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Living coyotes modify their behavior in the presence of larger carnivores, such as wolves. However, little is known about the effects of competitor presence or absence on morphological change in coyotes or wolves over long periods of time. We examined the evolution of coyotes and wolves through time from the late Pleistocene, during which many large carnivorous species coexisted as predators and competitors, to the Recent; this allowed us to investigate evolutionary changes in these species in response to climate change and megafaunal extinctions at the end of the Pleistocene. We measured postcranial skeletal morphologies of wolves (*Canis lupus*) and coyotes (*C. latrans*) from Pleistocene-aged tar deposits, as well as early, mid, and recent Holocene populations of both. We found few morphological differences between Pleistocene and Holocene wolf populations. Conversely, we found many differences in coyotes: Pleistocene coyotes were larger and more robust than Holocene populations. However, within 1,000 y of the megafaunal extinctions, coyotes are morphologically indistinguishable from modern populations. We cannot attribute these differences directly to climate change because modern coyotes do not follow Bergmann's rule, which states body size increases with decreasing temperature. Instead, we suggest that Pleistocene coyotes may have been larger and more robust in response to larger competitors and a larger-bodied prey base. Although we cannot separate competition from predator-prey interactions, this study indicates that the effects of biotic interactions can be detected in the fossil record.

Pleistocene extinctions | Canidae | Rancho La Brea

Recent studies of coyotes (*Canis latrans*) and gray wolves (*C. lupus*) demonstrate competition and antagonistic interactions between these species when they are sympatric (1–7). Coyotes often modify their behavior in response to antagonism from wolves (2, 3, 5, 6). However, coyotes and wolves also respond through body-size convergence when they are in direct competition for small- to medium-sized prey (8).

Antagonism arises from the similar diets in the two species, but wolves and coyotes differ significantly in their hunting styles. Wolves are large-prey specialists that hunt in packs by means of a long, enduring chase (9). In contrast, coyotes are commonly solitary predators of small mammals, such as rodents and rabbits; they kill by a pounce and subsequent shaking that breaks the neck (10). However, coyotes can be opportunistic hunters with highly plastic prey-killing behaviors because of their intermediate size (11) and adaptability (10), and animosity between wolves and coyotes occurs when their diets converge.

Ecologists studying species relationships tend to focus on biotic interactions (12, 13) over, essentially, an instantaneous moment in time, rather than on abiotic factors (for exceptions, see refs. 14–16). Paleoecologists take the principles of ecology and add the concept of deep time with varying levels of resolution (17). This latter approach may focus on biotic interactions but must also examine longer-scale abiotic factors, such as climate change, to explain broader changes in species or assemblages through time (12, 18). Coyotes and wolves have a clear recent ecological record of competition and antagonism. Has this relationship been the same throughout their evolutionary histories? Looking to the past may illuminate how these species interactions have evolved.

Coyotes in the Pleistocene (*C. latrans orcutti*) were morphologically distinct from extant coyotes. The skulls and jaws of *C. l. orcutti* are significantly thicker and deeper than in Recent populations. Pleistocene coyotes also had a shorter, broader rostrum and wider carnassial teeth used for processing meat (19–21): all adaptations for killing larger prey and dealing with higher stresses during food acquisition and processing (22–25). These characteristics suggest that *C. l. orcutti* was more carnivorous than modern coyotes.

C. l. orcutti is found in large numbers in late Pleistocene (∼40–11 Ka) deposits from three sites in Southern California (SoCal): Rancho La Brea (RLB), Maricopa Brea, and McKittrick tar seeps (21) (Fig. 1). Pleistocene coyotes were part of a carnivorous guild that contained multiple canids, including: foxes, the gray wolf, *C. lupus* (only at RLB), and the dire wolf, *C. dirus*, which was larger, more robust, and hunted larger prey than gray wolves (19, 26–28). *C. latrans* is also present in earliest Holocene-aged pit 10 at RLB (29, 30). Preliminary analyses of cranial material found pit 10 individuals to be smaller than those in older pits (19), suggesting morphological differentiation between Pleistocene and Holocene coyotes. However, to distinguish between biotic or abiotic factors requires, a more quantitative statistical approach.

Changes in gray wolf or coyote morphology between Pleistocene and Holocene populations may be attributable to either species interactions or climate change or both. Here, we examine wolves and coyotes across the Pleistocene–Holocene boundary, taking into account both biotic and abiotic effects that may have influenced their ecologies and morphologies. For our purposes, the key changes that occurred at the end of the Pleistocene are the major warming trend (abiotic) and the megafaunal extinctions (biotic, the cessation of interactions with a now extinct fauna).

We examine the postcranial morphology of wolves and coyotes from the Pleistocene, earliest Holocene, and Recent. We predict that if climate is directly causing morphological change, then a clear correlation will exist between body size and temperature (or latitude), also known as Bergmann's rule, in wolves and coyotes. This effect should not only be present over the Pleistocene–Holocene transition but also in modern species over a climate gradient. It is difficult to assess biotic interactions in the fossil record, but if climate change is not the direct cause of morphological disparity, then competition and predator/prey interactions in the Pleistocene must be considered as major factors.

Results

Wolves. Few differences were observed between Holocene and Pleistocene gray wolves. Tibial tuberosity length (TiSL) (Tables

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Fig. 1. Map of localities for coyote specimens used in this study. Modern sites are in black; fossil sites are in gray. Arrows indicate fossil sites and are numbered: RLB, 1; Maricopa, 2; McKittrick, 3; Idaho caves, 4. See Table S5 for localities.

S1 and S2) was significantly longer in RLB specimens than from Holocene cave sites in Idaho (∼3–5 Ka) and extant populations. Femur breadth (FeB) was significantly larger in RLB wolves than mid-Holocene wolves. No significant differences were found for any of the other 19 measurements.

Coyotes. Many significant differences were observed between Pleistocene and Holocene coyotes (Table 1, Table S4, and Fig. 2). SoCal coyotes were significantly smaller than other modern coyotes for 14 out of 21 measurements (Table S3). There were few significant differences within Pleistocene coyote populations; however, Maricopa had smaller means than the other two sites and were not significantly different from Holocene populations. Maricopa coyotes had high variances, potentially reflecting two different morphs in the population (Table 1). Pit 10 coyotes were smallest, followed by modern SoCal coyotes, other modern

coyotes, Holocene Cave coyotes, and Maricopa coyotes; McKittrick and RLB coyotes were largest.

RLB and McKittrick coyotes were significantly larger than modern coyotes (both groups), and Holocene coyotes for most measurements, but were not significantly different from each other. Surprisingly, all RLB coyotes, including Holocene coyotes from pit 10, had exceptionally short olecranon processes and were significantly different from all other groups. This measurement suggests that coyotes at RLB had exceptional cursorial abilities in both the Pleistocene and the early Holocene, despite the difference in body size between these two time intervals. See Table 1 for mean values for all measurements (all coyotes) and Table S4 for ANOVA P values for all Pleistocene coyotes.

