Ecological Changes in Coyotes (*Canis latrans*) in Response to the Ice Age Megafaunal Extinctions

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Abstract

Coyotes (*Canis latrans*) are an important species in human-inhabited areas. They control pests and are the apex predators in many ecosystems. Because of their importance it is imperative to understand how environmental change will affect this species. The end of the Pleistocene Ice Age brought with it many ecological changes for coyotes and here we statistically determine the changes that occurred in coyotes, when these changes occurred, and what the ecological consequences were of these changes. We examined the mandibles of three coyote populations: Pleistocene Rancho La Brean (13–29 Ka), earliest Holocene Rancho La Brean (8–10 Ka), and Recent from North America, using 2D geometric morphometrics to determine the morphological differences among them. Our results show that these three populations were morphologically distinct. The Pleistocene coyotes had an overall robust mandible with an increased shearing arcade and a decreased grinding arcade, adapted for carnivory and killing larger prey; whereas the modern populations show a gracile morphology with a tendency toward omnivory or grinding. The earliest Holocene populations are intermediate in morphology and smallest in size. These findings indicate that a niche shift occurred in coyotes at the Pleistocene/Holocene boundary – from a hunter of large prey to a small prey/more omnivorous animal. Species interactions between *Canis* were the most likely cause of this transition. This study shows that the Pleistocene extinction event affected species that did not go extinct as well as those that did.
Introduction

Coyotes (*Canis latrans*) are an important species for their ability to co-exist with humans in urban and suburban areas [1–3] where they provide ecosystem services such as control of populations of deer, rodents, and other pests; but also present challenges, such as spreading diseases to domestic animals and preying on pets [3, 4]. Because of the extirpation of larger carnivores such as bears, wolves, and mountain lions, coyotes are the current apex predator in many ecosystems in North America [3]. Coyotes are also a behaviorally labile species with the ability to change activity patterns and ecological niche depending upon their circumstances. Examples include changing pack size and prey preferences depending on whether competitors/predators, such as gray wolves, are present or absent [6–8].

Extant coyote subspecies in North America are also highly mobile, colonizing areas at a rapid rate [9–11]. This rapid colonization has led to most extant coyote subspecies being somewhat morphologically and genetically homogenous, which complicates subspecies distinctions [9, 10, 12].

As a labile species, coyotes did not always fill the same ecological niches that they fill today. The end of the Pleistocene epoch (circa 11,500 years ago) ushered in the demise of the large mammalian megafauna that roamed North America for millions of years, but also affected the species that did not go extinct, such as coyotes. Meachen and Samuels [12] examined the postcrania of Pleistocene and Holocene coyotes and found that late Pleistocene coyotes from western North America (*Canis latrans orcutti* ≈ late Pleistocene) were larger and more robust than Holocene coyotes. Using their results and the results of another paper on sociality in *Smilodon fatalis* [13], they concluded that the Pleistocene coyotes were more gregarious and hunted larger prey than Recent coyotes and that the end-Pleistocene megafaunal extinctions had a large effect on this niche shift.

Other studies have examined the crania of *C. l. orcutti* from Rancho La Brea and concluded that their crania were larger and more robust than modern coyotes, with shorter rostra and broader carnassial teeth for meat processing [14, 15]. However, these earlier cranial papers did not statistically test the changes that occurred in coyotes, when these changes may have occurred or what the ecological consequences of these changes may have been. In conjunction with the previous work on coyote postcrania, we explore the morphological changes that occurred in coyote crania at the Pleistocene/Holocene boundary that have shaped the roles that coyotes fill today.

Here, we examine the mandibles of seven subspecies of extant coyotes and compare them to the mandibles of coyotes from late Pleistocene Rancho La Brea and early Holocene Rancho La Brea to examine ecological differences in feeding adaptations between these three groups and when any ecological changes may have occurred. The mandible is a good indicator of feeding adaptations because it can be modeled as a two dimensional structure and contains functional information such as potential resistance to chewing forces [16] and relative proportions of grinding versus shearing dentition, which can indicate diet, or in the case of carnivores, prey killing preferences and hunting strategies [17–19].
Materials and Methods

