Microevolution of Jaw Shape in the Dire Wolf, *Canis dirus*, at Rancho La Brea

Alexandria L. Brannick, Julie A. Meachen, and F. Robin O’Keefe

ABSTRACT. The Rancho La Brea tar pits are classic fossil lagerstatten, famous for the deposition of episodic accumulations of large numbers of fossils over short intervals in the late Pleistocene. We analyzed *Canis dirus* hemimandibles from Rancho La Brea through a two-dimensional landmark-based morphometric analysis to examine size and shape changes through time. We scored 16 landmarks each on mandibles gathered from four pits: 61/67 (~13–14 ka), 13 (~17–18 ka), 2051 (~26 ka), and 91 (~28 ka). Analyses indicate size does change through time and shares a broad correlation with climate change. Largest body sizes are correlated with relatively warmer periods, whereas smaller body sizes are found in pits representative of colder climates. Shape variables—allometric size, coronoid process rotation, and molar position—also fluctuated from pit to pit. Additionally, some sexually dimorphic signals are also distinguishable among the mandibles. Global regressions of centroid size against specific molar distances indicated trends similar to those seen in the extant gray wolf (*Canis lupus*). While sexual dimorphism can be inferred, it appears to be constant over time, unlike other morphological aspects of the jaw.

INTRODUCTION

The Rancho La Brea tar pits are an excellent locality for examining late Pleistocene fossil communities. These asphaltic seeps range in age from ~50,000 to 10,000 years ago, spanning the late and terminal Pleistocene (O'Keefe et al., 2009). Each pit can be considered a distinct depositional episode in this larger time range; therefore, climate shifts can be broadly correlated with individual pits. This epoch saw numerous, extreme fluctuations in climate, as well as the demise of several genera of large mammals. The causality of this extinction event is contentious, but some combination of climate change and overkill by humans is the current consensus (Guthrie, 2006; Koch and Barnosky, 2006; Nogués-Bravo et al., 2008; Gill et al., 2009; MacDonald et al., 2012). By analyzing the structure of the fossil communities leading up to the end Pleistocene megafaunal extinction, a clearer interpretation of the causality of this extinction may be ascertained.

The dire wolf *Canis dirus* (Leidy, 1854) was one of the last Pleistocene species to disappear during the megafaunal extinction, with radiocarbon dates of Rancho La Brea specimens dating as recent as 9850 ± 550 BP (Dundas, 1999). Furthermore, specimens from other sites date as young as 8200 ± 260 BP (Hester, 1960). Carnivores are found in higher proportions in the pits at Rancho La Brea: a ratio of 10 carnivores for every one herbivore, the opposite of what is seen in nature and at most fossil sites (Stock, 1992; Binder and Van Valkenburgh, 2010). The disparity is due to the capture mode at the tar pits, wherein one herbivore became mired in the tar and attracted a large number of carnivores, which then became mired themselves. Carbone et al. (2009) suggested a carcass domination scenario, where large carnivores were more likely to become entrapped due to a higher success rate of defending trapped prey against other predators. A recent study supported this hypothesis by reporting significantly higher social carnivore abundance at Rancho La Brea compared with the fauna of Southern California and North America as a whole (McHorse et al., 2012). The most common species at Rancho La Brea is the dire wolf, comprising over 50% of the relative abundance of carnivores there (McHorse et al., 2012). Because of the large numbers of dire wolves, they are an excellent species for the examination of shape over time.
Here we use dire wolf mandibles to examine size and shape change and assess how these fluctuations may relate to climate change and other environmental factors.