A plot of coyote morphology versus time and climate (Fig. 3A) shows a morphological shift at the end-Pleistocene, concurrent with the megafaunal extinctions and climate change. A linear regression showed no correlation between body size and mean annual minimum temperature for modern coyotes (P value = 0.216; R^2 = 0.040) or when Pleistocene specimens were included (P value = 0.077; R^2 = 0.029) (Fig. 3B). This demonstrates that coyotes do not follow Bergmann's rule and suggests that climate is not the primary driving factor in coyote body size change.

Discussion

Wolves. Pleistocene wolves from RLB are not morphologically distinct from Holocene specimens. The only difference between the Pleistocene and Holocene populations is a larger tibial tuberosity, the insertion for the quadriceps and hamstring muscles. This suggests that Pleistocene gray wolves had larger and stronger muscles for take-off during a chase, but because there are no concomitant changes in any other measurements, this difference may not have any clear functional implications. Gray wolves are not common at the tar pits, and this may be attributable to behavioral modification or competitive exclusion of

Table 1. ANOVA results for *C. latrans* comparisons

Variable	SoCal Modern (n = 17)	Other Modern (n = 23)	Holocene Caves (n = 8–10)	Pit 10 (n = 12–15)	RLB (n = 31–58)	McKittrick (n = 9–12)	Maricopa (n = 4–7)
Humerus							
HuL	154.78 (6.90)	161.52 (8.41)	160.72 (6.90)	153.09 (5.51)	167.33 (6.70)	169.95 (7.08)	162.77 (10.67)
HuAPD	13.01 (0.84)	13.69 (1.05)	12.84 (1.22)	12.62 (0.79)	15.11 (0.97)	14.39 (0.86)	14.38 (1.44)
HuMLD	10.65 (0.70)	10.75 (0.56)	10.70 (0.82)	10.68 (0.73)	12.25 (0.86)	11.87 (0.32)	11.87 (0.66)
HuPCL	59.82 (3.48)	62.26 (4.45)	63.64 (6.93)	60.04 (4.57)	69.96 (5.00)	67.89 (3.73)	62.70 (3.97)
HuHTL	17.79 (1.63)	19.87 (1.69)	19.92 (1.37)	19.80 (0.81)	22.43 (1.14)	21.96 (0.97)	20.66 (1.65)
HuEB	28.26 (1.43)	29.37 (1.38)	29.27 (1.23)	27.89 (2.57)	32.04 (1.61)	32.32 (1.49)	31.14 (2.31)
Radius							
RaL	162.87 (5.92)	168.15 (8.52)	163.66 (6.63)	157.27 (6.80)	173.61 (7.89)	176.01 (8.34)	167.12 (4.77)
RaAPD	7.04 (0.58)	6.87 (0.48)	6.53 (0.67)	6.97 (0.66)	8.22 (0.83)	8.46 (0.62)	7.97 (0.11)
RaMLD	11.00 (0.86)	12.09 (0.75)	11.42 (0.91)	10.96 (0.64)	13.19 (1.00)	13.17 (0.90)	13.03 (0.15)
Ulna							
UlL	187.01 (8.06)	193.73 (9.79)	192.29 (8.17)	184.38 (12.85)	192.78 (7.37)	202.15 (7.51)	None
UlOL	24.42 (3.52)	25.38 (3.19)	25.71 (1.28)	18.85 (1.59)	19.99 (1.26)	27.47 (1.05)	None
Femur							
FeL	172.03 (6.77)	176.66 (8.48)	177.16 (5.98)	168.99 (8.24)	185.08 (7.37)	188.95 (9.58)	176.20 (9.76)
FeAPD	11.02 (0.79)	11.45 (0.89)	11.83 (1.37)	10.89 (0.99)	12.52 (0.92)	12.89 (0.60)	11.89 (0.33)
FeMLD	11.22 (0.58)	11.54 (0.78)	11.49 (0.99)	11.34 (0.75)	12.86 (1.12)	12.87 (0.59)	12.65 (0.18)
FeGTH	25.48 (4.02)	44.06 (8.94)	32.43 (8.09)	27.17 (2.18)	29.99 (3.99)	27.49 (2.66)	26.22 (3.35)
FeHD	16.03 (0.83)	16.87 (0.85)	16.96 (1.14)	15.92 (0.74)	17.77 (1.14)	18.28 (1.07)	17.39 (0.93)
FeB	27.05 (1.22)	28.50 (1.39)	28.92 (1.87)	26.32 (2.01)	30.42 (1.80)	31.11 (1.85)	29.33 (1.70)
Tibia							
TiL	181.84 (8.55)	190.44 (11.43)	182.15 (6.56)	174.76 (7.60)	193.32 (6.90)	196.83 (9.77)	191.46 (14.79)
TiAPD	11.48 (0.94)	12.14 (1.25)	11.66 (1.33)	10.94 (0.90)	12.99 (0.98)	13.06 (1.03)	12.25 (0.93)
TiMLD	11.09 (0.79)	12.09 (0.64)	11.14 (0.33)	10.72 (0.80)	12.80 (0.94)	12.32 (0.65)	11.95 (0.43)
TiSL	29.55 (2.58)	35.02 (5.04)	34.91 (4.91)	31.61 (2.93)	36.66 (3.02)	31.19 (2.78)	31.45 (4.47)

Mean ± SD for each locality and measurement used in this study. *N* for fossils is by individual element.
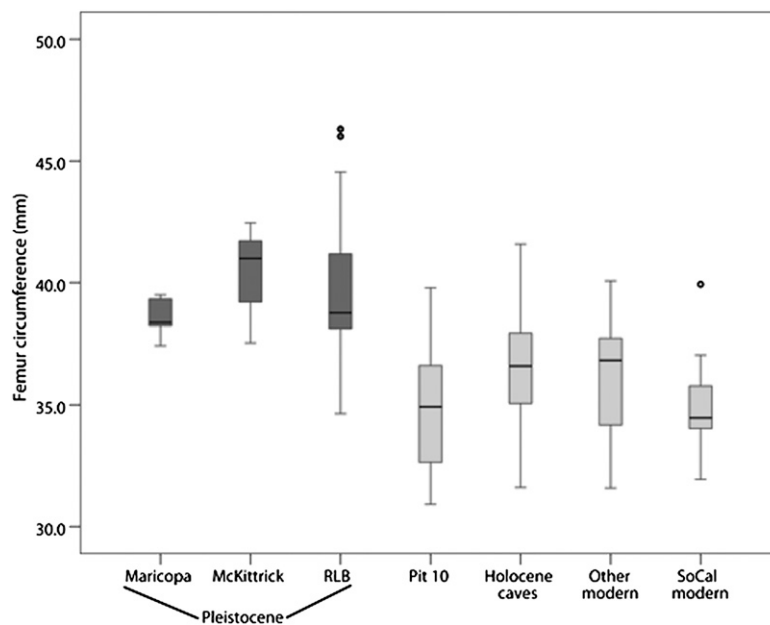
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Fig. 2. Box plot of femur circumference as a representative variable. Horizontal bars indicate the mean value; boxes indicate interquartiles, and whiskers (or dots) represent the extreme values for each group. Pleistocene groups are indicated with a darker shade of gray than Holocene groups.

gray wolves by dire wolves near the tar seeps. This is also indicated by their absence at McKittrick and Maricopa and is consistent with other studies (31, 32).