We sampled 76 coyote mandibles from seven extant subspecies from the Field Museum of Natural History (FMNH) including: *C. l. frustor*, *C. l. latrans*, *C. l. lestes*, *C. l. mearnsi*, *C. l. ochropus*, *C. l. texensis*, and *C. l. thamnos*. We also sampled 84 coyote mandibles from the Page Museum (LACMHC) from the Rancho La Brea tar pits (see Table 1 for specimens used). No permits were required for the described study, as no field work was performed to collect these data. Eighteen of these specimens belong to pit 10 at Rancho La Brea. Although some avian specimens from pit 10 are dated as Pleistocene, preliminary data on coyote material suggests that they were indeed early Holocene in age (B. Fuller and J. Southon, personal communication as a continuation of [20]), approximately 8–10 Ka. The remaining 66 mandibles were from Pleistocene pits that range in age from approximately 13–29 Ka [21], including the following pits: 91 (<29.1 thousand years before present (Kybp)), 16 (<26.4 Kybp), 3 (<18.5 Kybp), 13 (<16.2 Kybp), 4 (<14.5 Kybp), and 61/67 (<13 Kybp). Each pit date is a rough estimate rather than a distinct age due to an uncertain window of deposition and a lack of radiocarbon dates.

We analyzed *C. latrans* mandibular morphology using 2D geometric morphometrics (GM). Mandibular morphology captures many attributes of prey-killing and feeding style in carnivores [16, 22], and mandible fossils are numerous at RLB. Mandibles were digitized from digital photographs of the labial view of hemi-mandibles of *C. latrans*. Our photographing procedure followed published protocols as in [23]. For further discussion of the analysis of 2D representations of 3D structures see Zelditch et al. [24].

We digitized 13 landmarks on the labial view of each mandible in tpsDig2 (version 2.17) [25]. Landmark points were chosen to represent functional shape changes which may indicate response to feeding stresses and diet (Table 2; Fig. 1). Scalar data was collected by including the scale bar in every specimen photo and using the ‘measure’ tool in tpsDig2 and estimated using the centroid size computed from the landmark data. All sets of landmark coordinates were then aligned using a least-squares Procrustes average configuration of landmarks and the x, y-coordinates were used to obtain a consensus configuration. We generated partial warp scores (localized shape differences) by comparing individual landmarks to the mean configuration [24]. Mandible size and by-proxy overall size [26] were measured using centroid size, the scaling component of the Procrustes superimposition being a robust isometric size estimator [27]. A TPS file of all of our coyote mandibles can be downloaded on Dryad (www.datadryad.org), doi:10.5061/dryad.vn413.

A principal component analysis (PCA) run on the covariance matrix in pcagen7_14a [28] was then used to explore the distribution of mandibular shapes among the samples [24]. Using the PC axes as new variables describing shape variance in the data, we tested the hypotheses of equivalent shape means among pits by running multivariate analyses of variance (MANOVAs) on the resulting PC axes using Scheffé’s *post hoc* procedure for equal variance and Tamhane’s *post*
Table 1. Specimen numbers used in this analysis.

