HOW DID LA BREA SWAINSON'S HAWKS (*BUTEO SWAINSONI*) RESPOND TO CLIMATE CHANGE?

CASEY CLEAVELAND[1], DONALD R. PROTHERO[1,2], and V.J.P. SYVERSON[3]

[1]Department of Geological Sciences, Cal Poly Pomona, 3801 W. Temple Ave., Pomona, CA 91768 USA; ccleaveland@cpp.edu;
[2]Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, CA 90007;
[3]Dept. Earth and Physical Sciences, University of California, Davis, CA. 95616

Abstract—The Rancho La Brea tar pits are one of the richest fossil deposits in the world, with over 3 million fossils, including 85,000 bird fossils representing 133 species. These collections give us the opportunity to examine how Pleistocene birds responded to climate changes of the last 37 ka. The last glacial maximum occurred about 18 ka to 20 ka, causing the ecosystem of southern California to shift from chaparral to snowy coniferous forests. This change might be expected to impact body size and limb robustness (following Bergmann's Rule and Allen's Rule), but none of the La Brea birds examined so far display changes in body size or limb proportions. To further test this, we measured the leg bones of *Buteo swainsoni*, the Swainson's Hawk, and found stasis of size and limb robustness beginning 37 ka until the end of the Pleistocene, followed by fluctuations in robustness during the Holocene. The specimens from 27 ka years ago were the only ones that were significantly different from the pooled samples, but there was no size change during the peak cooling from 18 ka to 20 ka. These results agree with every other La Brea bird that has been studied in showing stasis and resistance to small-scale change, even in the face of major climate change, but altering in response to inferred post-Pleistocene ecological changes.

INTRODUCTION

Rancho La Brea tar pits (RLB) is an excellent place to study evolution over long times spans, since this oil seep deposit yields over 3 million fossils, spanning the interval from 37 ka to 9 ka. It yields an incredible numbers of Pleistocene-Holocene bird fossils, with over 85,000 individual bones representing at least 133 species (including 19 extinct species) (Howard, 1962). The tar is excellent at trapping and preserving their delicate bones, so there are enormous collections that represent many different species and many different time intervals ranging from about 50 ka to 9 ka (Akersten et al., 1983; Stock and Harris, 1992; Friscia et al. 2008).

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). The best evidence comes not from fossils of RLB itself, but from pollen samples from deep-sea cores drilled just offshore in the California continental shelf preserve an even better record of the changes in vegetation. Heusser's (1998) analysis of pollen grains found an alternation between an interglacial oak-chaparral flora and a snowy 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, then 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 region has been covered by the modern assemblage of oak-chaparral-herbaceous vegetation for the past 10,000 years. Oxygen and carbon isotopic analyses suggest there was increased seasonal aridity during the last interglacial and previous glacial (Coltrain et al., 2004).

In addition, many of the pits have been radiocarbon dated (Marcus and Berger, 1984; O'Keefe et al., 2009; Fuller et al., 2017), so we have a firm geochronology and sequence of ages for all the separate pit samples, and can determine which fossils represent the peak glacial about 18 ka to 20 ka, and which ones are from older and younger pits.

The RLB fossils are of particular interest, because they can potentially test various evolutionary models about bird evolution. Currently, most textbooks in evolution feature the Galápagos finch as a model of how species respond to climate change (Weiner, 1995; Grant and Weiner, 1999; Grant and Grant, 2007). These birds have been well documented, not only in their ability to change rapidly into different ecomorphs, once they were blown to unpopulated islands where they had no competition, but also in their rapid response over just a few years to short-term climate change. For example, after several years of drought, finches who had slightly more robust beaks survived, because they could break open the thick-walled seeds that had been previously ignored in years of abundant rainfall and plenty of seeds to eat. This kind of change over just a few years is frequently used as an exemplar of how species respond to environmental change over years to decades, and by extension, how speciation and adaption occur as a process. Similar rapid small-scale adaptations to environmental change have also been documented in other living birds, such as Siberian warblers, English sparrows, cuckoos, cowbirds, red-winged blackbirds, and many others (Weiner, 1995).

