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STASIS IN *NEOPHRONTOPS AMERICANUS* (EGYPTIAN VULTURES) FROM LA BREA TAR PITS DURING THE LAST GLACIAL-INTERGLACIAL CYCLE

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Abstract—According to conventional evolutionary theory, small changes in organisms from year to year, such as in the beaks of the Galápagos finches, are the mechanism by which birds evolve in response to environmental changes. Yet, all published studies of the fossil birds at Rancho La Brea have found no evidence of evolutionary responses to the glacial-interglacial cycle climate changes over the last 35,000 years. None of the birds exhibit any change in body size or limb proportions, even during the last glacial maximum about 18,000-20,000 years ago, when snowy coniferous forests replaced the southern California chaparral. To further assess this conclusion, we measured the leg bones of *Neophrontops americanus*, an extinct relative of the Egyptian vulture. We found complete stasis from 37,000 years ago until the end of the Pleistocene in size and limb robustness. This is consistent with the idea that small-scale changes, as seen in Galápagos finches, are random fluctuations around a mean and do not lead to speciation. Instead, the data show that speciation and lasting morphological change rarely occurs over short time scales and is only visible in long-term records of hundreds of thousands to millions of years.

INTRODUCTION

The Galápagos finch model of evolution is presented as an allopatric model with finches becoming isolated on islands near Galápagos and evolving to fit specific niches unique to their new localities (Weiner, 1995; Grant and Weiner, 1999; Grant and Grant, 2007). The finch anatomy did not overtly change on a major scale but instead on a very small scale. Singular morphological features adjusted to meet the needs of a new environment, such as beaks becoming elongated or more robust to better access novel and specific food supplies found on the new island habitats (Weiner, 1995; Grant and Weiner, 1999; Grant and Grant, 2007). The rapidity of the finch microevolution is due to being the first fauna to arrive on an empty island. Filling empty niches in these environments is conducive to rapid microevolution and new forms of finches (Weiner, 1995). As Weiner (1995) stated, "A woodpecker finch becomes possible only on an island without a woodpecker, a warbler finch only without a warbler."

Bird evolution has been previously thought of as a response to changing climate. However, the punctuated equilibrium model predicts morphological stasis over long spans of time despite environmental changes, including climate change (Eldredge and Gould, 1972). According to biological speciation theory, speciation is rare and difficult. As Eldredge and Gould (1972) explained, the catalyst for the rare speciation event is the occurrence of peripheral isolation and the resulting allopatric speciation. This happened when Darwin's finches became isolated on new islands where the gene pool became geographically separated from the original parental species (Weiner, 1995). This provides the inertia for complete speciation to reach novel homeostasis equilibria in a new environment (Eldredge and Gould, 1972).

Many multicellular animals exhibit stasis in the fossil record with rare and exceptional episodes of rapid morphological change, resulting in speciation (Jackson and Cheetham, 1999). Before significant extinction events, bursts of rare mass punctuated equilibria and exaptation transpired in the seas (Jackson and Cheetham, 1999). These are due to surviving animals filling important niches of dominant species slowly going extinct, causing chain reactions of speciation (Jackson and Cheetham, 1999). Corals and other Caribbean taxa experienced this over the course of 1 m.y. in the late Pliocene during glaciation and global cooling in the Northern Hemisphere (Jackson and Cheetham,

1999). Jackson and Cheetham (1999) wrote, "However, it is difficult to correlate biological change with any specific climatic event, although this is what one would expect if speciation and extinction occur as threshold events as implied by punctuated equilibria, rather than by gradual change."

Stasis is also typical of land animals as well. For example, most mammalian species persisted with no morphological change or speciation for 7 m.y. during the earliest Oligocene climatic crash, which was a severe climate event with a 13°C temperature drop, that led to a chain reaction of environmental and vegetational changes (Prothero and Heaton, 1996). The most common response of land mammals to an inhospitable environment is to move to a more habitable environment rather than to evolve gradually (Prothero and Heaton, 1996), another example of stasis as a result of punctuated equilibrium.