| Museum | Specimen number | Subspecies | Locality |
|--------|-----------------|------------|----------|
| FMNH   | 77208           | frustror   | USA; Arkansas; Miller Co. |
| FMNH   | 53694           | frustror   | USA; Oklahoma; Comanche Co. |
| FMNH   | 77209           | frustror   | USA; Arkansas; Miller Co. |
| FMNH   | 135222          | frustror   | USA; Kansas; Leavenworth Co. |
| FMNH   | 53695           | frustror   | USA; Oklahoma; Comanche Co. |
| FMNH   | 13246           | mearnsi    | USA; California; Tulare Co. |
| FMNH   | 13248           | mearnsi    | USA; California; Tulare Co. |
| FMNH   | 13247           | mearnsi    | USA; California; Tulare Co. |
| FMNH   | 53755           | mearnsi    | USA; California; San Bernardino Co., Yermo |
| FMNH   | 13249           | mearnsi    | USA; California; Inyo Co, Big Cottonwood meadow |
| FMNH   | 13251           | mearnsi    | USA; California; Los Angeles Co, Neenach |
| FMNH   | 53705           | mearnsi    | USA; Arizona; Pima Co. |
| FMNH   | 53706           | mearnsi    | USA; Arizona; Pima Co. |
| FMNH   | 53707           | mearnsi    | USA; Arizona; Pima Co. |
| FMNH   | 52860           | mearnsi    | USA; Arizona; Pima Co. |
| FMNH   | 135197          | lestes     | USA; Wyoming; Sweetwater Barrel Springs |
| FMNH   | 135199          | lestes     | USA; Wyoming; Sweetwater Barrel Springs |
| FMNH   | 135201          | lestes     | USA; Wyoming; Sweetwater Barrel Springs |
| FMNH   | 135198          | lestes     | USA; Wyoming; Sweetwater Barrel Springs |
| FMNH   | 105034          | lestes     | USA; Wyoming, Natrona Co. |
| FMNH   | 135200          | lestes     | USA; Wyoming; Sweetwater, Salazar Butte Quadrangle |
| FMNH   | 145970          | lestes     | USA; Wyoming, Sweetwater Co. |
| FMNH   | 160125          | lestes     | USA; Wyoming, Sweetwater Co. |
| FMNH   | 158709          | lestes     | USA; Wyoming, Sweetwater Co. |
| FMNH   | 160124          | lestes     | USA; Wyoming, Sweetwater Co. |
| FMNH   | 145971          | lestes     | USA; Wyoming, Sweetwater Co. |
| FMNH   | 18985           | lestes     | USA; Colorado, Boulder Co. |
| FMNH   | 52901           | lestes     | USA; Colorado, Mesa Co. |
| FMNH   | 18986           | lestes     | USA; California, Tulare Co. |
| FMNH   | 52902           | lestes     | USA; Colorado, Garfield Co. |
| FMNH   | 81499           | lestes     | USA; California, Tulare Co. |
| FMNH   | 20389           | lestes     | USA; Montana, Jefferson Co. |
| FMNH   | 25166           | lestes     | USA; Idaho, Custer Co., Salmon river |
| FMNH   | 20388           | lestes     | USA; Montana, Jefferson Co. |
| FMNH   | 52900           | lestes     | USA; Colorado, Garfield Co. |
| FMNH   | 42765           | latrans    | USA; South Dakota, Pennington Co. |
| FMNH   | 42766           | latrans    | USA; South Dakota, Pennington Co. |
| FMNH   | 42747           | latrans    | USA; South Dakota, Pennington Co. |
| FMNH   | 42764           | latrans    | USA; South Dakota, Pennington Co. |
| FMNH   | 42768           | latrans    | USA; South Dakota, Pennington Co. |
| FMNH   | 42769           | latrans    | USA; South Dakota, Pennington Co. |
| FMNH   | 42748           | latrans    | USA; South Dakota, Pennington Co. |
| FMNH   | 42767           | latrans    | USA; South Dakota, Pennington Co. |
| FMNH   | 13250           | ochropus   | USA; California, Kern Co. |
Table 1. Cont.