A small sample size of gray wolves may give a false-negative result, but Leonard et al. (31) also noted the gracile nature of the gray wolves at RLB (similar to living morphs) compared with end-Pleistocene Alaskan and Beringian wolves. Geist (33) found that living gray wolves in North America show a body size increase with increasing latitude, but only up to 65° N; then, they show a body size decrease again. In wolves, Geist argued that body size trends are not due to climate, but food availability. Other studies also suggest that body size gradients in carnivores are directly dependent upon prey size, prey availability, and interspecific interactions, rather than abiotic factors, such as climate (8, 11, 34–43).

Coyotes. We find a distinct morphological difference in coyotes across the Pleistocene–Holocene boundary (for a discussion of differences between Pleistocene sites, see *SI Results*). There was a large shift in morphology concurrent with the megafaunal extinctions and climate warming at the end of the Pleistocene (Fig. 2). However, we observed no relationship between body size and mean annual coldest temperature in modern coyotes (Fig. 3*B*); this provides additional evidence against Bergmann's rule. Our results are consistent with Thurber and Peterson (44), who found no correlation between latitude and body mass in coyotes.

If climate change was the direct cause of end-Pleistocene body size change in coyotes (that do not follow Bergmann's rule), why would this change not also appear in wolves (that do appear to follow Bergmann's rule) across the same time period? *C. l. orcutti* was larger and more robust than its extant relatives (Table 1 and Table S4), which can be corroborated by cranial evidence (19, 21). If living coyotes do not follow a simple pattern of larger body size in colder climates (i.e., Bergmann's rule), and we assume that this pattern was not different in the Pleistocene, then end-Pleistocene temperature change would not cause the body size changes seen here. This finding is somewhat unsurprising, considering that biotic interactions are responsible for a multitude of changes and trophic cascade effects that occur in modern ecosystems (for a review see 45). Two possible biotic reasons for the

morphological differences seen in *C. l. orcutti* are: (*i*) a larger prey base, both in body size and quantity; and (*ii*) competition with larger carnivores.

Interactions with Prey. Increased large-sized prey availability in the Pleistocene may have significantly contributed to the size differences seen at the Pleistocene–Holocene boundary.

Schmitz and Lavigne (8) found that both living coyotes and wolves changed in body size in response to prey availability. Coyotes are flexible in their prey-size preferences and increase the proportion of large prey in their diet as they approach 21–25 kg, the size at which carnivores switch from small prey to predominantly large prey (11). Bigger, more robust Pleistocene coyotes were approaching this critical size. Estimated mean mass of coyotes at Maricopa was 18 kg (46), and coyotes from McKittrick and RLB would have been even larger (see Table S4), suggesting *C. l. orcutti* hunted larger prey than its living conspecifics. In the Pleistocene, there were many prey species from which to choose, including horses, sloths, camels, llamas, and bison. Juveniles of one or more of those large-bodied species may have been suitable prey for coyotes, because modern coyotes are known to kill ungulate neonates when they are available (1).

C. l. orcutti also shows modifications of the crania and dentition for hunting and killing larger prey, including robust jaws and crania to accommodate large forces applied to the cranium and large molars and carnassial teeth for increased bone-cracking and meat-shearing capabilities, respectively (19–21, 24, 25). Van Valkenburgh and Hertel (28) found that coyotes at RLB had significantly more tooth breakage in their canines and premolars than their living counterparts. They concluded that *C. l. orcutti* had a higher frequency of tooth to bone contact than extant coyotes, from eating larger bones.

Interactions with Competitors. Extant coyotes change both social structure and diet in response to larger competitors/predators (47). When gray wolves were absent from northwestern Montana between 1980 and 1994, coyotes had minimal pack structure, were usually solitary (66%) or occasionally in pairs (29%), and ate mostly lagomorphs and rodents. Following wolf reintroductions in 1995, coyote pack size increased to pairs (48%) and
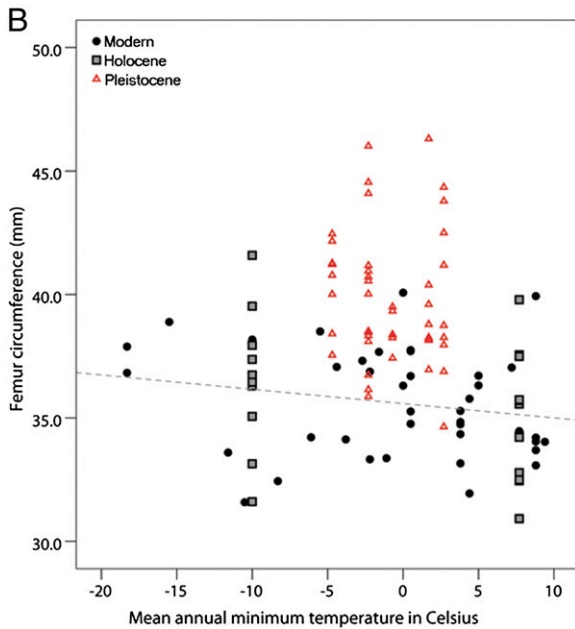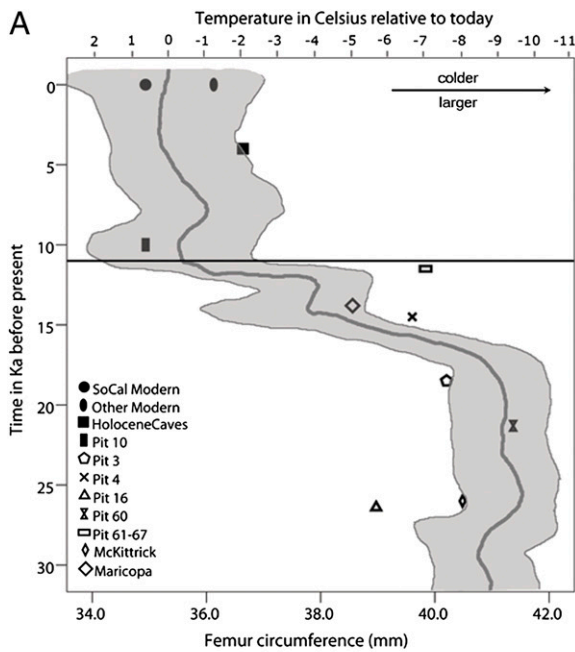
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Fig. 3. (A) Plot of femur circumference versus time in Ka before present. Data points correspond to morphology and time. All symbols are site averages. Solid symbols indicate Holocene groups, and open symbols indicate Pleistocene groups. The temperature curve was adapted from Jouzel et al. (75), and corresponds to time and temperature relative to the present; the mean is indicated with a gray curved line, and the confidence intervals of the curve are shaded. The horizontal black line indicates the end of the Pleistocene extinction events. (B) Plot of mean annual minimum temperature versus femur circumference to test for Bergmann's rule in coyotes. Points indicate individual specimens. The regression line is nonsignificant, is included only for illustrative purposes ($P = 0.216$; $R^2 = 0.04$), and includes only modern individuals.