The null hypotheses for this study are founded on the morphological variations seen in the extant gray wolf, Canis lupus. The wolf species are similar morphologically and behaviorally, making C. lupus an excellent model for the dire wolf. Previous studies on craniofacial measurements suggest that these two wolf species are not significantly different in most indices related to cranial proportions and jaw musculature, indicating similar feeding and killing behavior between the gray wolf and dire wolf (Biknevicius and Van Valkenburgh, 1996; Anyonge and Baker, 2006; Van Valkenburgh, 2007) However, C. dirus has larger dentition, including a more massive carnassial blade (Anyonge and Baker, 2006). Canis dirus also has broader zygomatic arches and relatively longer temporal fossae which suggest a slightly larger bite force from more massive temporalis muscles (Biknevicius and Van Valkenburgh, 1996; Anyonge and Baker, 2006). This dentition, in addition to larger, rounded canines, reveals that the dire wolf may have been able to resist the struggling of larger prey. Both species probably lived in packs, and they display cursorial hunting adaptations to a hypercarnivorous diet comprised primarily of ungulates, if available (Fox-Dobbs et al., 2007).

We have recently demonstrated significant shape and size difference in gray wolves with regard to geographic variation (O’Keefe et al., 2013). Gray wolves follow Bergmann’s rule, an ecological trend stating that body size increases with increasing latitude and decreasing temperature (Jolicoeur, 1959; Skeel and Carbyn, 1977; Blackburn et al., 1999; O’Keefe et al., 2013). However, recent work has suggested that size differences in gray wolves are related to resource availability rather than surface to volume ratio as was originally suggested by Bergmann’s rule (Geist 1987, McNab 2010). Although Bergmann’s rule is predominantly seen as a latitudinal trend, this pattern may be applied temporally (Gardner et al., 2011). If dire wolves follow a temporal version of Bergmann’s rule, we would expect to see the largest C. dirus specimens from pits with the coldest climates.

While climate may be influential in determining overall body size, other environmental effects may also affect the size and shape of dire wolf mandibles. Because canids almost solely rely on their crania in prey apprehension (Slater et al., 2009), mandibles should reflect functional changes as well. Functional changes may be induced by competition, nutritional stress, and prey preference change through time. Previous studies on dire wolf tooth breakage and wear show fluctuations between high and low breakage and wear frequencies (Binder et al., 2002; Binder and Van Valkenburgh, 2010; O’Keefe et al., 2014). High levels of breakage and wear indicate increased inter- and intraspecific competition and/or nutrient stress (decreased food availability) (O’Keefe et al., 2014; Binder et al., 2002; DeSantis et al., 2012). Because breakage and wear data reflect environmental effects, it is possible that the shape of the mandibles may change in response.

In addition to size patterns, sexual dimorphism is detectable in gray wolf skulls. Although levels of sexual dimorphism in canids are low, distinct characteristics are found in association with size variation among the sexes of C. lupus (Van Valkenburgh and Sacco, 2002). Females are smaller than males and have proportionally larger molars, whereas males have relatively larger coronoid processes (Jolicoeur, 1975; O’Keefe et al., 2013; O’Keefe et al., 2014). These features should be easily identifiable in the dire wolf mandibles if these ancient wolves displayed the same type and amount of sexual dimorphism. Assuming that sexual dimorphism does not vary over time, these particular signals should not segregate among pits.

Here we analyze dire wolf mandibular morphometrics to determine if shape and size remained static over time at Rancho La Brea. If change does occur, we explore these fluctuations in relation to Bergmann’s rule on a temporal scale, as well as other environmental factors, and attempt to disentangle possible causalities of any observed change.

METHODS AND MATERIALS

We used two-dimensional geometric morphometrics to analyze jaws of C. dirus. We analyzed 157 complete, adult C. dirus hemimandibles. Digital photographs were taken of the labial side of specimens from Pits 91 (~23–28 calibrated kyBP, majority of dates 27–28 kyBP; n = 22), 13 (~17–18 calibrated kyBP; n = 36), and 61/67 (~13–14 calibrated kyBP; n = 83) from the La Brea Tar Pits and Museum Hancock Collection (LACMHC), and Pit 2051 (~21–30 calibrated kyBP, mean 26 kyBP; n = 161) from the University of California Museum of Paleontology at Berkeley (UCMP). We analyzed left hemimandibles only for all pits, except Pit 2051, where right hemimandibles were examined. Specimens from Pit 2051 were horizontally inverted, using Adobe Photoshop CS2 v.9.0, before analysis. All specimens were laid flat and photographed with a 5-cm scale bar. While camera angle and distance were held constant photographing LACMHC specimens, scale bars present in photographs were used to size UCMP specimen images properly to LACMHC specimen images in Adobe Photoshop CS2 v.9.0 before landmark digitization.
We digitized 16 homologous landmarks on each specimen using the program tpsDig2 (Rohlf, 2013). Positions of landmarks were chosen to give a general outline of the mandible and capture information of functional relevance (Table 1, Fig. 1). Landmarks on the tooth row were placed on the tooth/mandible junction, so specimens with missing teeth could be included in our dataset. However, presence of the lower carnassial tooth was required in order to obtain landmark 5. Landmark 5 properly distinguishes the trigonid basin from the talonid basin of this tooth. The alveolus of the carnassial does not accurately differentiate between these basins, so the tooth itself must be present. All landmark data were collected by the same researcher (A.L.B.) to reduce bias and measurement error.