| Museum | Specimen number | Subspecies | Locality |
|--------|-----------------|------------|----------|
| FMNH   | 81498           | ochrops    | USA; California, Los Angeles Co. |
| FMNH   | 81495           | ochrops    | USA; California, Los Angeles Co. |
| FMNH   | 81497           | ochrops    | USA; California, Los Angeles Co. |
| FMNH   | 16019           | ochrops    | USA; California, Mendocino Co. |
| FMNH   | 81496           | ochrops    | USA; California, Los Angeles Co, Alhambra |
| FMNH   | 53053           | texensis   | USA; Texas, Nueces Co, Corpus Christi |
| FMNH   | 57504           | texensis   | USA; Texas, Howard Co |
| FMNH   | 83482           | texensis   | USA; Texas, Brewster Co |
| FMNH   | 83481           | texensis   | USA; Texas, Brewster Co |
| FMNH   | 53052           | texensis   | USA; Texas, Nueces Co, Corpus Christi |
| FMNH   | 53051           | texensis   | USA; Texas, Nueces Co, Corpus Christi |
| FMNH   | 154637          | thamnos    | USA; Illinois, Cook Co. O’Hare |
| FMNH   | 126805          | thamnos    | USA; Illinois, Cook Co. |
| FMNH   | 167044          | thamnos    | USA; Illinois, Cook Co. |
| FMNH   | 167068          | thamnos    | USA; Illinois, Du Page Co. Oak Brook |
| FMNH   | 167069          | thamnos    | USA; Illinois, Du Page Co. Oak Brook |
| FMNH   | 172552          | thamnos    | USA; Illinois, Kane Co. |
| FMNH   | 175313          | thamnos    | USA; Illinois, Du Page Co. Oak Brook |
| FMNH   | 196143          | thamnos    | USA; Illinois, Du Page Co. Hanover Park |
| FMNH   | 167043          | thamnos    | USA; Illinois, Will Co. |
| FMNH   | 23946           | thamnos    | USA; Illinois, Lake Co, Camp Logan |
| FMNH   | 129292          | thamnos    | USA; Illinois, Franklin Co. |
| FMNH   | 178025          | thamnos    | USA; Illinois, Douglas Co. |
| FMNH   | 13163           | thamnos    | USA; Minnesota, Nicollet Co. |
| FMNH   | 43961           | thamnos    | USA; Michigan, Marquette Co. |
| FMNH   | 24379           | thamnos    | USA; Wisconsin, Kenosha |
| FMNH   | 129293          | thamnos    | USA; Wisconsin, Oneida Co. |
| FMNH   | 19682           | thamnos    | USA; Wisconsin, Marinette Co. |
| FMNH   | 29513           | thamnos    | USA; Indiana, St. Joseph Co. |
| FMNH   | 154646          | thamnos    | USA; Wisconsin; Onieda Co. |
| FMNH   | 150782          | thamnos    | USA; Wisconsin, Douglas Co. Brule |
| LACMHC | HC 6171         | orcutti    | Pit 3 |
| LACMHC | 6172            | orcutti    | Pit 3 |
| LACMHC | 6170            | orcutti    | Pit 3 |
| LACMHC | 6180            | orcutti    | Pit 3 |
| LACMHC | 3201-L-8        | orcutti    | Pit 3 |
| LACMHC | 56861           | orcutti    | Pit 3 |
| LACMHC | 56862           | orcutti    | Pit 3 |
| LACMHC | 57404           | orcutti    | Pit 4 |
| LACMHC | 56915           | orcutti    | Pit 4 |
| LACMHC | 56916           | orcutti    | Pit 4 |
| LACMHC | 6187            | orcutti    | Pit 4 |
| LACMHC | 56931           | orcutti    | Pit 4 |
| LACMHC | 56918           | orcutti    | Pit 4 |
Table 1. Cont.

