HOW DID COUGARS AND BOBCATS RESPOND TO THE END OF THE ICE AGES? EVIDENCE FROM LA BREA TAR PITS

DANIELLA BALASSA[1], DONALD R. PROTHERO[2,3], and V.J.P. SYVERSON[4]

[1] Dept. Geological Sciences, California State University, Long Beach, CA 90840;
[2]Dept. Geological Sciences, California State Polytechnic University, Pomona, CA 91768;
[3]Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, CA 90007;
[4] Dept. Geosciences, Univ. Wisconsin, 1215 W. Dayton St., Madison, WI 53706

Abstract—At the end of the Pleistocene, most of the large mammals vanished from North America, including the predators (such as saber-toothed cats, dire wolves, American lions, and short-faced bears). Previous studies have shown that the coyotes of the late Pleistocene were bigger and more robustly built to contend with big predators for larger prey, and then grew smaller and more gracile in the Holocene when their large predator competition and large prey both disappeared. How did the surviving larger cats respond to this event? We compared cougars (*Puma concolor*) and bobcats (*Lynx rufus*) from the late Pleistocene Rancho La Brea asphalt deposits (35-9 ka) to their modern counterparts. The most common elements of these rarely fossilized cats— the lower first molar (m1), third metacarpal (MC3), and third metatarsal (MT3)—were measured with digital calipers. Even though the size range of Pleistocene La Brea specimens were contained within the modern range in most variables, on average the Pleistocene cougars were significantly larger in m1 and MC3 and significantly smaller in the MT3 (using Hotelling's T^2 test of bivariate significance). The m1 in Pleistocene and recent bobcats, on the other hand, were not statistically different, but the Pleistocene bobcat paws and feet were significantly larger, possibly because they had broader lynx-like feet for coping with the snows of the glacial interval. We conclude that Pleistocene cougars, like coyotes, competed with larger predators for larger prey during the Pleistocene, and therefore were more ecologically affected than bobcats by the megafaunal extinction.

INTRODUCTION

At the end of the Pleistocene, global climate transitioned from glacial conditions to the relatively warm stable conditions of the Holocene, and the high diversity of mammalian megafauna sharply decreased. In North America, the faunal landscape changed dramatically as most of the large herbivores (such as mastodons, mammoths, horses, camels, and ground sloths) vanished completely, along with the large predators that probably fed on these animals (such as saber-toothed cats, American lion, short-faced bear, and dire wolf). The disappearance of the megaherbivores left only the familiar large mammals of the Holocene dominating the landscape (bison, moose, elk, deer, and pronghorns), preyed upon by the smaller felids such as cougars (*Puma concolor*) and bobcats (*Lynx rufus*), as well as canids (gray wolves and coyotes) and ursids (black bears and brown bears).

What effects did the climate change and the loss of the megafauna have on the mammal species that persisted through the megafaunal extinction? In some cases, the intraspecific changes were substantial. For example, coyotes from the Pleistocene of Rancho La Brea (RLB) were significantly larger, with jaws more suitable to attacking large prey, and that these features disappeared in Holocene coyote populations (Meachen and Samuels, 2012; Meachen et al., 2014). Black bears elsewhere in North America also shrank in size during the Holocene (Graham, 1991; Wolverton and Lyman, 1998). In most cases, individuals from modern populations of large prey species are significantly smaller than their conspecifics from the late Pleistocene: white-tailed deer got smaller (Purdue, 1989), as did bighorn sheep (Harris and Mundel, 1974), wapiti/elk (Lyman, 2006, 2010), and pronghorns (Adams et al., 1999), while the large Pleistocene *Bison antiquus* was replaced by the much smaller modern species, *Bison bison* (McDonald, 1981; Raymond and Prothero, 2011). Most of this size reduction in the Holocene can be explained by Bergmann's Rule, which predicts large body sizes in colder climates, and indeed, for many of these animals which are clinally distributed over a wide range of latitudes, like bears, cougars, and bison, there is a strong Bergmann's Rule effect even today.