A Procrustes superimposition was performed on raw landmark x-y coordinates in Morphologika. A set of new x-y coordinates, with rotation and translation between specimens removed, was then used to calculate interlandmark relationships (Zelditch et al., 2004). To determine if the large sample size in Pit 61/67 affected the resulting Procrustes coordinates, 30 specimens from Pit 61/67 (total of 104 specimens) were randomly selected and subjected to a Procrustes superimposition. This process was replicated three times. No significant difference between the replicates and the original sample was detected; further analyses were conducted using the original sample of all 157 total specimens. Centroid size, a scaling variable, was also calculated and provided a relative representation of mandible size for each specimen. Since mandible size and overall body size in carnivorans have been shown to be highly correlated (Figueirido et al., 2011), we use centroid size as a proxy for overall body size. Differences in size between pit samples were determined through an analysis of variance (ANOVA) on centroid size.

A principal component analysis (PCA) was conducted on the Procrustes coordinates to investigate jaw shape variation within and between the pits sampled (Zelditch et al., 2004). The PCA was run in pcagen7_14a (Sheets, 2005), as well as the program JMP. A Procrustes mean specimen was generated through least squares fitting based on all data. Partial warp scores were then computed using that Procrustes mean specimen. Principal components were calculated from the covariance matrix of partial warp scores generated in pcagen7_14a and JMP. Principal component (PC) axes were used as shape variables to describe variance in shape among the specimens. Specimens were then identified by pit along each PC axis to evaluate mandibular shape. Both a Student’s t-test and a set of analyses of variance (ANOVA) on the first four PC scores were used to determine significant differences in shape among the pits.

Shape changes along PC axes were visualized as vectors of mean landmark position differences by 0.1 units in the positive direction (unless

Table 1 Descriptions of the 16 homologous landmarks placed on Canis dirus hemimandibles.