| Museum     | Specimen number | Subspecies | Locality |
|------------|-----------------|------------|----------|
| LACMHC     | 56919           | orcutti    | Pit 4    |
| LACMHC     | 6186            | orcutti    | Pit 4    |
| LACMHC     | 6252            | orcutti    | Pit 4    |
| LACMHC     | 56920           | orcutti    | Pit 4    |
| LACMHC     | 56921           | orcutti    | Pit 4    |
| LACMHC     | 56922           | orcutti    | Pit 4    |
| LACMHC     | HC 6219         | orcutti    | Pit 10   |
| LACMHC     | 6220            | orcutti    | Pit 10   |
| LACMHC     | 6221            | orcutti    | Pit 10   |
| LACMHC     | 6222            | orcutti    | Pit 10   |
| LACMHC     | 6223            | orcutti    | Pit 10   |
| LACMHC     | 6224            | orcutti    | Pit 10   |
| LACMHC     | 6225            | orcutti    | Pit 10   |
| LACMHC     | 6226            | orcutti    | Pit 10   |
| LACMHC     | 6227            | orcutti    | Pit 10   |
| LACMHC     | 6228            | orcutti    | Pit 10   |
| LACMHC     | 6229            | orcutti    | Pit 10   |
| LACMHC     | 57056           | orcutti    | Pit 10   |
| LACMHC     | 57059           | orcutti    | Pit 10   |
| LACMHC     | 57061           | orcutti    | Pit 10   |
| LACMHC     | 57062           | orcutti    | Pit 10   |
| LACMHC     | 57063           | orcutti    | Pit 10   |
| LACMHC     | 57064           | orcutti    | Pit 10   |
| LACMHC     | 57066           | orcutti    | Pit 10   |
| LACMHC     | 57142           | orcutti    | Pit 13   |
| LACMHC     | HC 6210         | orcutti    | Pit 13   |
| LACMHC     | 3201-R-5        | orcutti    | Pit 13   |
| LACMHC     | 57149           | orcutti    | Pit 13   |
| LACMHC     | 57147           | orcutti    | Pit 13   |
| LACMHC     | 57151           | orcutti    | Pit 13   |
| LACMHC     | 57146           | orcutti    | Pit 13   |
| LACMHC     | 57152           | orcutti    | Pit 13   |
| LACMHC     | HC 6213         | orcutti    | Pit 16   |
| LACMHC     | 57250           | orcutti    | Pit 16   |
| LACMHC     | 57251           | orcutti    | Pit 16   |
| LACMHC     | 6255            | orcutti    | Pit 16   |
| LACMHC     | 57253           | orcutti    | Pit 16   |
| LACMHC     | 57256           | orcutti    | Pit 16   |
| LACMHC     | 6254            | orcutti    | Pit 16   |
| LACMHC     | 6211            | orcutti    | Pit 16   |
| LACMHC     | 57257           | orcutti    | Pit 16   |
| LACMHC     | 57259           | orcutti    | Pit 16   |
| LACMHC     | 57262           | orcutti    | Pit 16   |
| LACMHC     | HC 6183         | orcutti    | Pit 61   |
hoc procedure for unequal variances in SPSS 22 [29]. Additionally, we ran a homogeneity of variance test to determine if variances were equal or unequal. A qualitative evaluation of the average shape among pits is accomplished using an animation that shows the movement of each landmark configuration's mean shape from one pit to another. Arranging the pits in temporal sequence reveals the coyote jaw shape change over geologic time (See S1 Video).

**Results**

We ran MANOVAs on the PCs of all possible combinations of coyote groups (modern subspecies, between Pleistocene pits, all groups measured) and found that the comparison between the following three groups were statistically

| Museum    | Specimen number | Subspecies | Locality |
|-----------|-----------------|------------|----------|
| LACMHC    | 6192            | orcutti    | Pit 61   |
| LACMHC    | 6191            | orcutti    | Pit 61   |
| LACMHC    | 6185            | orcutti    | Pit 61   |
| LACMHC    | 6175            | orcutti    | Pit 61   |
| LACMHC    | 6174            | orcutti    | Pit 61   |
| LACMHC    | 3201-R-2        | orcutti    | Pit 61   |
| LACMHC    | 57349           | orcutti    | Pit 61   |
| LACMHC    | 57350           | orcutti    | Pit 61   |
| LACMHC    | 6184            | orcutti    | Pit 61   |
| LACMHC    | 57376           | orcutti    | Pit 67   |
| LACMHC    | 6199            | orcutti    | Pit 67   |
| LACMHC    | 6173            | orcutti    | Pit 67   |
| LACMHC    | 6197            | orcutti    | Pit 67   |
| LACMHC    | 6200            | orcutti    | Pit 67   |
| LACMHC    | 57384           | orcutti    | Pit 67   |
| LACMHC    | 6201            | orcutti    | Pit 67   |
| LACMHC    | 57378           | orcutti    | Pit 67   |
| LACMHC    | 57379           | orcutti    | Pit 67   |
| LACMHC    | 57380           | orcutti    | Pit 67   |
| LACMHC    | 57381           | orcutti    | Pit 67   |
| LACMHC    | 57383           | orcutti    | Pit 67   |
| LACMHC    | 57403           | orcutti    | Pit 67   |
| LACMHC    | 39573           | orcutti    | Pit 91   |
| LACMHC    | 24001           | orcutti    | Pit 91   |
| LACMHC    | 13139           | orcutti    | Pit 91   |
| LACMHC    | 22036           | orcutti    | Pit 91   |
| LACMHC    | 31790           | orcutti    | Pit 91   |

Museum legend: FMNH, Field Museum, Chicago, IL; LACMHC, Rancho La Brea, Page Museum Hancock collection, Los Angeles, CA.