These notions of species which are infinitely responsive to environmental change, and evolve in a matter of just years or decades, directly contradicts the "punctuated equilibrium" model of evolution, which predicts stasis over centuries to thousands to millions of years, despite environmental change (Eldredge and Gould, 1972; Eldredge, 1999; Gould, 2002). Fifty years of research has confirmed that nearly all multicellular animals show stasis (Jackson and Cheetham, 1999; Gould, 2002; Jablonski, 2000, 2008; Geary, 2009; Princehouse, 2009; Hallam, 2009; Sepkoski and Ruse, 2009; Hunt et al., 2015), with almost no examples of gradual change over longer time scales. Some of these studies demonstrate that, even during intervals of climate change, most organisms are static and do not change size or shape in response to century- to millennium-term changes in climate (*e.g.* Coope, 1979; Davis, 1983; Bennett, 1990; Prothero and Heaton, 1996; Prothero, 1999; Prothero et al., 2012).

So how would we expect birds of RLB to respond to the dramatic changes from 18 ka to 20 ka and the last glacial maximum? One response might be shorter limbs and other appendages in colder climates (Allen's Rule). Another might be size increase, following Bergmann's rule, which predicts larger body size in colder climates. Body size should peak when Rancho La Brea was at its coldest and snowiest during the last glacial maximum. Clinal size variation consistent with Bergmann's rule

is present in modern populations of most of the birds at RLB, so we know that today they have certain climate preferences, and their body size is changed accordingly. For example, the most commonly preserved bird in the tar pits, the Golden Eagle (*Aquila chrysaetos*), shows considerable clinal variation today, with larger-bodied subspecies in higher latitudes in both Siberia and North America (Brown, 1968; Johnsgard, 1990). Yet Golden Eagles show no indication of larger body sizes during the peak glacial interval at 18-20 ka (Molina and Prothero, 2011). There were no size differences over the same period in the third most common bird, the extinct California Condor *Gymnogyps amplus* (Syverson and Prothero, 2010), nor in the second most common bird, the extinct California turkey (*Meleagris californica*), the bald eagle (*Haliaeetus leucocephalus*), or the La Brea caracara (*Caracara plancus prelutosus*) (Fragomeni and Prothero, 2011). According to Gillespy et al. (2016) there are no size or shape changes in the huge extinct condor-like *Teratornis merriami*. There was complete size and shape stasis in the Black Vultures (*Coragyps occidentalis*) (Long et al., 2016), in the Great Horned Owls (*Bubo virginianus*) (Madan et al., 2015), in the Barn Owls (*Tyto alba*) (Madan et al., 2016), the Burrowing Owl (*Athene cunicularia*) and the Long-Eared Owl (*Asio otus*) (Madan et al., 2018). For the last 35,000 years, all the commonly preserved birds at RLB have maintained steady size and shape. Even the small birds (Western Meadowlark, *Sturnella neglecta*; Raven, *Corvus corax*; and Yellow-Billed Magpie, *Pica nuttalli*), usually expected to be more sensitive to environmental change, did not change during the climate transition (Long et al., 2020).

Another bird which could potentially test this idea is Swainson's Hawk (*Buteo swainsoni*). A medium-sized hawk which preys mainly on insects (especially grasshoppers and locusts), their modern populations spend their Northern Hemisphere springs and summers in grasslands of central and western North America, then migrate to Argentina in the Austral Summer (November-February), and avoid winter in the Northern Hemisphere (Brown, 1968; Johnsgard, 1990). It is abundantly represented by specimens from many different pits at RLB, so it offers an opportunity to further test our conclusion that birds at RLB did not change size or shape in response to Late Pleistocene climate change. However, migratory birds tend not to follow Bergmann's Rule compared to sedentary birds (Meiri and Dayan, 2003), so we might not see the same patterns with these highly migratory birds that we see with the rest of the birds.

MATERIALS AND METHODS

We measured the all the well-dated complete adult tarsometatarsi (TMTs) of *Buteo swainsoni* in the RLB collections (which were all identified and curated by Hildegard Howard over much of the twentieth century). Of all the skeletal measurements, the tarsometatarsus is by far the most robust element in the bird skeleton and therefore 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 in the La Brea condor (*Gymnogyps amplus*) and found no differences between the trends shown in TMT measurements and those of the other parts of the skeleton.