However, not all species responded to the shift in climate so clearly. Many small rodents, such as woodrats (*Neotoma* spp.) (Smith and Betancourt, 1998, 2003, 3006; Smith et al., 2014, 1998), deer mice (*Peromyscus maniculatus*) (Holbrook, 1998), and pocket gophers (*Thomomys* and *Geomys*) (Hadly, 1997) showed complex changes over this period. This has been extensively investigated in birds present in the RLB collections (Prothero et al., 2012). The condor *Gymnogyps amplus* was replaced by the smaller modern California condor *G. californianus* (Syverson and Prothero, 2011); however, the size reduction did not happen until the mid-Holocene, apparently not in immediate response to the lack of megamammal carcasses in the early Holocene, possibly as a result of dietary plasticity (Chamberlain et al., 2005; Fox-Dobbs et al., 2006; Perrig et al., 2019). The most common bird at La Brea, the golden eagle (*Aquila chrysaetos*), became slightly larger during the Holocene (Molina and Prothero, 2011). There were no size differences between Pleistocene and modern populations of Great Horned Owls (*Bubo virginianus*) (Madan et al., 2015), Barn Owls (*Tyto alba*) (Madan et al., 2016), or Black Vultures (*Coragyps occidentalis*) (Long et al., 2016), and there are no significant size changes in the smaller owls, such as the Burrowing Owl (*Athene cunicularis*) or Long-Eared Owl (*Asio otus*) (Madan et al., 2019), or the smaller Passeriformes (Long et al., 2020). In short, birds show no consistent trend toward larger or smaller body size with the Pleistocene-Holocene transition.

Because predators tend to occur at lower abundances than herbivores in living populations, they are usually poorly represented in the fossil record. According to Kurtén and Anderson (1980), cougars (also known as the puma or mountain lion, *Puma concolor*), and the bobcat (*Lynx rufus*) are known from only a handful of North American Pleistocene localities, although the FAUNMAP database now lists 57 Rancholabrean localities with bobcats and 29 with cougars, so the sampling has improved since 1980. Kurtén and Anderson (1980, pp. 195-196) suggested that late Pleistocene cougars were slightly larger in body size, with smaller canine teeth than Recent animals, but provided no evidence for this claim. These authors did not discuss how Pleistocene bobcats might compare to Recent populations.

The largest samples of Pleistocene fossils of both of these cats are at the RLB tar pits, world famous as one of the richest and most diverse fossil assemblages known, and certainly the richest in the Pleistocene (Stock and Harris, 1992; Akersten et al., 1983). At RLB, both species are common, although less abundant than other extinct carnivorans such as *Smilodon fatalis*, *Panthera atrox,* and *Canis dirus*. Not only does RLB provide large samples of many different animals, but most deposits are dated to within ± 5 k.y. (Marcus and Berger, 1991; O'Keefe et al., 2009; Fuller et al., 2015), and the climate history of the region is well established based on the pollen grains preserved in deep-sea cores just off the coast of Los Angeles (Heusser, 1998). Many studies have been published on the more abundant predators of RLB, especially *Smilodon fatalis* and *Canis dirus*, but very little has been written about the cougars and bobcats. Thus, in this study we ask how cougars and bobcats from the California coastal region respond to the climatic transition from the Pleistocene to the Holocene.

MATERIALS AND METHODS

We measured fossil specimens of *P. concolor* and *L. rufus* from the RLB asphalt deposits at the La Brea Tar Pits and Museum (formerly the George C. Page Museum of La Brea Discoveries). Modern specimens used in this study were measured at the Department of Mammalogy at the Natural History Museum of Los Angeles County (LACM), and the University of California Museum of Vertebrate Zoology in Berkeley (UCMVZ); these are drawn from a wider sampling area, but still primarily represent California and western North America. We chose to focus only on these geographically restricted collections to avoid the well-known phenomenon of geographic clines in size and shape of both cougars and bobcats.

For both species, there are fewer than twenty of any single skeletal element in the La Brea collections. Thus, it was not possible to get the huge sample sizes that are available for common La Brea mammals like *S. fatalis* or *C. dirus*. Nor was it possible to compare only one pit sample of one age from La Brea, since no single pit produced more than a few specimens. The most common elements were partial mandibles, so we measured the first lower molar (m1) or carnassial, which is present in all mature specimens and has been shown to give the best single-tooth estimate of body size in carnivorans (Finarelli and Flynn, 2006). We measured the maximum length and width of the entire m1 in all unbroken specimens (Fig. 1A). The only common postcranial bones were metapodials, so we measured all the third metacarpals (MC3) and third metatarsals (MT3) available. Although these bones were chosen for their availability, they are both suitable to this analysis, as their diaphysis cross-sectional areas scale close to isometrically with mass in felids (Doube et al., 2009). On these elements, we measured maximum length and midshaft diameter in the dorso-plantar direction (Fig. 1B). We were very careful to make sure that MC3s were not mixed with MT3s in the collection, since in some cats they are of similar size and shape. Measurements were made with digital calipers to the nearest 0.1 mm. Data were analyzed in Excel and R, using Hotelling's T^2 test for significant differences between the means of two multivariate distributions (package "hotelling").