The Rancho La Brea tar pits (RLB) yield a collection of almost 3 million fossils available to test evolutionary responses during recent climate changes. The RLB oil seeps are rich in well-preserved bird fossils from the Pleistocene-Holocene, with over 133 species represented by over 85,000 individually preserved bones (Howard, 1962). Delicate bird bones, usually destroyed in diagenesis or by crushing, have been superbly preserved at RLB. With great care, these fossils have been added to the enormous collection from RLB, including multiple species from 50 ka to 9 ka (Akersten et al., 1983; Stock and Harris, 1992; Friscia et al., 2008). Radiocarbon dates have been determined from 16 RLB pits using mostly bone-derived collagen, which did not exchange carbon with the tar environment (O'Keefe et al., 2009).

Rancho La Brea also preserves an excellent climatic record based on data from snails, pollen, plant macrofossils, and oxygen isotopes (Warter, 1976; Coltrain et al., 2004; Ward et al., 2005). Drilling off the California continental shelf has produced deep-sea cores full of pollen samples, which preserve an excellent record of vegetation changes. Heusser's (1998) analysis of pollen grains found an alternation between an interglacial oak-chaparral flora and a glacial conifer forest in southern California over the past 60,000 years. About 59 ka, there was a change from oak and chaparral vegetation to pine-juniper-cypress woodlands, culminating about 24 ka. Between 24 and 14 ka (the last glacial maximum), the vegetation changed to a closed-cone juniper-ponderosa forest with abundant winter snow. During the glacial-interglacial transition from 14 to 10 ka, the landscape

returned to dominant oak-chaparral and coastal sagebrush with pulses of alder. The modern assemblage of oak-chaparral-herbaceous vegetation has covered the region for the past 10,000 years. Oxygen and carbon isotopic analyses suggest increased seasonal aridity during the last interglacial and previous glacial (Coltrain et al., 2004).

Bergmann's Rule predicts body size should peak when Rancho La Brea was at its coldest and snowiest during the last glacial maximum about 18,000-20,000 years ago. Clinal variation in size consistent with Bergmann's rule is present in most modern populations of the birds found at RLB. The most common bird from the tar pits, *Aquila chrysaetos* (Golden Eagle), shows considerable clinal variation today. There are larger-bodied subspecies in higher latitudes in Siberia and North America (Brown, 1968; Johnsgard, 1990). Yet there is no indication of larger body sizes in *A. chrysaetos* during the peak glacial interval of 18 ka to 20 ka (Molina and Prothero, 2011). Over that same period, no size differences were found in *Gymnogyps amplus* (ancestral California Condor), an extinct New World vulture and the third most common bird at RLB (Syverson and Prothero, 2010). Again and again, stasis occurs with no shape or size differences in the RLB birds. Examples include *Meleagris californica* (extinct California Turkey and the second most common RLB bird), *Haliaeetus leucocephalus* (Bald Eagle), *Caracara plancus prelutosus* (La Brea Caracara) (Fragomeni and Prothero, 2011), *Teratornis merriami* (extinct condor-like bird) (Gillespy et al., 2016), *Coragyps occidentalis* (Black Vulture) (Long et al., 2016), *Bubo virginianus* (Great Horned Owl) (Madan et al., 2015), *Tyto alba* (Barn Owl) (Madan et al., 2016), *Athene cunicularia* (Burrowing Owl), and Long-Eared Owl (*Asio otus*) (Madan et al., 2018). All the commonly preserved birds at RLB from the last 35,000 years have maintained stasis in size and morphology. Even the smallest birds, which have the smallest geographic range and might be expected to be more sensitive to climate change, showed no evolution during the climate transition. These birds include *Sturnella neglecta* (Western Meadowlark), *Corvus corax* (Raven), and *Pica nuttalli* (Yellow-Billed Magpie) (Long et al., 2020).