groups of three or more (33%), and they showed a major shift in diet from small prey to ungulates (47). Arjo and Pletscher (47) hypothesized that this pack structure change was for defense against wolves, and the dietary change was an increase in scavenging of carcasses left by wolves. Increased pack size in coyotes

also has important offensive consequences for prey-killing, and many studies have documented that coyotes in large packs kill ungulate prey (10, 48–50).

In the Pleistocene, *C. l. orcutti* coexisted with both gray wolves and the larger, more robust dire wolf (19). From a competition standpoint, the observed size increase in *C. l. orcutti* seems suboptimal in the presence of both wolf species. However, if dire wolves competitively excluded gray wolves (31, 32), larger coyotes would have been able to move into the "empty" gray wolf niche. Nowak (21) also suggested that *C. l. orcutti* was filling a more wolf-like role in the environment. Additional evidence that Pleistocene coyotes were hunting in packs comes from their large sample size at RLB. Coyotes are the third-most common species found at RLB, after dire wolves and *Smilodon*, the saber-toothed cat. Carbone et al. (51) suggested that *Smilodon* was a social hunter at RLB because of its numbers at that site. They based this hypothesis on African playback experiments in modern carnivores, where they found that only the largest, pack-hunting species responded to distress calls of herbivores and fighting noises of carnivores. They proposed a similar type of scenario for RLB, where one herbivore would become mired in the tar, drawing attention only from groups big enough to defend themselves from the other carnivores present.

Humans As Competitors/Predators? Humans migrated to North America at the end of the Pleistocene and may have impacted coyote morphology, either directly or indirectly. Humans were present at RLB, represented by the skeleton of a human female recovered from pit 10, dated at 10.08 Ka (52). Recent humans actively select against the biggest carnivores in an ecosystem, which are seen as a threat to domestic animals and themselves. If Pleistocene coyotes were more wolf-like, they may also have been more aggressive. Therefore, it is possible that many of the larger individuals of *C. l. orcutti* were killed by humans at the end of the Pleistocene. This would leave smaller individuals behind to repopulate, resulting in the morphology that we see today. However, humans would have also competed with much larger and more ferocious carnivores at the end-Pleistocene, such as saber-toothed cats and dire wolves, rendering coyotes less threatening. Indeed, there is no direct evidence of humans hunting coyotes in the Pleistocene. Instead, humans may have had indirect effects on large coyotes by killing off their prey base.

Conclusions

A large body of literature deals with the evolution of species or communities attributable to species interactions, competition, and predator–prey interactions on decadal time scales (53–57). Still, few studies have demonstrated morphological evolution attributable to species interactions (16, 58, 59). This study shows that relatively rapid evolution in a large mammal can be attributed to biotic interactions.

C. l. orcutti was a larger, more robust, and more wolf-like coyote than Holocene populations. The earliest Holocene coyotes from RLB pit 10 show a distinct change in morphology within 1,000 y of the megafaunal extinctions. We show climate was not directly affecting coyote size; therefore, climate change at the end of the Pleistocene was unlikely the major cause of this morphological shift. We do not dispute the effects of climate change on coyote evolution; our results show that climate change was not the direct cause of morphological change in coyotes. Although climate was not directly responsible for this change, it likely had indirect effects that would be hard to separate from biotic interactions. The end-Pleistocene extinctions are thought to be a product of climate change, which would have caused a trophic cascade in all mammalian assemblages that both survived the event and went extinct (45).

Biotic interactions are the most likely cause for morphological evolution in coyotes, but we cannot discern whether prey dis-

appearance or competitive release was responsible for this shift. Previous studies show that carnivore body size is influenced by both competitors (38–42, 60) and prey species (8, 11, 34–36). In this case, it was probably a combination of both. For example, competition with larger predators causes coyotes to form larger packs for defense (47), which makes them better able to catch larger prey as a team (48–50).

The end-Pleistocene extinctions not only extirpated large mammal species but also had a profound effect on the species that did not go extinct (45). It is important to understand how ecosystems function and change through time, and species interactions are an integral part of any ecosystem (61–64). Some of the carnivore species that were present at RLB are still extant today (e.g., coyotes, gray wolves, mountain lions, etc.). However, the niches that these predators filled in the Pleistocene may have changed because of missing interactions with a now extinct fauna and because abiotic conditions differ.

Modern studies comparing gray wolves to coyotes show that removal of one apex predator has dramatic top-down effects on other predator species, as well as prey species (1–3, 5, 44, 45). *C. l. orcutti* was a larger-prey specialist than living coyotes, a trait that made *C. l. orcutti* better able to compete and survive in the carnivore-laden Pleistocene. Both modern ecosystems and Pleistocene ecosystems highlight the importance of species interactions, revealing the delicate balance that exists in both carnivore–carnivore and predator–prey interactions. Eradication of a single (or multiple) carnivore species has profound effects on the remaining species.

Methods

We measured fore- and hind-limbs of coyotes from different localities through time (Table S2 and Fig. S1). See Table S5 for locations and sample sizes. These specimens included *C. l. orcutti* from the RLB tar pits, from pit 3 (approximate mean age, 18.5 Ka), pit 4 (~14.5 Ka), pit 16 (~26.4 Ka), pit 60 (~21.3 Ka), and pits 61/67 (~11.5 Ka) (30). An ANOVA was performed comparing individual pits. Significant differences were found in humerus length (pit 4 was significantly larger than pit 61) and radius length (pit 4 was significantly larger than pits 3 and 61/67; pit 16 was also significantly larger than pit 61/67). No other significant differences were found for any measurements between any Pleistocene pits at RLB. Therefore, Pleistocene RLB specimens were treated as one group in subsequent analyses. Additionally, specimens were measured from earliest Holocene pit 10 (~6–10 Ka) to determine if these specimens are morphologically distinct from older RLB coyotes.

