2	12.5	119.0	21.6	5	0.11	2.02-2.57	0.919
14 ka vs. 12 ka	118.7	188	118.9	14.5	8	-0.14	186-2.31	0.446
12 ka vs. modern	*118.9*	*14.5*	*113.6*	*10.4*	*49*	*5.96*	*1.67-2.01*	*<0.01*

Table 3. Pairwise t-tests of significance of differences of bone lengths at the 95% confidence level (alpha = 0.05) between temporally sequential pit samples of *Gymnogyps*. Mean and variance of older sample are in the first pair of columns; those of the younger sample in the second pair of columns. All samples were normally distributed, and had significantly equal variances (as established by an F- test), so t-test for equal variances was used. DF = degrees of freedom. None of the comparisons are statistically different at the 95% confidence level (t-stat greater than t-critical), except for those in *Italic*, which are the comparisons between the youngest Pleistocene sample of *G. amplus* and most of the modern *G. californianus* samples.

	df	F value	Fcritical	P value
Carpometacarpus				
LENGTH				
RLB only	2	0.773	3.133	0.465
Plus modern	3	4.457	2.706	0.005
PROXIMAL WIDTH				
RLB only	2	0.274	3.133	0.761
Plus modern	3	2.965	2.706	0.036
MIDSHAFT WIDTH				
RLB only	2	2.145	3.133	0.124
Plus modern	3	8.328	2.706	0.000
MIDSHAFT DEPTH				
RLB only	2	0.398	3.133	0.672
Plus modern	3	4.601	2.706	0.004
DISTAL DEPTH				
RLB only	2	0.055	3.133	0.945
Plus modern	3	4.842	2.706	0.003
Femur				
LENGTH				
RLB only	2	2.345	3.209	0.107
Plus modern	3	5.734	2.700	0.001
PROXIMAL WIDTH				
RLB only	2	0.014	3.209	0.985
Plus modern	3	5.179	2.700	0.002
MIDSHAFT WIDTH				
RLB only	2	2.629	3.209	0.207
Plus modern	3	3.361	2.700	0.021
MIDSHAFT DEPTH				
RLB only	2	1.382	3.209	0.261
Plus modern	3	6.699	2.700	0.572
DISTAL DEPTH				
RLB only	2	1.321	3.214	0.302
Plus modern	3	47.230	2.700	0.000
Tibiotarsus				
LENGTH				
RLB only	2	3.135	3.153	0.051
Plus modern	3	24.006	2.721	0.000
PROXIMAL WIDTH				
RLB only	2	3.121	3.153	0.051
Plus modern	3	6.160	2.721	0.001
MIDSHAFT WIDTH				
RLB only	2	0.078	3.153	0.925
Plus modern	3	17.791	2.721	0.000
MIDSHAFT DEPTH				
RLB only	2	1.154	3.153	0.322
Plus modern	3	11.012	2.721	0.000
DISTAL DEPTH				
RLB only	2	0.331	3.153	0.719
Plus modern	3	24.991	2.721	0.065

Tarsometatarsus				
LENGTH				
RLB only	5	0.291	2.262	0.926
Plus modern	6	7.713	2.143	0.001
PROXIMAL WIDTH				
RLB only	5	2.140	2.259	0.062
Plus modern	6	2.822	2.139	0.001
MIDSHAFT WIDTH				
RLB only	5	2.257	2.259	0.020
Plus modern	6	11.772	2.139	0.000
MIDSHAFT DEPTH				
RLB only	5	2.288	2.392	0.017
Plus modern	6	5.890	2.139	0.000
DISTAL DEPTH				
RLB only	5	2.297	2.592	0.002
Plus modern	6	5.827	2.139	0.000

Table 4. One-way ANOVA results comparing temporally sequential samples of *Gymnogyps* to determine whether the different pit samples have significantly different means (null hypothesis = no difference in mean). df = degrees of freedom. P level = 0.05. RLB only = Pleistocene samples; Plus modern = Pleistocene plus Recent specimens. All the RLB samples yield no significant differences among the different pit assemblages (F value < Fcritical in each case), while when the modern specimens are added to the total sample, the differences are significant (F value > F critical).

Sample	Combined	RLB only	Modern only
HUMERI			
Total length	2.8	2.5	2.4
Prox. Width	4.5	3.6	4.2
Prox. Depth	10.2	3.9	5.0
Midshaft Width	6.1	5.5	4.2
Midshaft Depth	6.6	5.5	6.8
Distal Width	4.2	3.8	3.5
Distal Depth	5.3	5.3	5.2
Prox. Area	13.1	6.7	8.6
Midshaft Area	11.5	9.4	10.2
Distal Area	8.3	8.2	8.2
FEMORA			
Total length	7.9	2.9	2.3
Prox. Width	7.3	4.5	8.6
Prox. Depth	9.1	6.1	9.5
Midshaft Width	8.2	7.5	9.5
Midshaft Depth	5.2	4.8	6.3
Distal Width	5.0	3.6	3.8
Distal Depth	7.9	4.3	6.4
Prox. Area	13.5	8.5	8.0
Midshaft Area	11.6	9.0	3.2
Distal Area	12.3	7.3	8.5

Table 5. Comparison of coefficients of variation (CV) of representative bones of the condors in this study, showing that some of the CV values of the combined RLB and modern sample are too large for a single population (typically, CV > 10), but the RLB and modern samples each have a much lower CV typical of a single population.