MATERIALS AND METHODS

We measured all the well-dated complete adult tarsometatarsi (TMTs) of *Neophrontops americanus* in the RLB collections (Figs. 1, 2). These specimens were identified and curated by Dr. Hildegard Howard over many decades as the curator of the bird collections. Based on counts of unique skeletal elements, the minimum number of individuals represented in the collection is 142 individuals of *N. americanus* (Howard, 1962, table 1).

Using the museum's Excel database for all RLB birds, we determined the pit number of each specimen. Pit 16, which has widely scattered radiocarbon ages (Marcus and Berger, 1984; O'Keefe et al., 2009; Fuller et al., 2015), produces a high percentage of the bird bones from RLB (Howard, 1962), but the dating is too poor to be used for time-series studies like this one, so all specimens from Pit 16 were excluded.

Of all the skeletal measurements, the tarsometatarsus is the most robust element in the bird skeleton, and therefore, it is the most likely to be preserved intact. The TMT is considered a good proxy for within-species body size variation and has been widely used by ornithologists and paleo-ornithologists for that purpose. Syverson and Prothero (2010) made a more extensive set of measurements for *Gymnogyps amplus*. They found no differences between the trends shown in TMT measurements and those of the other parts of the skeleton. We measured only complete, undeformed adult TMTs to avoid artifacts resulting from breakage or ontogenetic growth. For comparison, we also measured both TMTs of a single specimen of the living Egyptian vulture, *Neophron percnopterus*, from the American Museum of

Natural History in New York. This individual was not included in the statistical analyses but is plotted in Figure 3.

We measured a total of 138 *Neophrontops americanus* TMTs and two *Neophron* TMTs with digital metric calipers. Two dimensions were measured (Fig. 2): maximum shaft length between the lengthiest proximal-distal ends of the TMT; and midshaft transverse width of the TMT. As is visible in Figure 2, the TMT of *Neophrontops* is approximately square at midshaft (transverse and anteroposterior width are approximately the same). This attribute allowed us to examine shape and size by calculating a robustness index, the cross-sectional area (the square of the width) divided by the length.

Once the pit dates were added to the spreadsheet, we performed fundamental statistical analysis using Excel and R. Almost none of the samples from the pits were normally distributed (Shapiro-Wilk method, threshold $p < 0.05$), so we used the nonparametric Kruskal-Wallis test. This allowed us to determine whether any pit samples were significantly different from the pooled mean of all other measurements. The time series of each measurement was also fit to evolutionary models (directional random walk, undirected random walk, stasis, and strict stasis) in R using the *paleoTS* package.

RESULTS

The basic statistics of the three different TMT samples are shown in Table 1 and plotted in Figures 3 and 4. The results from the statistical comparisons are shown in Table 2, and the results from time series analysis in Table 3. Examining Figures 3 and 4, it is clear that size and robustness are static, despite all the climate changes going on through this time interval. None of the species were significantly different in size or shape between the 37 ka and the Holocene. This was supported by the analysis of variance done with the Kruskal-Wallis test for non-parametric data, which found no significant difference between sample medians. In other words, no individual sample of *Neophrontops*

FIGURE 1. Mounted skeleton of *Neophrontops americanus* and a restoration of the bird behind it, on display at the La Brea Tar Pits Museum. (Photo by D.R. Prothero)

FIGURE 2. Image of a *Neophrontops americanus* TMT, showing the measurement landmarks. Note approximately square midshaft cross-section. Scale bar in cm.

FIGURE 3. Plot of length of tarsometatarsi of La Brea *Neophrontops americanus* and AMNH *Neophron percopterus* through the last 37 ka at RLB. Open diamonds are individual specimens; solid squares indicate mean. Note that the 0 ka sample is a single modern individual of *Neophron percopterus*.