Based on counts of unique skeletal elements, the minimum number of individuals represented in the collection is 130 individuals of *Buteo swainsoni* (Howard, 1962, Table 1). We measured only complete, undeformed adult TMTs to avoid artifacts resulting from breakage or ontogeny. For comparison, we also measured TMTs of extant populations of *Buteo swainsoni* in the collections of the University of California Museum of Comparative Zoology.

Using the Page Museum's database of RLB bird specimens, we determined the pit number of each specimen. Pit 16, which has problematic, widely scattered radiocarbon ages (Marcus and Berger, 1984; O'Keefe et al., 2009), 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.

This amounted to 200 TMTs that were suitable for analysis (counting both right and left TMTs), corresponding to a minimum number of 101 individuals. Two dimensions were measured (Fig. 1) using digital metric calipers: maximum shaft length between the longest proximal-distal ends of the TMT; and midshaft transverse width of the TMT. These values allowed us to calculate a robustness index, the cross-sectional area (calculated from the width) divided by the length, to examine shape as well as size.

Once the pit dates had been added to the spreadsheet, we performed basic statistical analysis using Excel, PAST and R. The significance of differences between samples was tested using the Kruskal-Wallis nonparametric ANOVA. Any samples that had significant differences were also tested for differences in their distribution from the rest of the data set using a pairwise Mann-Whitney U test. 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 *B. swainsoni* data are shown in Table 1. The results are plotted in Figures 2 and 3. As is apparent from these plots, there is no obvious response in the length of the TMT or its robustness at the peak glacial around 18 ka to 20 ka, when some kind of change might be predicted. According to Allen's rule, the limbs should get more robust, and according to Bergmann's rule, overall body size should increase in colder climates, but neither appears to happen.

Testing for normality (Shapiro-Wilk test, $p = 0.05$) showed that, although the whole data set for each measurement was normally distributed, most of the individual pit samples were not, with the exception of the 9 ka and 0 ka samples. We therefore used the nonparametric Kruskal-Wallis ANOVA to determine whether any pit sample was significantly different from the pooled mean of all other measurements. The results, given in Table 2, indicated significant differences between samples in both width and robustness at the $p = 0.00625$ (i.e., $p = 0.05$ with Bonferroni correction). These results did not change when the modern (0 ka) specimens were omitted. However, when all Holocene (9 ka and 0 ka) specimens were omitted, the differences between the remaining groups were not significant.

We proceeded to a pairwise test for differences to determine which samples were significantly different, using a Mann-Whitney U test at p = 0.00625 to test each age group against all other specimens combined. The results are summarized in Table 3. As expected from the ANOVA results, there were no significant differences in length for any group. The distributions of width and robustness were significantly different for the 27 ka, 9 ka, and 0 ka groups. Since length was not distinguishable, differences in width naturally translate to differences in robustness, so the significantly different groups were the same for width and robustness. The 27 ka and 0 ka groups were wider than the mean of all other groups, and the 9 ka group was narrower. This result was also unchanged when the modern (0 ka) specimens were omitted.

Time series analysis was performed using R package paleoTS; the results, given in Table 4, showed that stasis was the best model for all measurements. This reflects the presence of uncorrelated variation around a constant mean and a lack of any steady upward or downward trend in the distributions of any measurement. However, the strict stasis model, which

FIGURE 1. Image of a La Brea *Buteo swainsoni* TMT, Page Museum catalog number G3364, showing the measurement landmarks. Scale bar in cm.
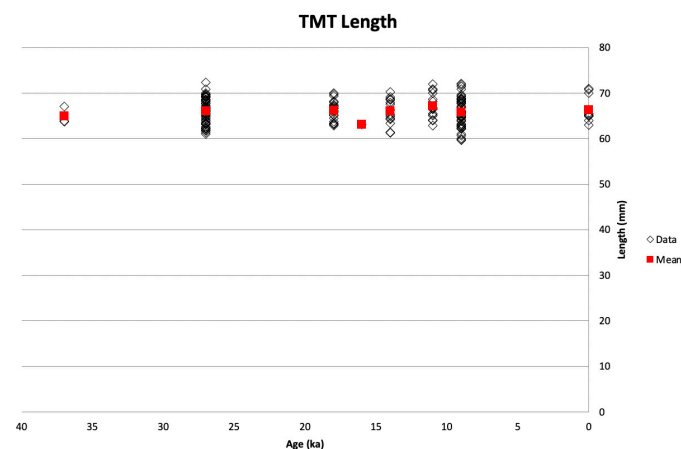