We also measured coyotes from California Pleistocene tar seeps: (*i*) McKittrick tar pits; and (*ii*) Maricopa Brea. McKittrick has two radiocarbon dates on plant material at 38 K ± 2.5 Kybp and 12.2 K ± 250 ybp (46, 65). Maricopa Brea also has two radiocarbon dates which range in age from 36 K ± 3.9 Kybp (dire wolf) to 13.8 K ± 420 ybp (wood) (66).

We measured *C. latrans* from two pre-European Holocene sites in Idaho [Middle Butte Cave (< 8 Ka) and Moonshiner Cave (~3 Ka) (67)] and from extant populations from Arizona, California, Colorado, Montana, North Carolina, Nebraska, North Dakota, and Wyoming (Fig. 1). Extant subspecies included *C. l. latrans*, *C. l. lestes*, *C. l. mearnsi*, *C. l. merriami*, *C. l. ochropus*, and *C. l. frustor* (n = 40). These subspecies likely represent present diversity in coyotes. We analyzed the SoCal coyote subspecies (*C. l. ochropus*; n = 17)

separately from all other subspecies because this group likely represents the descendants of the Pleistocene coyote populations.

All other coyotes were included together as one group. To determine whether this grouping was acceptable, we compared the total group variation to the variation in the largest non-California group, North Carolina (n = 14/23 total). The sample from North Carolina was large and varied enough that the morphological diversity of the other modern coyotes measured fell within the North Carolina range (>90%) and were as large as coyotes from all of the other states. Given this predominant similarity, we treated all of the remaining extant coyote subspecies as a single group in subsequent analyses.

Although sexual dimorphism is not extreme in canids, it is present (68); thus, for all modern samples, we attempted to measure equal numbers of males and females.

C. lupus was analyzed from RLB, the two Holocene cave sites in Idaho, and recent populations from Alaska, Arizona, Montana, Nebraska, North Carolina, and North Dakota (Table S6). There has been some debate as to whether Eastern wolves are a different species from gray wolves (69). However, the one wolf specimen from North Carolina fell within the range of variation of other gray wolf specimens; thus, all modern wolves were treated as a single group in subsequent analyses. No gray wolf specimens were available from McKittrick, Maricopa, or RLB pit 10.

We chose limb measurements based upon their ability to predict locomotor mode and functional performance in carnivores (70, 71) and rodents (72). We analyzed these measurements with multiple one-way ANOVA tests using Tamhane (for unequal variance) and Scheffé (for equal variance) post hoc procedures. We performed a Levene test of homogeneity of variances to determine which post hoc test was appropriate. We performed all statistical analyses using SPSS version 19 (SPSS). We used raw measurements instead of ratios, and we did not perform any multivariate analyses, because of the fact that fossil specimens are disarticulated and random, and measurements that compare two bones (e.g., radius length to humerus length) would only be possible using averages; this method would effectively reduce the sample size of each group to one. To visualize where each of these groups fell in shape space, we constructed bivariate plots with time on the y axis and morphology on the x axis, with climate overlaid on top (Fig. 3A).

To examine the effects of climate, we plotted femur circumference, a good proxy for body size in canids (73, 74), against mean annual coldest temperature for each locality to look for correlations. We obtained mean annual coldest temperatures for modern specimens by identifying the nearest town (within 5 miles) to the collection locality of each coyote using the most precise data available (either the county in which it was collected or latitude and longitude coordinates) and looking up average temperature data for this town on the National Weather Service website (www.weather.gov). For fossil sites, we identified the weather conditions for the locality in the present, and then using data from Jouzel et al. (75) and the approximate age for the locality, we subtracted the appropriate number of degrees Celsius.

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Supporting Information

Meachen and Samuels 10.1073/pnas.1113788109

SI Results and Discussion

We found variation between the Pleistocene sites; however, this variation is low compared with the variation between the Pleistocene and the Holocene. From the data currently available, we cannot rule out taphonomic processes as a cause for some of the intra-Pleistocene site variation.

RLB coyotes were significantly larger than living conspecifics for most measurements. However, the differences between McKittrick and Maricopa Brea, and modern coyotes, are not quite as pronounced. These three pits are thought to be similar in age, but with different entrapment biases. At RLB the asphalt seeps both trapped and preserved the animal fauna, disproportionately preserving a large number of carnivores that were attracted to herbivores stuck in the tar (1). At McKittrick and Maricopa, the asphalt did not trap animals very frequently; there is less evidence for "baited" herbivore traps like those at RLB (2). Therefore, Maricopa and McKittrick have fewer large carnivores than RLB. Additionally, small carnivores (weasels, skunks, etc.) are found in greater abundance at Maricopa and McKittrick than at RLB (3).

Pleistocene coyotes were smallest at Maricopa, where mud and clay were trapping animals, facilitating their preservation in the asphalt (4). Conversely, the entrapment bias at RLB was selecting for larger, more wolf-like coyotes at that site. The preliminary radiocarbon dates from Maricopa are Pleistocene in age. However, the high variances from the ANOVAs on the Maricopa coyotes suggest the possible presence of a mixed Pleistocene–Holocene assemblage or two types of coyotes coexisting at this site during the Pleistocene (Table 1). Mired ungulates may have attracted the larger coyotes, whereas the smaller coyotes were trapped when pursuing smaller prey.

Curiously, Holocene pit 10 coyotes are smaller than all other groups analyzed, including the modern SoCal population. This marked size decrease at the Pleistocene–Holocene boundary may be a plastic or adaptive response by coyotes to a major shift in both ecological interactions and climate change. Plastic response has been seen in Holocene cave fauna in response to climate change (5). Alternatively, this size decrease could indicate the extinction of *C. l. orcutti* and replacement by a population of coyotes of more diminutive body size from elsewhere. In either case, it indicates that the larger morphology was no longer optimal after the Pleistocene.

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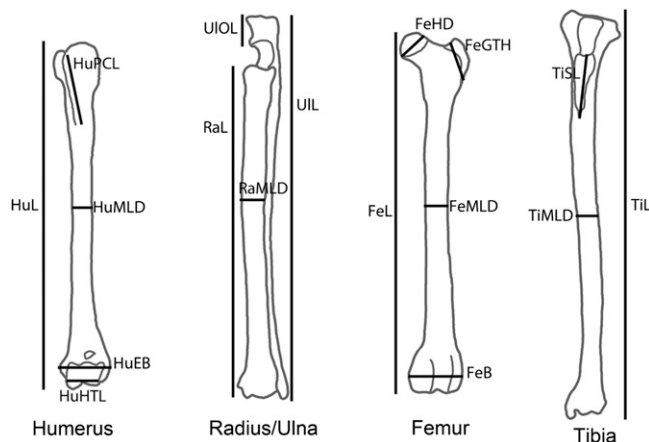
Fig. S1. Diagram of measurements used in this study. Detailed descriptions of measurements are included in Table S2.