FIGURE 4. Plot of calculated robustness of tarsometatarsi of La Brea *Neophrontops americanus* and AMNH *Neophron* through the last 37 ka at RLB. Open diamonds are individual specimens; solid squares indicate mean. Note that the 0 ka sample is a single modern individual of *Neophron*.

americanus was statistically different from the pooled samples of all the measurements. Thus, *N. americanus* did not change in size or shape, even at the last glacial maximum at 18-20 ka, when the climate at La Brea was much colder and snowier. There was no increase in body size as might be expected from Bergmann's Rule, or were the limbs more robust as might be expected from Allen's Rule. The TMTs of the single individual of *Neophron percopterus* are both substantially shorter and proportionally narrower than the *Neophrontops* means, resulting in a similar shape to the *Neophrontops* TMTs.

DISCUSSION

Significant clinal size variations due to Bergmann's Rule have been previously documented in Golden Eagles (Molina and Prothero, 2011), Bald Eagles and Caracaras (Fragomeni and Prothero, 2011), Great Horned Owls (Madan et al., 2015), Barn Owls (Madan et al., 2016), and Burrowing Owls (Duncan, 2003; König and Weick, 2008) as well as all three smaller passerine birds analyzed by Long et al. (2018). This leads to the expectation of declining size and robustness spanning the last glacial maximum and the early Holocene, the time covered by the RLB specimens. However, neither the body size nor limb robustness was significantly greater in these birds during glacial periods (18-20 ka) of coniferous forests and frequent snow at low elevations, compared to the near-modern hot Mediterranean climate and chaparral vegetation around 15-10 ka.

All of the larger RLB mammals exhibit similar stasis throughout the same climate transition, none of which have size or shape differences within the last 35 ka (Prothero and Raymond, 2008, 2011; DeSantis et al., 2011; Raymond and Prothero, 2011; Madan et al., 2011; Prothero et al., 2012). Numerous studies
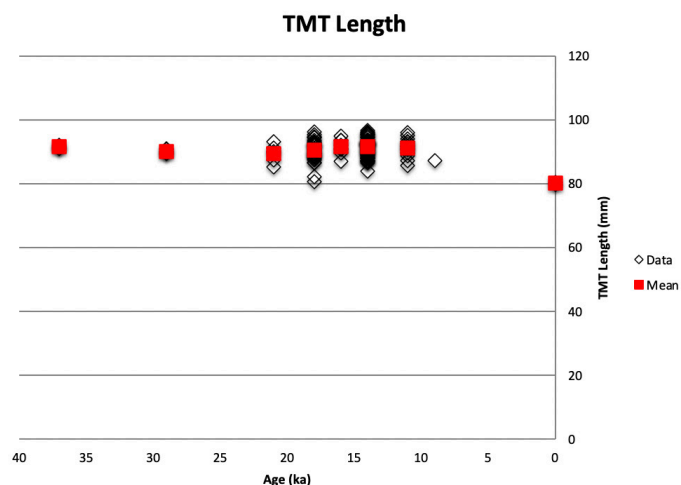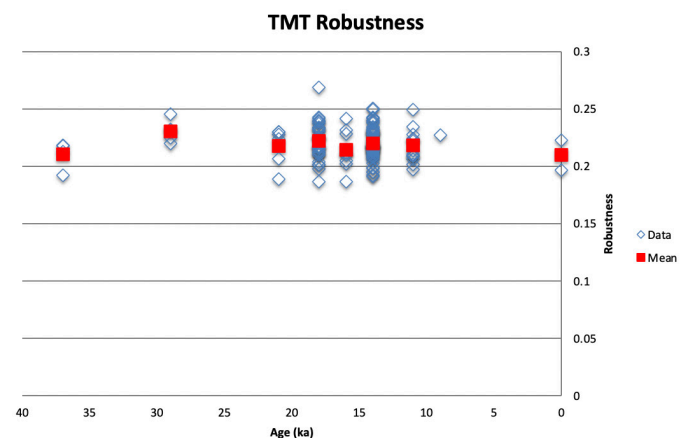
have documented stasis (Barnosky, 1994, 2005) of body size in nearly every Pleistocene mammal lineage at other fossil sites; many of these species even ranged throughout several glacial-interglacial cycles. Clearly, Pleistocene birds and mammals of all sizes show no expected increases in size or robustness during climate changes during the last several glacial-interglacial cycles.