FIGURE 2. Plot of the lengths of Swainson's hawk TMTs through time. Open diamonds = individual specimens; red squares = mean for each pit.

expects both no overall trend and no real differences between samples, was not favored, consistent with the pairwise Mann-Whitney U test results. When the modern (0 ka) specimens were omitted, the favored model for length switched to strict stasis, which expects no trend and no uncorrelated variation; when the Holocene (9 ka and 0 ka) specimens were omitted, strict stasis was favored for all measurements.

DISCUSSION

Our results for the Swainson's hawks are interesting because they constitute an exception to the pattern found in most of the animals measured at Rancho La Brea. However, the differences between age groups do not indicate a decrease in body size or robustness between the last glacial period and the interglacial, which we would expect to occur between the 18 ka and 11 ka samples. Instead, the Pleistocene is significantly different from either of the Holocene samples, which are also different from each other.

As mentioned above, none of the RLB birds examined so far show any statistically significant change in size or limb robustness during the last glacial maximum, when Ponderosa pines and winter snow covered the area that is now Hollywood and Rancho La Brea (Syverson and Prothero, 2010; Fragomeni and Prothero, 2011; Molina and Prothero, 2011; Madan et al., 2015; Gillespy et al., 2016; Long et al., 2016; Madan et al., 2016; Madan et al., 2018; Long et al., 2020). Similar stasis through this climate transition is documented in all the larger mammals of RLB (Prothero et al., 2012; Prothero and Raymond,
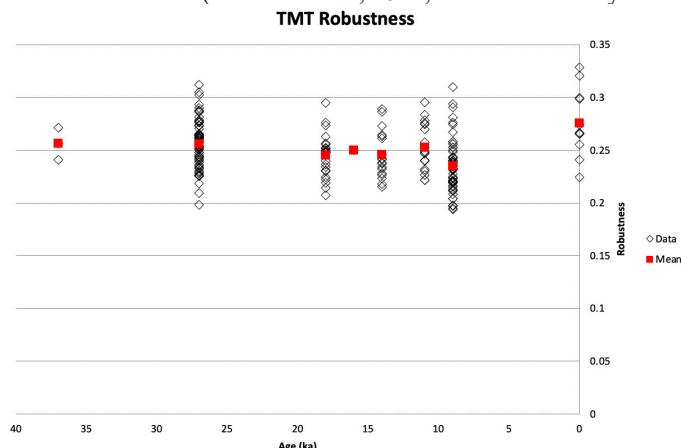