Table S1.   ANOVA results for *C. lupus* comparisons

	Mean ± (SD)			P value for comparison with RLB	
Variable	Modern	Mid-Holocene	RLB	Modern	Mid-Holocene
Humerus					
HuL	215.66 (26.10)	197.17 (6.59)	212.02 (11.54)	0.978	0.072
HuAPD	20.41 (2.03)	19.14 (1.10)	20.84 (1.34)	0.881	0.192
HuMLD	15.56 (0.81)	15.26 (1.10)	15.77 (0.68)	0.907	0.599
HuPCL	90.37 (12.36)	84.73 (6.79)	94.13 (6.41)	0.756	0.230
HuHTL	29.15 (3.17)	27.35 (2.00)	28.66 (1.62)	0.934	0.646
HuEB	43.66 (5.75)	40.21 (2.82)	42.99 (2.14)	0.956	0.505
Radius					
RaL	210.53 (17.83)	193.22 (9.70)	194.78 (4.64)	0.073	0.973
RaAPD	10.55 (0.94)	12.10 (2.37)	12.16 (0.84)	0.282	0.998
RaMLD	16.97 (1.13)	15.87 (2.66)	18.14 (1.19)	0.591	0.167
Ulna					
UlL	249.12 (26.69)	236.52 (14.37)	236.06 (11.39)	0.743	1.000
UlOL	34.91 (7.03)	36.78 (2.71)	33.94 (3.47)	0.974	0.808
Femur					
FeL	229.78 (22.40)	216.01 (7.10)	224.95 (2.87)	0.889	0.082
FeAPD	16.49 (1.58)	16.05 (1.14)	16.17 (0.32)	0.911	0.995
FeMLD	16.61 (1.35)	15.95 (0.96)	16.92 (0.88)	0.900	0.452
FeGTH	56.75 (7.97)	51.35 (7.82)	62.67 (2.36)	0.406	0.081
FeHD	24.54 (2.83)	23.37 (1.02)	24.99 (1.13)	0.968	0.170
FeB	40.95 (4.31)	38.98 (1.30)	42.05 (1.05)	0.852	**0.012**
Tibia					
TiL	234.31 (22.38)	218.62 (12.60)	230.70 (9.65)	0.962	0.183
TiAPD	17.11 (1.13)	16.38 (0.87)	17.48 (0.65)	0.774	0.106
TiMLD	16.20 (0.92)	15.97 (1.32)	16.57 (0.84)	0.813	0.692
TiSL	46.94 (5.21)	46.52 (5.45)	60.15 (4.20)	**<0.001**	**0.001**

Mean ± SD for each locality and measurement used in this study. Values in bold indicate significance at the α = 0.05 level.

Table S2.   Osteological measurements used in analyses

Measurement	Abbreviation
Humerus	
Greatest length	HuL
Midshaft anteroposterior diameter	HuAPD
Midshaft mediolateral diameter	HuMLD
Length of the deltopectoral crest	HuPCL
Breadth of the trochlea and condyle	HuHTL
Breadth of the epicondyles	HuEB
Radius	
Greatest length	RaL
Midshaft anteroposterior diameter	RaAPD
Midshaft mediolateral diameter	RaMLD
Ulna	
Greatest length	UlL
Length of the olecranon process	UlOL
Femur	
Greatest length	FeL
Midshaft anteroposterior diameter	FeAPD
Midshaft mediolateral diameter	FeMLD
Height of the greater trochanter	FeGTH
Head diameter	FeHD
Breadth of the epicondyles	FeB
Tibia	
Greatest length	TiL
Midshaft anteroposterior diameter	TiAPD
Midshaft mediolateral diameter	TiMLD
Length of the tibial tuberosity	TiSL

Data are illustrated in Fig. S1.

Table S3. ANOVA *P* values for a comparison of modern SoCal coyotes versus all other modern coyotes in this study

Variable	*P* value
HuL	**0.010**
HuAPD	**0.035**
HuMLD	0.624
HuPCL	0.069
HuHTL	**<0.001**
HuEB	**0.018**
RaL	**0.035**
RaAPD	0.328
RaMLD	**<0.001**
UlL	**0.027**
UlOL	0.824
FeL	0.074
FeAPD	0.121
FeMLD	0.154
FeGTH	**<0.001**
FeHD	**0.003**
FeB	**0.002**
TiL	**0.013**
TiAPD	0.076
TiMLD	**<0.001**
TiSL	**<0.001**

For all significant values, SoCal coyotes are smaller. Values in bold indicate significance at the $\alpha = 0.05$ level.

Table S4.   ANOVA *P* values for comparisons of Pleistocene coyotes to other sites