RESULTS

For the cougar m1 data (Figure 2A), the fossil specimens all fall within the range of the much larger sample of modern cougars, but the fossils are all at the large end of the range,

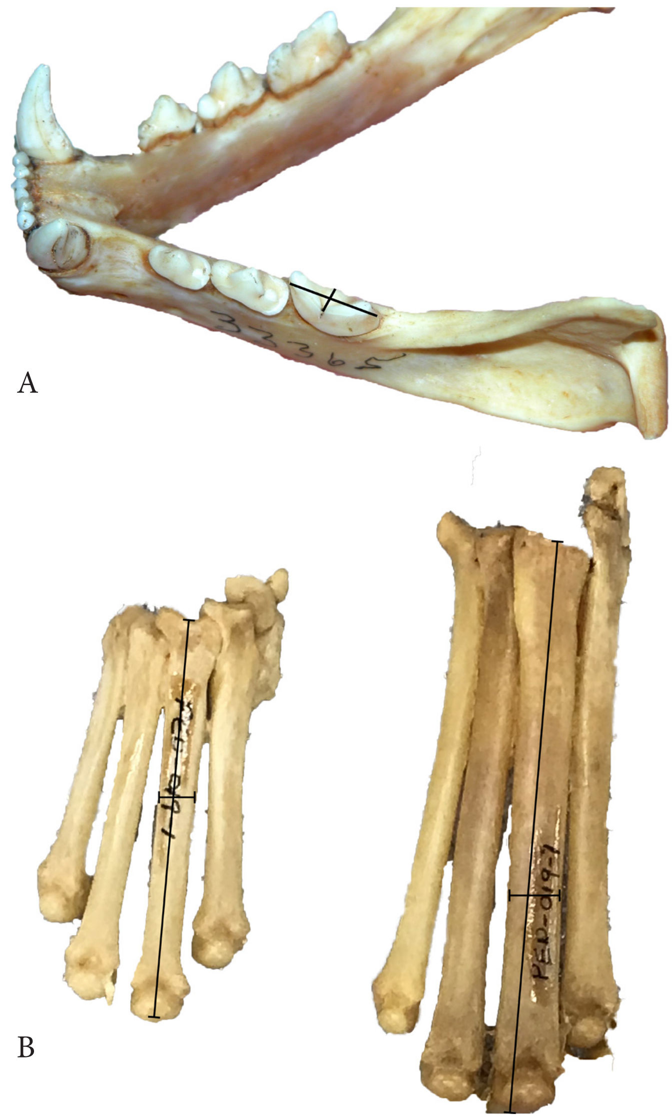

FIGURE. 1. Measurement landmarks. **A**, Bobcat mandible, showing the position of the measurement of maximum m1 length and width. **B**, Bobcat metacarpals (left) and metatarsals (right), showing the location of the measurements of the maximum length and midshaft width of the middle metapodial (MC3 and MT3).

and mean length and mean width of m1 are both significantly larger ($p<0.02$) in Pleistocene cougars than in modern cougars (Tables 1 and 3). This is consistent with the results reported by Samuels et al. (2013), where the bones of RLB cougars they measured were larger than those of modern cougars. The same pattern is true of MC3 (Fig. 2B); again, the distributions of the fossil and modern specimens overlap, but the mean values for Pleistocene specimens are significantly larger ($p<0.007$) (Tables 2 and 3). However, the distribution of MT3 length and width in cougars are significantly smaller ($p<0.0001$) in the Pleistocene than in the modern (Table 3); in fact, their distributions barely overlap with the modern samples (Fig. 2C). As expected, the MT3 lengths are significantly longer than the MC3 lengths, the normal condition for most felids (Tables 1, 2).