FIGURE 3. Plot of the robustness (midshaft cross-sectional area divided by length) of Swainson's hawk TMTs through time. Symbols as in Figure 2.
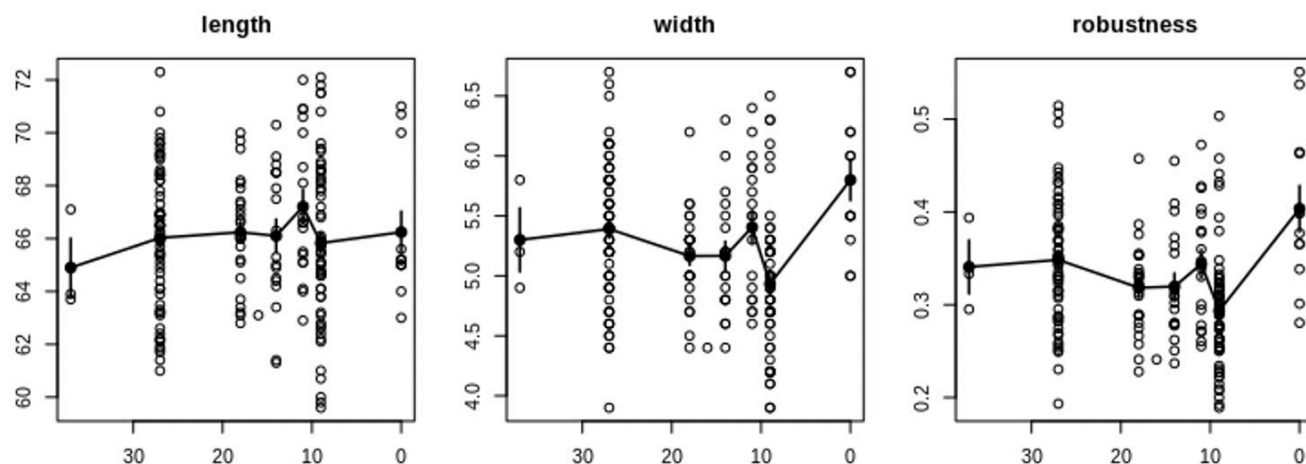
Buteo swainsoni TMT

FIGURE 4. Time series of *Buteo swainsoni* TMT length, width, and robustness. Open circles are specimens; filled circles connected by lines are averages for each age cohort.

TABLE 1. Basic statistics of La Brea *Buteo swainsoni* TMTs. SD = Standard Deviation; CV = Coefficient of Variation (= 100 x SD/Mean)

Character	Age (ka)	N	Mean	SD	CV
Length	37	3	64.9	1.9	2.9
	27	62	66.0	2.7	4.0
	18	25	66.2	2.0	3.0
	16	1	63.1	—	—
	14	17	66.1	2.7	4.0
	11	17	67.2	2.7	4.1
	9	57	65.8	3.0	4.7
	0	11	66.2	2.7	4.1
Midshaft transverse width	37	3	5.3	0.5	8.7
	27	62	5.3	0.6	10.9
	18	25	5.2	0.4	7.4
	16	1	4.4	—	—
	14	17	4.2	0.5	9.8
	11	17	5.4	0.6	10.6
	9	57	4.9	0.6	12.0
	0	11	5.8	0.6	10.1

2008, 2011; DeSantis et al. 2011; Raymond and Prothero 2011; Madan et al. 2011). Most measurements on most species are static, in some cases they have some random variation, but in no case have we documented the trend toward larger or more robust individuals during the cold times of 18 ka to 20 ka that would be predicted by Bergmann's or Allen's rule. Numerous other studies (Barnosky, 1994, 2005) document stasis in body size in nearly every Pleistocene mammal lineage at other fossil sites, even though many of these species ranged through several glacial-interglacial cycles. Taken together, it is clear that Pleistocene birds and mammals of all sizes show none of the expected increases in size or robustness during climate changes over the entire span of several glacial-interglacial cycles.

These results demonstrate a departure from this pattern in the case of the Swainson's hawks at RLB. When the Pleistocene

TABLE 2. Kruskal-Wallis nonparametric analysis of variance for all groups. Width and robustness have groups significantly different from mean at the corrected p-value of 0.00625.

	K-W chi-squared	df	p-value	significant (p<0.00625)
LENGTH	5.25	7	0.62922491	0
WIDTH	33.1	7	2.537e-05	1
ROBUSTNESS	36.09	7	6.96e-06	1

TABLE 3. Mann-Whitney *U* test comparing specimens in each age category to those in the union of all other age categories, for those measurements for which the Kruskal-Wallace non-parametric ANOVA found significant differences between groups (Table 2). The width and robustness of the 27ka, 9ka, and modern groups of specimens are significantly different from the sample overall at the corrected p-value of 0.00625 indicates significance at the p<0.00625 level.