	SoCal Modern	Other Modern	Holocene Caves	Pit 10	RLB	McKittrick	Maricopa
RLB							
HuL	**<0.001**	0.140	0.343	**<0.001**	N/A	0.982	0.876
HuAPD	**<0.001**	**<0.001**	**<0.001**	**<0.001**	N/A	0.639	0.775
HuMLD	**<0.001**	**<0.001**	**<0.001**	**<0.001**	N/A	0.891	0.949
HuPCL	**<0.001**	**<0.001**	**0.029**	**<0.001**	N/A	0.954	**0.033**
HuHTL	**<0.001**	**<0.001**	**<0.001**	**<0.001**	N/A	0.984	0.109
HuEB	**<0.001**	**<0.001**	**0.002**	**<0.001**	N/A	1.000	0.959
RaL	**0.001**	0.233	0.075	**<0.001**	N/A	0.993	0.965
RaAPD	**<0.001**	**<0.001**	**<0.001**	**<0.001**	N/A	0.988	1.000
RaMLD	**<0.001**	**<0.001**	**0.001**	**<0.001**	N/A	1.000	1.000
UlL	0.608	1.000	1.000	0.712	N/A	0.720	None
UlOL	**0.001**	**<0.001**	**<0.001**	0.987	N/A	**0.003**	None
FeL	**<0.001**	**0.026**	0.264	**<0.001**	N/A	0.953	0.378
FeAPD	**<0.001**	**0.002**	0.976	**0.002**	N/A	0.985	0.128
FeMLD	**<0.001**	**<0.001**	**0.038**	**<0.001**	N/A	1.000	1.000
FeGTH	**0.014**	**<0.001**	1.000	0.102	N/A	0.742	0.575
FeHD	**<0.001**	0.094	0.521	**<0.001**	N/A	0.954	0.993
FeB	**<0.001**	**0.011**	0.416	**<0.001**	N/A	0.985	0.906
TiL	**0.001**	0.999	**0.006**	**<0.001**	N/A	0.998	1.000
TiAPD	**0.001**	0.136	**0.049**	**<0.001**	N/A	1.000	0.933
TiMLD	**<0.001**	0.106	**<0.001**	**<0.001**	N/A	0.759	0.995
TiSL	**<0.001**	0.975	1.000	**<0.001**	N/A	**<0.001**	0.891
McKittrick							
HuL	**<0.001**	0.160	0.239	**<0.001**	0.982	N/A	0.670
HuAPD	0.072	0.758	0.070	**0.007**	0.639	N/A	1.000
HuMLD	**0.012**	**0.018**	0.058	**0.021**	0.891	N/A	1.000
HuPCL	**0.008**	0.141	0.672	**0.015**	0.954	N/A	0.552
HuHTL	**<0.001**	**0.013**	0.080	**0.021**	0.984	N/A	0.691
HuEB	**<0.001**	**0.003**	**0.017**	**<0.001**	1.000	N/A	0.934
RaL	**0.011**	0.340	0.094	**<0.001**	0.993	N/A	0.896
RaAPD	**0.001**	**<0.001**	**<0.001**	**0.002**	0.988	N/A	0.992
RaMLD	**<0.001**	0.159	**0.018**	**<0.001**	1.000	N/A	1.000
UlL	0.203	0.789	0.720	0.241	0.720	N/A	None
UlOL	0.638	0.893	0.959	**0.005**	**0.003**	N/A	None
FeL	**0.001**	**0.032**	0.133	**<0.001**	0.953	N/A	0.180
FeAPD	**<0.001**	**0.002**	0.630	**0.001**	0.985	N/A	**0.042**
FeMLD	**<0.001**	**0.003**	**0.046**	**0.002**	1.000	N/A	1.000
FeGTH	0.980	**<0.001**	0.886	1.000	0.742	N/A	1.000
FeHD	**0.001**	0.098	0.289	**0.001**	0.954	N/A	0.850
FeB	**<0.001**	0.051	0.322	**<0.001**	0.985	N/A	0.722
TiL	**0.006**	0.879	**0.010**	**<0.001**	0.998	N/A	1.000
TiAPD	**0.020**	0.428	0.150	**<0.001**	1.000	N/A	0.936
TiMLD	**0.012**	0.995	0.062	**<0.001**	0.759	N/A	0.995
TiSL	0.935	0.132	0.675	1.000	**<0.001**	N/A	1.000
Maricopa							
HuL	0.424	1.000	0.999	0.211	0.876	0.670	N/A
HuAPD	0.169	0.863	0.145	**0.027**	0.775	1.000	N/A
HuMLD	**0.041**	0.061	0.116	0.060	0.949	1.000	N/A
HuPCL	0.933	1.000	1.000	0.958	**0.033**	0.552	N/A
HuHTL	**0.002**	0.931	0.973	0.921	0.109	0.691	N/A
HuEB	0.055	0.523	0.601	**0.020**	0.959	0.934	N/A
RaL	0.997	1.000	0.999	0.824	0.965	0.896	N/A
RaAPD	0.785	0.606	0.350	0.747	1.000	0.992	N/A
RaMLD	0.175	0.914	0.528	0.178	1.000	1.000	N/A
UlL	None	None	None	None	None	None	N/A
UlOL	None	None	None	None	None	None	N/A
FeL	0.973	1.000	1.000	0.756	0.378	0.180	N/A
FeAPD	**0.028**	0.786	1.000	0.134	0.128	**0.042**	N/A
FeMLD	**<0.001**	**<0.001**	0.094	**0.001**	1.000	1.000	N/A
FeGTH	1.000	**<0.001**	0.672	1.000	0.575	1.000	N/A
FeHD	0.212	0.968	0.993	0.189	0.993	0.850	N/A
FeB	0.231	0.977	1.000	0.053	0.906	0.722	N/A

Table S4. Cont.

	SoCal Modern	Other Modern	Holocene Caves	Pit 10	RLB	McKittrick	Maricopa
TiL	0.999	1.000	0.999	0.904	1.000	1.000	N/A
TiAPD	0.944	1.000	0.989	0.565	0.933	0.936	N/A
TiMLD	0.700	1.000	0.801	0.275	0.645	0.995	N/A
TiSL	1.000	0.994	0.998	1.000	0.891	1.000	N/A

Values in bold indicate significance at the $\alpha = 0.05$ level.

Table S5. All coyote specimens used in these analyses including: age, locality, sample size, and specimen numbers

Age	Locality	n	Museum and specimen numbers
Modern	Kern County, CA	5	LACM 51300, 52276, 52277, 52278, 52279
Modern	Los Angeles County, CA	2	LACM 30358, 31164
Modern	Los Angeles County, Lincoln Park	1	LACM 83
Modern	Los Angeles County, Griffith Park	1	LACM 52253
Modern	Los Angeles County, Beverly Hills	1	LACM 52254
Modern	Los Angeles County, Agoura	1	LACM 87635
Modern	Orange County, CA	2	LACM 31244, 87420
Modern	San Diego County, CA	1	LACM 52176
Modern	San Diego County, El Cajon	1	UCLA 13789
Modern	Santa Barbara County, Lompoc	1	UCLA 13851
Modern	Ventura County, CA	1	LACM 85735
Modern	Cherokee County, NC	1	NCSM 8183
Modern	Columbus County, NC	1	NCSM 7116
Modern	Duplin County, NC	1	NCSM 5282
Modern	Haywood County, NC	1	NCSM 8326
Modern	Henderson County, NC	1	NCSM 8191
Modern	Hyde County, NC	2	NCSM 8204, 8207
Modern	Iredell County, NC	1	NCSM 5564
Modern	Macon County, NC	1	NCSM 8963
Modern	Polk County, NC	1	NCSM 15024
Modern	Tyrrell County, NC	2	NCSM 7830, 5825
Modern	Wayne County, NC	1	NCSM 15026
Modern	Randolph County, NC	1	NCSM 8205
Modern	Elgin, AZ	2	UCLA 15414, 15415
Modern	Grand Canyon, AZ	1	LACM 22588
Modern	Delta, CO	1	USNM 533111
Modern	Morton County, ND	2	USNM 291937, 291938
Modern	Fort Kearney, NE	1	USNM A01326
Modern	Beaver Head, MT	1	LACM 54172
Modern	Afton, WY	1	USNM 263786
Mid-Holocene (~3–5 Ka)	Middle Butte Cave, ID	6 each element	IMNH 47001, 47002, 47003, 47004, 47005, 47006, 47015, 47016, 47017, 47022, 47023, 47024, 47025, 47026, 47027, 47028, 47034, 47035, 47036, 47037, 47038, 47043, 47044, 47045, 47046, 47047, 47048, 47049, 47050, 47051, 47052, 47053, 47054, 47055, 47056, 47057, 47303, 47304, 47305, 47306, 47307, 47308
Mid-Holocene (~3–5 Ka)	Moonshiner Cave, ID	4 each element	IMNH 20028, 20029, 20032, 20034, 20035, 20037, 20038, 20040, 20041, 20042, 20043, 20044, 47228, 47234, 47007, 47008, 47009, 47010, 47011, 47012, 47013, 47014, 47018, 47019, 47020, 47021, 47229, 47230, 47231, 47232, 47233, 47235, 47236, 47237, 47238, 47239, 47240
Late Pleistocene	Maricopa Brea, CA	4–7 each element (except ulnae)	LACM 17720, 7721, 17729, 17731, 17734, 17735, 17866, 17867, 17868, 21826, 22114, 22573, 22573, 22573, 27142, 6731–1, 6731–2, 6731–3, 6731–4, 6731–5
Late Pleistocene	McKittrick Tar Pits, CA	9–12 each element	LACM 101332, 101333, 101336, 101337, 101338, 101339, 101342, 101375, 101376, 101377, 101464, 101466, 101467, 101469, 101472, 101473, 101474, 101475, 101476, 101565, 101567, 101570, 102239, 102240, 102241, 102242, 102243, 102244, 102247, 102248, 102362, 102363, 102367, 102368, 102369, 102370, 102371, 102372, 102374, 102376, 102377, 102381

Table S5. Cont.