In bobcats, by contrast, all fossil m1 specimens are completely within the size distribution of the modern specimens, and there is no significant difference between the means of the two samples (Fig. 3A, Table 3). Even though there is a lot of overlap of the two distributions, mean values for both MC3 and

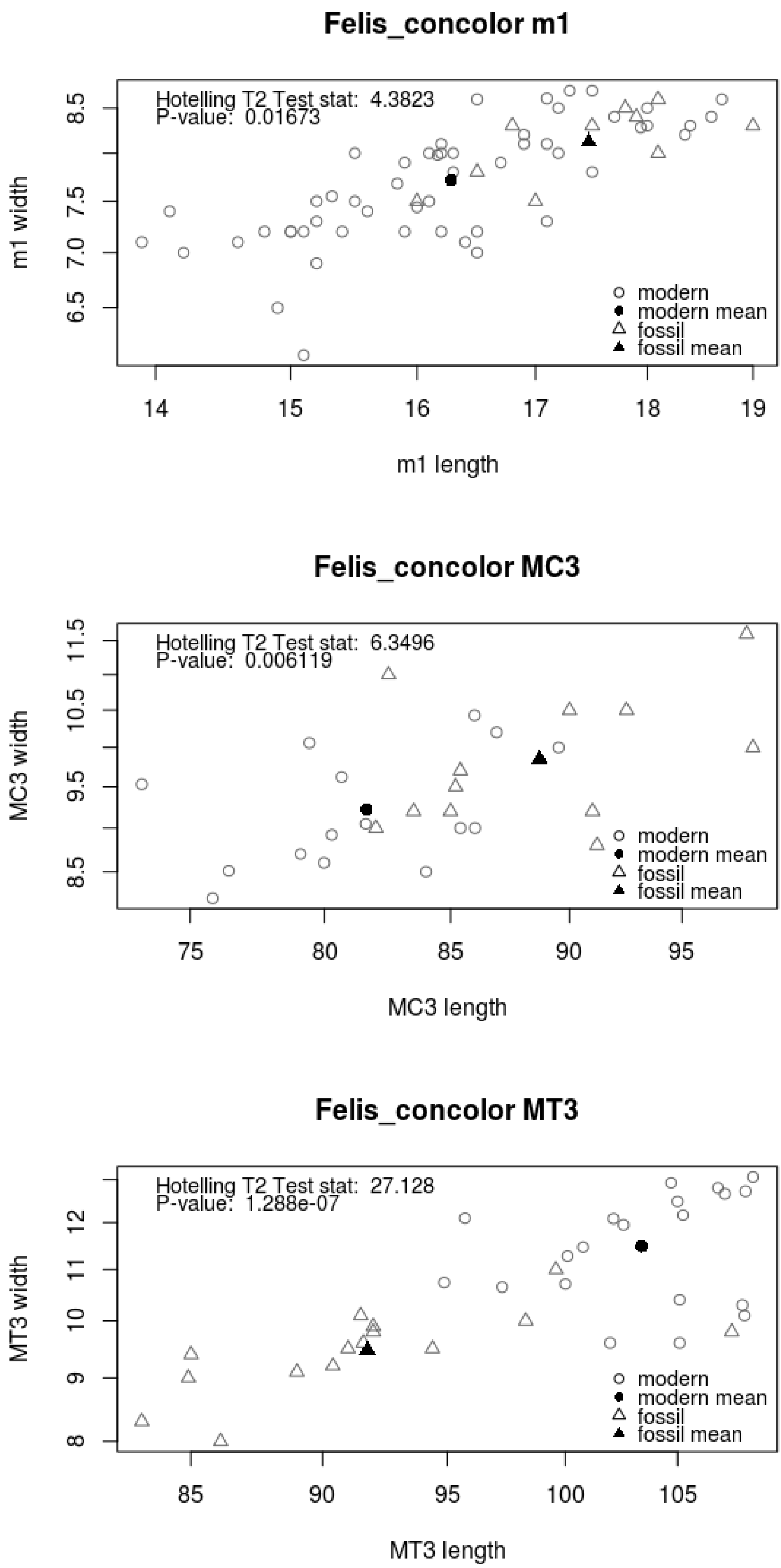

FIGURE 2. Bivariate plots comparing Pleistocene cougars from La Brea with modern cougars. **A**, m1. **B**, MC3. **C**, MT3.