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significant: Pleistocene individuals (all pits together – except 10), Pit 10 individuals, and extant individuals (all subspecies taken together) (Table 3), so it is these results that we will focus on for the remainder of the study. No significant differences were found between the PCs of extant coyote subspecies, suggesting that extant coyote jaws show few morphological differences over their geographic range in North America. For the Pleistocene Rancho La Brean coyotes, pits 3 and 61/67 were significantly different on PC 4 (p=0.032), but no other statistically significant differences were found between Pleistocene pits.

When we compared modern coyotes (all 7 subspecies together in one group), Pit 10 early Holocene coyotes and Pleistocene RLB coyotes (all Pleistocene pits), our principal components analysis yielded 20 principal components that explained 100% of the variance, however, only the first 3 PCs showed meaningful differences between the three groups. So we chose to focus only on the first 3 PC axes, plus centroid size (CS) for this statistical comparison.

### Table 2. Landmarks used in this study.

| Landmark | Description |
|----------|-------------|
| 1        | Anterior edge of mandible, before the incisors. |
| 2        | Anterior edge of the canine tooth at the tooth/mandible junction. |
| 3        | Posterior edge of the canine tooth at the tooth/mandible junction. |
| 4        | Anterior edge of the p1 at the tooth/mandible junction. |
| 5        | Point where the talonid basin (grinding surface) begins at the tooth/mandible junction, can be estimated at roughly 2/3 the length of the m1 (carnassial). |
| 6        | Posterior edge of the m3 or alveolus at the tooth/mandible junction. |
| 7        | Top-most point of the coronoid process |
| 8        | Basin of the mandibular notch, used in conjunction with coronoid process to measure coronoid height. |
| 9        | Posterior most point of the mandible at the condyloid process. |
| 10       | Tip of the angular process |
| 11       | Bottom edge of mandible directly below landmark 6, measured with a straight edge |
| 12       | Bottom edge of mandible directly below landmark 5, measured with a straight edge |
| 13       | Bottom edge of mandible directly below landmark 4, measured with a straight edge |

Also see Fig. 1 for graphical representation.

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**Fig. 1.** Coyote mandible landmarks used in this study. Also see table 2 for descriptions.

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We found a striking pattern of shape variation between these three coyote groups. On PC1 (22% variance explained), Pit 10 coyotes grouped together with Pleistocene coyotes, with negative values (Fig. 2). The Holocene/Pleistocene Rancho La Brea group had dorso-ventrally deeper mandibles under the pre-molar (shearing) arcade, shallower mandibles under the molar (grinding) arcade, a relatively longer shearing arcade and a relatively short grinding arcade and slightly truncated coronoid processes; whereas all modern coyotes showed the opposite pattern with positive values on PC1– shallow mandibles under the premolars and deeper mandibles under the molars, a relatively short premolar arcade and a relatively longer molar arcade, and a heightened coronoid process. On PC2 (16% variance explained), pit 10 coyotes were significantly different from modern and Pleistocene groups – although the two other groups were not different from each other. Pit 10 coyotes had negative scores with relatively larger canines. Pleistocene coyotes had positive values with smaller canines, while modern coyotes did not differ from the consensus shape on PC2 (Figs. 2 & 3). Due to the possible negative allometry of pit 10 coyotes, relative to Pleistocene coyotes on PC2, we ran a reduced major axis regression of PC2 versus log10 centroid size and found that Pleistocene coyotes had the highest slopes with Pit 10 coyotes showing a negative allometric trend and Recent coyotes showing distinct negative allometry from the Pleistocene population (Table 4).

Along PC3 (13% variance explained), Pit 10 and modern coyotes grouped together and are significantly distinct from the Pleistocene sample (see Table 3 for p-values) (Fig. 3). Pleistocene coyotes had negative scores on PC3, with again, shortening of the grinding area arcade, and an antero-ventral movement of the coronoid process. Positive scores on PC3, consistent with modern specimens, were indicative of shallow mandibles and a postero-dorsal movement of the coronoid process. Pit 10 coyotes did not differ significantly from the consensus