Age	Locality	n	Museum and specimen numbers
Earliest Holocene (~10 Ka)	Pit 10, RLB	12–15 each element	LACMHC 9638, 9642, 9644, 9648, 9796, 9797, 9799, 9800, 9801, 9822, 9823, 9834, 9835, 9836, 9837, 9839, 9840, 9841, 9856, 9910, 9916, 9918, 9939, 9940, 9945, 9946, 9947, 9948, 9949, 9950, 9968, 9973, 9984, 9985, 9987, 10010, 10018, 10024, 10025, 10026, 10031, 10032, 10051, 10055, 10057, 10062, 10063, 10064, 10065, 10069, 10070, 10071, 10072, 10073, 10074, 10075, 10094, W-639
Late Pleistocene (~11.5 Ka)	Pit 61/67, RLB	10–15 each element	LACMHC 118907, 118909, 118910, 119843, 120352, W-09, W-112, W-117, W-118, W-129, W-261, W-262, W- 66, W-267, W-268, W-269, W-273, W-274, W-275, W- 76, W-36, W-498, W-499, W-500, W-505, W-506, W- 82, W-585, W-586, W-654, W-657, W-658, W-666, W- 67, W-668, W-671, W-674, W-676, W-7, W-757, W-760, W-775, W-776, W-791, W-793, W-9, X-9657, X-9660, X-9672, X-9776, X-9777, X-9785, X-9789, X-9791, X-9793, X-9794, X-9795, X-9797, X-9799, X-9801, X-9807, X-9879, X-9888, X-9894, X-9895
Late Pleistocene (~14.5 Ka)	Pit 4, RLB	8–15 each element	LACMHC 117976, 120341, W-199, W-200, W-202, W-203, W-204, W-205, W-206, W-213, W-214, W-215, W-473, W-475, W-476, W-477, W-478, W-479, W-480, W-481, W-624, W-625, W-627, W-628, W-630, W-632, W-634, W-635, W-636, W-637, W-67, W-68, W-74, W-76, X-9631, X-9632, X-9635, X-9742, X-9743, X-9744, X-9745, X-9746, X-9749, X-9751, X-9753, X-9755, X-9756, X-9775, X-9845, X-9957
Late Pleistocene (~18.5 Ka)	Pit 3, RLB	7–15 each element	LACMHC W-144, W-184, W-185, W-186, W-187, W-189, W-190, W-191, W-193, W-195, W-196, W-197, W-198, W-468, W-469, W-471, W-541, W-544, W-545, W-546, W-61, W-65, W-713, W-714, W-715, W-718, W-719, W-720, W-721, W-722, W-807, X-9624, X-9732, X-9733, X-9734, X-9736, X-9737, X-9739, X-9740, X-9944, X-9956
Late Pleistocene (~21.3 Ka)	Pit 60, RLB	1–3 each element	LACMHC W-239, W-496, W-497, W-572, X-9887, X-9991, X-9993
Late Pleistocene (~26.4 Ka)	Pit 16 RLB	5–10 each element	LACMHC W-639, W-227, W-228, W-229, W-230, W-231, W-232, W-233, W-236, W-489, W-490, W-492, W-493, W-494, W-644, W-645, W-646, W-647, W-648, W-649, W-650, W-651, W-711, W-712, X-9551, X-9646, X-9647, X-9648, X-9649, X-9650, X-9652, X-9653

IMNH, Idaho Museum of Natural History; LACM, Natural History Museum of Los Angeles County; LACMHC, George C. Page Museum of Tar Pits Discoveries; NCSM, North Carolina Museum of Natural Sciences; UCLA, Donald R. Dickey Collection at University of California, Los Angeles; USNM, Smithsonian Institution National Museum of Natural History.

Table S6. All gray wolf specimens used in these analyses including age, locality, sample size, and specimen numbers

Age	Locality	n	Museum and specimen numbers
Modern	Santa Cruz County, AZ	2	UCLA 16403, 16404
Modern	Tyrrell County, NC	1	NCSM 5284
Modern	Anchorage, AK	2	USNM 324994, A00977
Modern	Fort Union, ND	1	USNM 977
Modern	Fort Kearney, NB	1	USNM A01308
Modern	Montana, Upper Missouri River	1	USNM A03497
Modern	Gallatin County, MT	1	USNM 271651
Modern	Locality unknown	1	LACMHC PED-047–1
Mid-Holocene (∼3–5 Ka)	Middle Butte Cave, ID	3–5 each element	IMNH 23992, 24728, 24729, 24730, 24731, 24732, 47029, 47030, 47031, 47032, 47033, 47058, 47059, 47060, 47066, 47067, 47068, 47069
Mid-Holocene (∼3–5 Ka)	Moonshiner Cave, ID	4–5 each element	IMNH 19869, 19870, 19871, 19872, 19873, 19875, 19876, 19877, 19878, 19881, 19882, 19884, 21223, 21338, 47242, 47243, 47244, 47245, 47246, 47247, 47248, 47249, 47250, 47251, 47252, 47253, 47254, 47255, 47256, 47257, 47258, 47259, 47260
Late Pleistocene (∼21.3–11.5 Ka)	RLB (Pits 3, 13, 60, 61/67)	2–6 each element	LACMHC 14442, 14443, 14444, 14445, 14457, 80862, 95310, 97455, 97456, 97457, 97458, 102812, 126459, E-215, E-24, H-1193, H1201, H-1214, H-1537, H-1638, H2121, H-633, H-675, H-744, H772, I-5820, I-6386, I- 587, I-6613, I-6621, I-6702, I-6925, I-7394, I-9441, I-9853, W-6799

IMNH, Idaho Museum of Natural History; LACMHC, George C. Page Museum of Tar Pits Discoveries; NCSM, North Carolina Museum of Natural Sciences; UCLA, Donald R. Dickey Collection at University of California, Los Angeles; USNM, Smithsonian Institution National Museum of Natural History.