TABLE 1. Measurement of La Brea and modern cougar (*Puma concolor*) elements.

SAMPLE	N	MEAN	ST.DEV.
All m1 lengths pooled	67	17.47	1.23
All m1 widths pooled	67	8.12	0.59
La Brea m1 lengths	14	16.47	0.89
La Brea m1 widths	14	7.78	0.39
Modern m1 lengths	53	16.28	1.19
Modern m1 widths	53	7.71	0.60
All MC3 lengths pooled	27	85.00	6.06
All MC3 widths pooled	27	9.52	0.82
La Brea MC3 lengths	12	88.62	5.83
La Brea MC3 widths	12	9.85	0.91
Modern MC3 lengths	15	81.62	4.53
Modern MC3 widths	15	9.22	0.68
All MT3 lengths pooled	33	98.21	7.77
All MT3 widths pooled	33	10.59	1.41
La Brea MT3 lengths	14	91.76	4.19
La Brea MT3 widths	14	9.48	1.14
Modern MT3 lengths	19	103.37	6.37
Modern MT3 widths	19	11.49	0.73

TABLE 2. Measurement of La Brea and modern bobcat (*Lynx rufus*) elements

SAMPLE	N	MEAN	ST.DEV.
All m1 lengths pooled	88	11.25	1.31
All m1 widths pooled	88	4.73	0.43
La Brea m1 lengths	10	11.37	1.32
La Brea m1 widths	10	4.74	0.40
Modern m1 lengths	78	11.22	1.22
Modern m1 widths	78	4.72	0.65
All MC3 lengths pooled	27	48.51	4.40
All MC3 widths pooled	27	4.40	0.50
La Brea MC3 lengths	12	50.24	2.47
La Brea MC3 widths	12	9.85	0.39
Modern MC3 lengths	15	47.28	4.52
Modern MC3 widths	15	3.43	0.52
All MT3 lengths pooled	33	69.36	4.32
All MT3 widths pooled	33	5.39	0.93
La Brea MT3 lengths	14	72.09	4.81
La Brea MT3 widths	14	3.16	0.44
Modern MT3 lengths	19	66.99	5.91
Modern MT3 widths	19	4.23	0.88

TABLE 3. Hotelling's T-squared test for significance of difference between two bivariate samples. Values in bold face are statistically significant (p = 0.05).

SAMPLE	N	T-squared	P-value
COUGARS			
m1 length vs. width	**88**	**4.3823**	**0.017**
MC3 length vs. width	**27**	**6.3496**	**0.006**
MT3 length vs. width	**33**	**27.128**	**<0.001**
BOBCATS			
m1 length vs. width	88	0.06451	0.938
MdC3 length vs. width	**27**	**5.1021**	**0.016**
MT3 lengths vs. width	**33**	**14.3**	**<0.001**

MT3 are significantly longer and narrower in the fossil bobcats than in the modern specimens, with a larger and more significant difference in the metatarsals (Fig. 3B and 3C, Table 3).

DISCUSSION

Using m1 as the best available proxy for body size in carnivorans (Finarelli and Flynn, 2006), cougars were indeed significantly larger in the late Pleistocene. One explanation might be the changing climate, and that Pleistocene cougars were larger due to Bergmann's Rule for the size of animals in cold climates. Another possibility is that larger body size would have been advantageous to Pleistocene cougars in contending with large Pleistocene prey animals and competitors, but less useful after the megafaunal extinction, similar to the pattern observed in coyotes (Meachen and Samuels, 2012; Meachen et al., 2014). This is consistent with the results of previous carbon and nitrogen isotope analysis (DeSantis et al., 2019) and dental microwear texture analysis (DeSantis and Haupt, 2014), which showed that RLB cougars were eating the same kinds of prey as *Smilodon fatalis* and *Panthera atrox*, mostly prey that lived in forested, closed habitats.

By contrast, bobcats show no significant size difference in the mean values of m1, so we conclude that bobcats did not shrink in body size after the Pleistocene. This suggests that Pleistocene bobcats preyed on the same smaller animals (rodents, rabbits, birds, and other small animals) as modern bobcats, and therefore did not see much change in prey size into the Holocene.