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**Table 3. p-values for MANOVAs on the principal component scores and centroid size (CS).**

| Variable | Comparison groups               | p-value |
|----------|--------------------------------|---------|
| PC1      | Modern vs Pleistocene           | <0.001  |
|          | Modern vs Pit 10                | <0.001  |
|          | Pit 10 vs Pleistocene           | 0.179   |
| PC2      | Modern vs Pleistocene           | <0.001  |
|          | Modern vs Pit 10                | 0.007   |
|          | Pit 10 vs Pleistocene           | 0.004   |
| PC3      | Modern vs Pleistocene           | 0.208   |
|          | Modern vs Pit 10                | <0.001  |
|          | Pit 10 vs Pleistocene           | 0.008   |
| CS       | Modern vs Pleistocene           | 0.429   |
|          | Modern vs Pit 10                | 0.006   |
|          | Pit 10 vs Pleistocene           | 0.005   |

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

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shape. For centroid size (CS), pit 10 coyotes were the smallest and were significantly smaller than the Pleistocene sample, but not the modern sample. An animation depicting average pit shape change through time in coyote mandibles can be found in the supplementary materials (S1 Video).

Discussion

Our findings mirror the postcranial findings of Meachen and Samuels [12]. Pleistocene coyotes from Rancho La Brea are larger and more robust, and modern coyotes are the most gracile, suggesting a change in functional use of the mandible. Our findings also reflect the work of Koblmuller et al. [9] and Thurber and Peterson [10] indicating that modern coyote subspecies are relatively homogeneous. Although the individual specimens of a single subspecies cluster together in morphospace, these clusters are broadly overlapping among subspecies and are not distinct.

Pleistocene coyotes have reduced grinding areas, with an expanded shearing arcade, indicating increased carnivory. Notably, the Pleistocene specimens have thickening of the mandibular corpus directly under the carnassial (apex occurring in pit 61/67), reflecting the increased chewing forces that occurred here [16, 22]. This indicates higher feeding stresses in the mandible, and mandibular thickening continues under the m1–m2 junction which may indicate a higher proportion of durophagy, including large bones in the diet. Van Valkenburgh and Hertel [30] also argued for increased bone consumption in the coyotes of Rancho La Brea as they found a significant increase in tooth breakage. An increase in eating large bones would also necessitate a slightly larger gape, accomplished by the shorter
coronoid process. Pleistocene specimens also show corpus thickening at the anterior end, under the first few premolars, when compared with Recent specimens. This anterior mandibular corpus thickening is indicative of increased forces on the anterior mandible, reflecting the “leap and bite” strategy employed by canids when hunting larger prey [19, 31].

Our mandibular results suggest that Pleistocene specimens were large, but not significantly larger than modern specimens. This is slightly different than the findings of Meachen and Samuels [12] that found that Pleistocene coyotes were significantly larger than Recent coyotes. Since postcrania are a better predictor of body mass and overall body size than crania in carnivores [32], we will defer to the postcranial results in this case.

Pit 10 coyotes showed an interesting pattern. These specimens were significantly smaller than all others (as were the postcrania – [12]), but they showed morphological traits closer to their Pleistocene precursors rather than the Recent coyotes; while the subspecies that occurs in southern California today,

**Table 4.** Reduced major axis regression results for PC2 versus log10 CS.

| Group  | RMA intercept | slope   | Slope 95% CI | R²   |
|--------|---------------|---------|--------------|------|
| Pleistocene | -2.126        | 0.651   | 0.49–0.81    | 0.0528 |
| Pit 10  | -1.870        | 0.572   | 0.27–0.87    | >0.001 |
| Recent  | -1.210        | 0.371   | 0.29–0.45    | 0.0920 |
*Canis latrans ochropus* grouped with the other Recent specimens. Pit 10 coyotes retain the deep mandibular corpus proportions of their predecessors but the relative proportions of shearing versus grinding teeth starts to change. In grinding versus shearing, Pit 10 specimens show an intermediate condition between Pleistocene and Recent populations, the same as the consensus shape. This may indicate a shift away from larger, more difficult prey – the dwindling megafauna, to smaller prey like rabbits and rodents. Additionally, PC2 shows a negatively allometric signal through time. This axis reveals larger canines relative to mandibular size in Pit 10 coyotes, while the larger, Pleistocene coyotes have a relatively smaller canine to mandible size ratio. This may reflect a developmental signal being captured in the earliest Holocene. Neoteny in pit 10 coyotes may be the result of truncated growth in the absence of the large quantity of protein that was available in the Pleistocene. This negative trend continues into the Recent coyote populations.