A lively and long-lasting debate continues in the 50 years since the original punctuated equilibria model was introduced by Eldredge and Gould (1972) about the mechanisms that provoke evolution and the prevalence of stasis. Short-term and small-scale changes, such as beak size changes in Galápagos finches, have been the modern neontologists' preferred model for how evolution occurs (Weiner, 1995). Yet, long-term stasis in the RLB mammals and birds conflicts with the notion that climate change is the culprit for evolutionary change. Stasis throughout deep time in the geological timescale is the emerging consensus and is consistent with our results. According to Hunt et al. (2015), when examining an array of geological time series, 38% of best fit by stasis models have a wide range of taxa and

TABLE 1. Basic statistics of La Brea *Neophrontops americanus* (roman) and AMNH *Neophron* (italics) TMTs. SD = Standard Deviation; CV = Coefficient of Variation (= 100 x SD/Mean). Note that all premodern specimens are *Neophrontops americanus* and all modern specimens are *Neophron*.

Character	Age (ka)	N	Mean	SD	CV
Length	37	4	91.6	0.4	0.5
	29	5	90.2	3.0	0.6
	21	6	89.6	2.8	3.1
	18	33	90.6	2.4	3.7
	16	8	91.6	3.4	2.6
	14	68	91.7	2.7	2.9
	11	14	89.9	0.6	3.3
	0	*2*	*80.2*	*0.4*	*0.5*
Midshaft transverse width	37	4	6.1	0.4	5.8
	29	5	6.6	0.3	4.7
	21	6	6.2	0.5	7.6
	18	33	6.4	0.4	6.6
	16	8	6.3	0.5	8.2
	14	68	6.4	0.4	6.2
	11	14	6.2	0.5	7.7
	0	*2*	*5.3*	*0.5*	*9.2*

TABLE 2. Nonparametric analysis of variance (Kruskal-Wallis test) for *N. americanus* TMTs. No measurement had a significant difference between any two pit samples, so no further analysis was performed. The modern Egyptian vulture specimen was excluded from this analysis.

	K-W chi-squared	df	p-value	significant (p<0.00625)
LENGTH	8.44	7	0.2953	0
WIDTH	5.08	7	0.6498	0
ROBUSTNESS	6.5	7	0.483	0

TABLE 3. Results of time series analysis. No directional trend was supported for either measurement. Midshaft transverse width was best fit by the strict stasis model, and length by random walk (URW). The calculated robustness was also best modeled as strict stasis. The modern Egyptian vulture specimen was excluded from this analysis.

GRW	URW	Stasis	StrictStasis
0.017	0.548	0.394	0.042
0.003	0.098	0.098	0.801
0.003	0.098	0.098	0.801

temporal resolutions, especially for sub-million-year fluctuation time-series driven by global temperatures.

There are many attempts to explain such widespread stasis in the fossil record, but few are successful. Estes and Arnold (2007) consider the cause of stasis to be stabilizing selection, in which a population is pushed towards a mean trait, to understand and explain divergence. However, stabilizing selection is not applicable over geological time scales, and assumes the environment is stable (Lieberman and Dudgeon, 1996). In our case, the environment changes drastically and is not stable. Inhibition of minor evolutionary change by developmental canalization has been suggested as an explanation of stasis in the past, but has since been out of favor (Gould, 2002; Eldredge et al., 2005). The theory of developmental canalization that inhibited small-scale changes to explain stasis has gone out of favor (Gould, 2002; Eldredge et al., 2005). The suggestion of organisms not responding due to the rapidity of climate changes of the Pleistocene has been suggested (Bennett, 1990, 1997). However, the Galápagos finch populations changed over a few years, which is a much shorter time scale.