The changes in the metapodials are not so easily explained. Our results indicate clearly that the Pleistocene cougars at RLB had larger front paws relative to their modern descendants, but smaller hind paws relative to modern cougars. If the front and hind paws of cougars, like m1, had both been larger in the Pleistocene, then it could be explained as an effect of allometric scaling, but instead we find that Pleistocene cougars' hind feet were smaller than those of their modern counterparts. It is possible that pouncing and attacking larger prey may have required larger front paws, but cougars did not require such large hind feet for running, which might be necessary to catch such smaller prey as cougars must capture today.

The pattern in bobcats is also interesting. Although the size distribution of m1 (our proxy for overall body size) did not change in size from Pleistocene to modern, their front and rear paws were longer in the Pleistocene, suggesting larger paw size. These specimens are mostly from pits dated to the last glacial maximum around 18-20 ka, when the climate at La Brea were significantly colder and snowier, with open conifer forests in the Los Angeles Basin, like those of our high-elevation

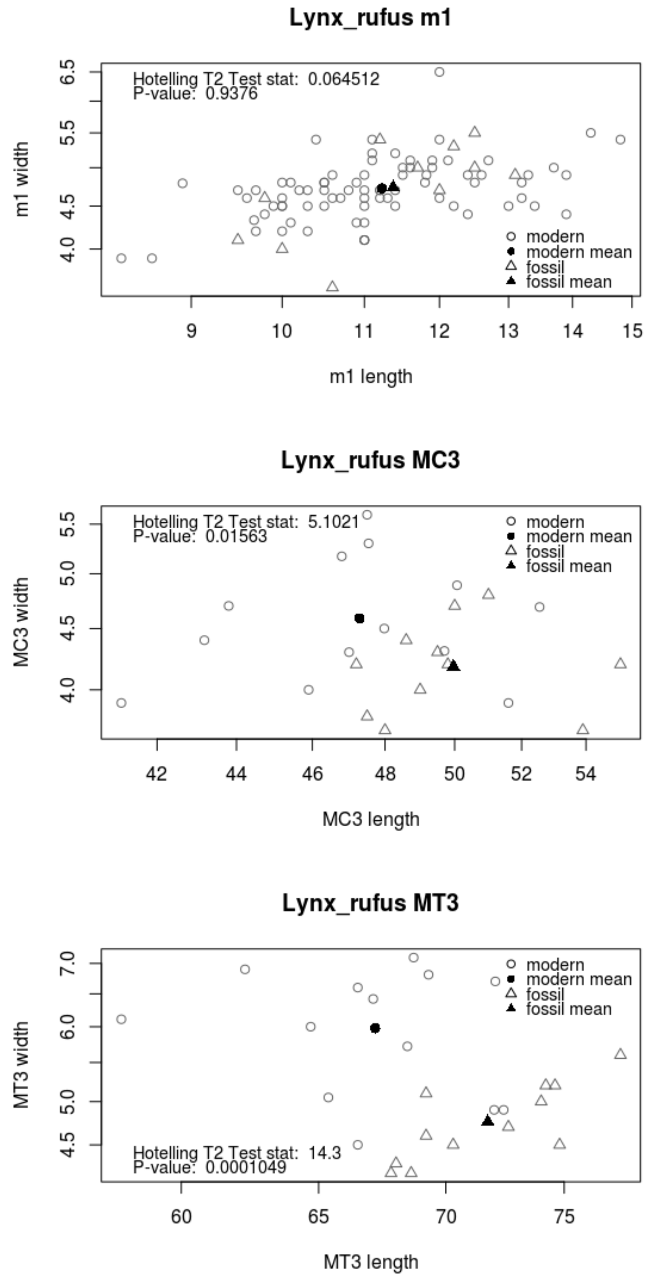

FIGURE 3. Plots comparing Pleistocene bobcats from La Brea with modern cougars. **A**, m1. **B**, MC3. **C**, MT3.

mountains, while the present vegetation is oak-chaparral, much like the vegetation we have today (Heusser, 1998). Larger paws in Pleistocene might have several advantages, including being able to run faster and jump higher, and capture larger prey. Another possibility is that if bobcats of the peak glacial forests had to run across winter snow, their larger feet might have been an advantage in behaving like snowshoes, as in their close relatives, the Canada lynx (*Lynx canadensis*) (Parker et al., 1983). However, it is not clear that snow was common in the Los Angeles Basin even at the last glacial maximum; open conifer forests are characteristic of the coastal mountains of California at higher latitudes today, where snow is rare.

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