Age (ka)	Width.U	Width.p	Robustness.U	Robustness.p
37	315.5	0.831687	346	0.602903
27	5327.5	0.005686*	5451	0.002023*
18	2155	0.732243	2144.5	0.704064
16	15	0.1453	16	0.150961
14	1500.5	0.582077	1501	0.584271
11	1929	0.197836	1881.5	0.279502
9	2423	6e-06*	2319	2e-06*
0	1729.5	0.001662*	1736	0.001512*

and Holocene data are all analyzed together, the 27 ka sample stands out as significantly different from the rest in its width distribution, as do the 9 ka and 0 ka samples. However, the 27 ka sample is much larger than the others (N = 63, compared to N = 66 for all other Pleistocene samples combined), and therefore its statistical significance will tend to be overemphasized in this analysis. The 9 ka sample is also very large (N = 58). If the Holocene samples are omitted, it is apparent that the 27 ka sample is not significantly different from the other Pleistocene data, which suggests that the difference being detected is primarily between the Pleistocene specimens (dominated by the 27 ka sample), which are more robust on average, and the 9 ka specimens, which are more gracile. The modern specimens, however, are more robust than any other group, which forecloses the possibility that this is the Allen's rule climate-driven evolutionary trend that we were looking for. Instead, these results indicate stasis through Late Pleistocene climatic change followed by changes in response to the ecological disruptions of the Holocene.

In the 50 years since the original "punctuated equilbria" model was introduced by Eldredge and Gould (1972), there has been a long debate over how evolution occurs, and what the prevalence of stasis means. Conventional neontologists have focused on small-scale changes like the beak sizes in Galápagos finches and other small birds as the exemplar of how evolution occurs in birds and other animals (Weiner, 1995). However, the evidence of long-term stasis in all the birds and mammals of RLB despite strong selection from climate change conflicts with this notion of the changes powering evolutionary change. These results, however, are consistent with an emerging consensus about the prevalence of stasis over paleontological timescales. Looking at a wide array of paleontological time series, Hunt et al. (2015) found that 38% of them best fit by a stasis model across a wide range of taxa and temporal resolutions, but especially for time series driven by sub-million-year fluctuations in global temperature.

How to explain such stasis? Stabilizing selection has been proposed (Estes and Arnold 2007), but this doesn't work, because the environment is not stabilizing but in fact changing

dramatically (Lieberman and Dudgeon, 1996). Some have suggested that organisms might not respond to the extremely rapid climate changes of the Pleistocene (Bennett, 1990, 1997). However, this is contradicted by observation of population means shifting over just a few years, such as in the Galápagos finches, whereas the Pleistocene fossil record spans tens to hundreds of thousands of years. More recently, Uyeda et al. (2011) looked at a wide range of morphological time series from paleontological and neontological studies on scales from years to tens of millions of years. They found that the small-scale changes seen by neontologists over the periods of years to decades amounted to nothing more than fluctuations around a mean, which were generally constrained and did not accumulate over long periods of time (what they called "bounded fluctuations"). True lasting evolutionary changes only occurred over longer time scales (>1 million years), when rare but substantial bursts of phenotypic change go beyond the normal bounded fluctuations. Uyeda et al. (2011) argued that these rare bursts of change represent shifts in adaptive zones, but that the small-scale changes seen in Galápagos finches and other small birds do not add up to permanent evolutionary changes.

While the Pleistocene stasis is typical of RLB birds, the Holocene populations of *B. swainsoni* are unusual. *Gymnogyps* and *Teratornis* (Syverson et al., 2010; Gillespy et al., 2016) as well as *Canis latrans* (Meachen et al., 2012, 2014) also decrease in size between Pleistocene and Holocene populations, but the increase in size between 9 ka and modern specimens is unique among the species studied. Ecological factors may account for the differences between Swainson's hawks and other RLB birds. Swainson's hawks are long-distance migrators that travel annually between the North American plains and the South American pampas (Brown, 1968). Nonbreeding adults also prey primarily on large insects with cyclic populations, like grasshoppers and locusts, rather than on the usual raptor prey of rodents and reptiles. Their habitat and prey population are therefore both highly susceptible to the effects of the profound land-use changes in the Americas over the last few millennia, in ways not characteristic of any of the other birds represented at RLB. We suggest that changes in prey and habitat availability

may have contributed to the notable increase in robustness of *B. swainsoni* TMTs from early Holocene to modern populations.

ACKNOWLEDGMENTS

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