The intermediate condition in the earliest Holocene coyotes, plus mandibular morphology that closely resembles the Pleistocene specimens, but with negative allometry, suggests an adapting population, rather than immigration from elsewhere. However, we cannot test this hypothesis without a DNA analysis.

Recent coyotes have large but gracile mandibles compared with the older populations. They also have a longer grinding arcade and a shorter shearing arcade compared to earlier populations. The mandibular corpus in the Recent coyotes is also relatively shallow, with a slight thickening under the grinding arcade, posterior 1/3 of m1, m2 and m3, which better reflects their diet today – omnivorous with a focus on smaller prey such as rodents and rabbits, but with occasional large prey, such as deer [3, 7, 8, 33, 34].

In a previous paper Meachen and Samuels [12] discuss the interplay between canids in the late Pleistocene and early Holocene. From late Pleistocene fossil records, gray wolves (*Canis lupus*) are rare in Southern California (and in the lower 48 states), but dire wolves (*Canis dirus*) are common [35, 36]. It is likely that when dire wolves went extinct at the end of the Pleistocene a niche opened up in North America and gray wolves moved across from Eurasia to fill this niche. This transition would have had important ecological consequences for coyotes, which would have a new competitor with a smaller overall body size than dire wolves. This size shift in a major competitor may have forced coyotes to get smaller themselves. In fact, antagonistic relationships have plagued gray wolves and coyotes for centuries, with gray wolves actively hunting and exterminating larger coyote individuals [37–43]. It is not unreasonable to think that the megafaunal extinction would have changed the balance between coyotes and larger species of *Canis* in North America.

Additionally, Recent coyote populations also do not seem to follow Bergmann’s rule – a positive relationship between latitude and body size [10, 12] (sometimes presented as a negative relationship between climate and body size). The larger size in Pleistocene coyotes seems to be an anomaly when plotted on a graph of temperature and body size in this species, suggesting that biotic interactions rather than climate are directly responsible for the changes in this species [12].
Conclusions

Here we show, on average, Pleistocene coyotes were experiencing stronger dorso-ventral forces on the mandible during feeding and hunting than living coyotes. This suggests that Pleistocene coyotes were hunting larger prey more frequently and incorporating harder food (such as bone) into their diet. While it is possible that coyotes were scavenging more than hunting, the shape of the thickened anterior corpus suggests that they were also hunting with a higher frequency. This anterior mandibular thickening is also seen in modern canid species that hunt large prey with regularity, due to the repeated “leap and bite” strategy that transmits forces from the prey to the front of the face in canids [19, 31]. Additionally, since coyotes are the third most common fossil at the Rancho La Brea tar pits, they were trapped with high frequency, which was the argument for sociality that Carbone et al. [13] used in their study. The prior study by Meachen and Samuels [12] suggested that in the Pleistocene coyotes were larger, more carnivorous, and traveled in social packs. Here, we concur with that finding, and from the shape of the mandibular corpus we also suggest that coyotes were not mainly scavenging, but actively hunting larger prey. Meachen and Samuels [12] showed that the major environmental changes that occurred at the end of the Pleistocene were the major drivers for this change, including possibly both the extinction (Canis dirus) and influx (C. lupus) of other predators and the extinction of many possible prey species.

Coyotes have clearly changed since the Pleistocene and in conjunction with the end-Pleistocene extinction events. Present day species interactions between coyotes and gray wolves give us insight into the evolution of the coyote from what it was in the past into what we see today. Extinction events do not just affect the species that go extinct, but also affect many of the species that remain. For coyotes, interactions between closely related competitors are likely the driving force behind major evolutionary changes.

Supporting Information

S1 Video. Animation that shows the movement of each landmark configuration’s mean shape change through time in Canis latrans from approximately 38,000 years ago to present.
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Author Contributions
Conceived and designed the experiments: JAM. Performed the experiments: JAM ACJ JEA. Analyzed the data: JAM ACJ JEA. Contributed reagents/materials/analysis tools: RWS. Contributed to the writing of the manuscript: JAM RWS.

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