Uyeda et al. (2011) examined wide ranges of paleontological and neontological morphological time-series studies, spanning years to tens of millions of years. Small-scale change studies observing years to decades by neontologists were best described as bounded fluctuations, which are variations around a generally constrained mean and not accumulated over long periods (Uyeda et al., 2011). Long-lasting changes due to evolution arises over deep time and spans millions of years, transpiring with extremely infrequent yet substantial phenotypic bursts of change far beyond the time scales of bounded fluctuations. Although Uyeda et al. suggest that occasional short-term bursts of phenotypic change can result in permanent shifts in adaptive zones, our results show no sign of any such shifts persisting over the 1000+ year timescale even during intervals of significant environmental fluctuations.

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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., 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 University Press, Cambridge.

Brown, L., 1968, Eagles, Hawks, and Falcons of the World: McGraw-Hill, New York.

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.

DeSantis, S.N., Prothero, D.R., and Gage, G.L., 2011, Size and shape stasis in late Pleistocene horses and camels from Rancho La Brea during the last glacial-interglacial cycle: Bulletin of the New Mexico Museum of Natural History, v. 53, p. 505-510.

Eldredge, N., 1999, The Pattern of Evolution: W. H. Freeman, New York.

Eldredge, N., and Gould, S.J., 1972, Punctuated equilibria: an alternative to phyletic gradualism; in Schopf, T.J.M., ed., Models in Paleobiology: Freeman, Cooper and Company, San Francisco, p. 82-115.

Eldredge, N., Thompson, J.N., Brakefield, P.N., Gavrilet, S., Jablonski, D., Jackson, J.B.C., Lenski, R.E., Lieberman, B.S., McPeek, M.A., and Miller, W., 2005, The dynamics of evolutionary stasis: Paleobiology, v., 31, p. 133-145.

Estes, S., and Arnold, S., 2007, Resolving the paradox of stasis: models with stabilizing selection explain evolutionary divergence on all timescales: American Naturalist, v. 169, p. 227-244.

Fragomeni, A., and Prothero, D.R., 2011, Stasis in late Quaternary birds from the La Brea tar pits during the last glacial-interglacial cycle: New Mexico Museum of Natural History, Bulletin 53, p. 511-516.

Fuller, B.T., Harris, J.M., Farrell, A.B., Takeuchi, G., and Southon, J.R., 2015, Sample preparation for radiocarbon dating and isotopic analysis of bone from Rancho La Brea: Natural History Museum of Los Angeles County, Science Series, n. 42, p. 151-167.

Friscia, A.R., Van Valkenburgh, B., Spencer, L., Harris, J.M., 2008, Chronology and spatial distribution of large mammal bones in Pit 91, Rancho La Brea: Palaios, v. 23, p. 35-42.

Geary, D.H., 2009, The legacy of punctuated equilibrium; in Allmon, W.D., Kelley, P.H., Ross, RM, eds., Stephen Jay Gould: Reflections on His View of Life: Oxford University Press, Oxford, p. 127-147.

Gillespy, D.H., Prothero, D.R., and Syverson, V.G.P., 2016, Stasis in teratorns from the La Brea tar pits during the last glacial-interglacial cycle: New Mexico Museum of Natural History, Bulletin 74, p. 67-71.

Gould, S.J., 2002, The Structure of Evolutionary Theory: Harvard University Press, Cambridge, Massachusetts.

Grant, P.R., and Weiner, J., 1999, The Ecology and Evolution of Darwin's Finches: Princeton University Press, Princeton.

Grant, P.R., and Grant, B.R., 2007, How and Why Species Multiply: The Radiation of Darwin's Finches: Princeton University Press, Princeton.

Hallam, A., 2009, The problem of punctuational speciation and trends in the fossil record; in Sepkoski, D., and Ruse, M., eds., The Paleobiological Revolution: University of Chicago Press, Chicago, 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., 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.

Hunt, G., Hopkins, M.J., and Lidgard, S., 2015, Simple versus complex models of trait evolution: Proceedings of the National Academy of Sciences, v. 112, p. 4885-4890.