<table>
<thead>
<tr>
<th>Landmark</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Anterior edge of the canine at the tooth/mandible junction.</td>
</tr>
<tr>
<td>2</td>
<td>Posterior edge of the canine at the tooth/mandible junction. Together landmarks 1 and 2 will give the anteroposterior width of the canine.</td>
</tr>
<tr>
<td>3</td>
<td>Anterior edge of p1 at the tooth/mandible junction.</td>
</tr>
<tr>
<td>4</td>
<td>Posterior edge of the p4 at the tooth/mandible junction. Together landmarks 3 and 4 will give the length of the premolar arcade.</td>
</tr>
<tr>
<td>5</td>
<td>Point on the tooth/mandible junction directly below anterior edge of the talonid basin of the m1. Together landmarks 4 and 5 will give the length of the shearing area of m1.</td>
</tr>
<tr>
<td>6</td>
<td>Tooth/mandible junction of the posterior edge of m1. Together landmarks 5 and 6 will give the length of the grinding area of m1.</td>
</tr>
<tr>
<td>7</td>
<td>Posterior edge of m2/m3 at the tooth/mandible junction. Together landmarks 5 and 7 will give an estimate for the grinding area.</td>
</tr>
<tr>
<td>8</td>
<td>Anterior edge of the masseteric fossa. Disregard landmark movement in the coronal plane and focus only on movement in the anteroposterior plane.</td>
</tr>
<tr>
<td>9</td>
<td>Top edge of the coronoid process.</td>
</tr>
<tr>
<td>10</td>
<td>Point where the coronoid process meets the condyloid process. Together landmarks 8 and 10 give the total width of the masseteric fossa.</td>
</tr>
<tr>
<td>11</td>
<td>Posterior edge of the condyloid process. Together landmarks 1 and 11 give an estimate of the total jaw length.</td>
</tr>
<tr>
<td>12</td>
<td>Posterior edge of the angular process.</td>
</tr>
<tr>
<td>13</td>
<td>Point where the ramus of the jaw moves from a horizontal plane to a vertical plane to the angle of the jaw. Together landmarks 9 and 13 will give the height of the coronoid process.</td>
</tr>
<tr>
<td>14</td>
<td>Edge of mandible, directly below landmark 7. When taken with landmark 7, gives the height of the jaw in the coronal plane post-m1.</td>
</tr>
<tr>
<td>15</td>
<td>Edge of mandible, directly below landmark 5. When taken with landmark 5, gives the height of the jaw in the coronal plane post-p4.</td>
</tr>
<tr>
<td>16</td>
<td>Edge of mandible, directly below landmark 4.</td>
</tr>
</tbody>
</table>
described otherwise). The pcagen7_14a program was used to create the landmark vectors. The vectors showed the relative direction and magnitude of landmark displacement, allowing for a clearer interpretation of shape change along each PC axis. Additionally, distances between Procrustes coordinates for specific landmark combinations were calculated. These distances included the length of the grinding portion of the carnassial (between landmarks 5 and 6), the length of the second molar (between landmarks 6 and 7), and the coronoid height (between landmarks 9 and 13). Measurements of these features were analyzed to determine whether or not sexually dimorphic signals similar to those seen in C. lupus skulls were detectable (O’Keefe et al., 2013). The interlandmark distances chosen were regressed against centroid size to establish significant patterns of these elements in relation to overall body size. Regressions against centroid size first included all specimens and were not separated by pit. To ensure that patterns were consistent throughout all pits, regressions against centroid size were then separated by pit and examined.

**RESULTS**

The ANOVA of centroid size showed that overall body size varied among the pits (Fig. 2). Pit 61/67 displayed the largest size but was significantly larger than only Pits 2051 and 13. The smallest body size was from Pit 13 and was significantly smaller than from all of the other pits. Although Pit 91 body size did not differ from either Pit 2051 or Pit 61/67, that from Pit 2051 was significantly smaller than Pit 61/67.

Thirty-two PCs resulted from the PCA, with PC1–PC6 explaining 67.2% of the variance (Table 2). While performing a PCA on the Procrustes coordinates should minimize the effect of size on shape variables, size significantly varied among the pits and should be taken into account when examining shape. For example, knowing the relationship between size and a PC axis may alter the interpretation of that axis. The first and fourth principal components are positively correlated with centroid size (p < 0.001, $R^2 = 0.099$ and p < 0.0001, $R^2 = 0.090$, respectively), whereas PC3 is negatively correlated with centroid size (p < 0.0335, $R^2 = 0.0288$; Table 2). Principal component 2 is not correlated with centroid size.

![Figure 1](image1.png)  
*Canis dirus* hemimandible in labial view. Locations of 16 landmarks are also shown. See Table 1 for corresponding list and descriptions for landmark placement.

![Figure 2](image2.png)  
Plot of ANOVA of centroid size among pits; n = 157 hemimandibles. The red lines represent the estimates of the mean for each pit. Black lines indicate 95% confidence intervals. Pit 13 has a significantly smaller overall body size compared with the other three pits.
Principal component 1 explains 17.9% of variance and is interpreted to represent posterior jaw size increase. Principal component 1 is also correlated with size. Dire wolves scoring high on the PC1 axis have a larger jaw, largely represented by vectors from landmarks 8–13, in relation to the size of their teeth, as represented by vectors from landmarks 1–7. Negative values on the PC1 axis indicate animals with small jaws relative to tooth size. Significant differences among pits on PC1 were identified. Pit 91 significantly segregated from all other pits, as did pit 2051. Pits 13 and 61/67 were not different on PC1.