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: Smithsonian Institution Press, Washington, DC.

Lieberman, B.S., and Dudgeon, S., 1996, An evaluation of stabilizing selection as a mechanism for stasis: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 12, 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.

Long, K.L., Prothero, D.R., and Syverson, V.J.P., 2016, Stasis in Rancho La Brea black vultures (Coragyps occidentalis) over the last glacial-interglacial cycle: New Mexico Museum of Natural History, Bulletin 74, p. 121-125.

Long, K. L., Prothero, D. R., and Syverson, V. J. P., 2020, How do small birds evolve in response to climate change? Data from the long-term record at La Brea tar pits: Integrative Zoology, v. 15, p. 249-261.

Madan, M., Prothero, D.R., and Sutyagina, A., 2011, Did felids from Rancho La Brea change size or shape in the last Pleistocene? New Mexico Museum of Natural History, Bulletin 53, p. 554-563.

Madan, M., Prothero, D.R., and Syverson, V.J.P., 2015, Stasis in great horned owls from the La Brea tar pits during the last glacial-interglacial cycle: New Mexico Museum of Natural History, Bulletin 65, p. 221-225.

Madan, M., Prothero, D.R., and Syverson, V.J.P., 2016, Stasis in barn owls from the La Brea tar pits during the last glacial-interglacial cycle: New Mexico Museum of Natural History, Bulletin 74, p. 153-157.

Madan, M.A., Prothero, D.R., and Syverson, V.J.P., 2019, Stasis in smaller owls from Rancho La Brea during the last glacial-interglacial climate change: Palaeontologica Electronica, v. 22, no. 3, p. 1-12. Doi.org/10.26879/960

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. University of Chicago Press, Chicago, p. 159-188.

Molina, S., and Prothero, D.R., 2011, Evolutionary stasis in late Pleistocene golden eagles: New Mexico Museum of Natural History, Bulletin 53, p. 64-569.

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.

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. University of Chicago Press, Chicago, p. 149-175.

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., and Raymond, K.R., 2008, Variability and sexual size dimorphism in Pleistocene ground sloths (Xenarthra): New Mexico Museum of Natural History, Bulletin 44, p. 331-334.

Prothero, D.R., and Raymond, K.R., 2011, Stasis in late Pleistocene ground sloths (*Paramylodon harlani*) from Rancho La Brea, California: New Mexico Museum of Natural History, Bulletin 53, p. 624-628.

Prothero, D.R., Syverson, V.J.P., Raymond, K.R., Madan, M.A., Fragomeni, A., Molina, S., Sutyagina, A., DeSantis, S., and Gage, G.L., 2012, Stasis in the face of climatic change in late Pleistocene mammals and birds from Rancho La Brea, California: Quaternary Science Reviews, v. 56, p. 1-10.

Raymond, K.R., and Prothero, D.R., 2011, Did climate change affect size in late Pleistocene bison? New Mexico Museum of Natural History, Bulletin 53, p. 636-640.

Sepkoski, D., and Ruse, M., eds., 2009, The Paleobiological Revolution: University of Chicago Press, Chicago.

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.P., and Prothero, D.R., 2010, Evolutionary patterns in late Quaternary California condors: PalArch Journal of Vertebrate Paleontology, v. 7, no. 10, p. 1-18.

Uyeda, J.C., Hansen, T.F., Arnold, S., and Pienaar, J., 2011, The million-year wait for macroevolutionary bursts: Proceedings of the National Academy of Sciences, v. 108, p. 15908-15913.

Ward, J.W., Harris, J.M., Cerling, T.E., Wiedenhoeft, A., Lott, M.J., Dearing, M., Coltrain, J.B., and Ehleringer, J., 2005, Carbon starvation in glacial trees recovered from the La Brea tar pits, southern California: Proceedings of the National Academy of Sciences, v. 102, no. 3, 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, v. 2, p. 32-39.

Weiner, J., 1995, The Beak of the Finch: A Story of Evolution in our Own Time. Vintage. New York.