The second principal component represents significant reorientation of the jaw. Principal component 2 explains 13% of the variance and also displays segregation among groups. Negative loading on PC2 is associated with two shape changes: (1) the coronoid process and posterior portion of the jaw shifting both anteriorly and ventrally in a counterclockwise fashion and (2) the anterior portion of the jaw near the canine shifting posteriorly and dorsally in a clockwise rotation (Fig. 3). Positive loadings are associated with the anterior and posterior portions of the jaw rotating away from each other. Pit 2051 differed from all other pits, displaying the highest degree of the anterior and posterior portions of the jaw rotating in toward each other. Pit 61/67 differentiated from Pit 13 as well, with Pit 13 specimens displaying more reorientation of the anterior and posterior portions of the jaw toward each other than those from 61/67. However, Pit 13 did not differ significantly from Pit 91. A plot of the scores of the first two PCs can be seen in Figure 3.

Principal component 3 explains 11.9% of the variance and shows no significant differences among pits. Negative loadings on PC3 are associated with increases in canine size and length of the tooth row relative to the somatic jaw. Molars shift together posteriorly, with a slight decrease in size of the second molar. Positive loadings are associated with decreases in canine size and overall tooth row length.

Principal component 4 explains 9.9% of the variance and is correlated with size. Positive values on PC4 are associated with slight increases in jaw and tooth row length. Negative values are associated with a decrease in jaw size, especially the coronoid height, and a shift of the molar arcade forward. On this axis, wolves from Pit 91 are distinct from all other pits. Pit 61/67 differs from Pit 13, but not Pit 2051. Pits 13 and 2051 are not distinct. It is important to note that the landmark 13 vector dominates this PC axis; this is relevant because the variance of this landmark in the x dimension regarding the Procrustes coordinates is an order of magnitude greater than any other landmarks’ variance in the x or y dimension. The placement of landmark 13 is more significant than the x dimension.
subjective in the x dimension than any other landmark. However, landmark 13 still contributes to size decrease with negative values on the x-axis. The variance of landmark 13 in the y-dimension was similar to that of the other landmarks; this is important because the main purpose of the landmark 13 was to acquire coronoid height in conjunction with landmark 9.

The length of the grinding portion of the carnassial and the length of the second molar were negatively correlated with centroid size \((p = 0.0023, R^2 = 0.058; p = 0.0003, R^2 = 0.082, \text{ respectively})\). These patterns were consistent throughout each pit. In terms of sexual dimorphism, these results are consistent with trends seen in the extant gray wolf. *Canis lupus* males have relatively larger body sizes and relatively smaller molars. The trend of decreasing molar size with increasing centroid size can be seen in both of these regressions (Fig. 4). While it is not possible to discern *C. dirus* male specimens from female specimens, these trends suggest that the dire wolf displayed the same degree of sexual dimorphism in their molars as extant gray wolves.

The same result does not hold for coronoid height. Male gray wolves have been shown to have relatively taller coronoid processes. As such, we expected to see a positive correlation of coronoid height with centroid size based on these trends. Regressions against centroid size, both...
separated and not separated by pit, do not display a significant trend (global regression: $p = 0.302$, $R^2 = 0.007$).

**DISCUSSION**

Both shape and size in *C. dirus* change through time in Rancho La Brea, showing that evolution is occurring. Mean body size averages vary from pit to pit; the largest body size occurs in Pit 61/67, and wolves from Pit 91 are only marginally smaller than those from 61/67. Significantly smaller wolves are found in Pit 13. By examining Greenland Ice Core Project (GRIP) and North GRIP (NGRIP) climate records, we can begin to evaluate size and climate relationships, such as Bergmann’s Rule (NGRIP, 2004). Pit 61/67 had the warmest climate, overlapping in deposition with the Bølling-Allerød warm interval, whereas Pit 13 was deposited during a relatively cool interval near the last glacial maximum. According to NGRIP data, Pit 2051 represents the coldest interval of this sequence, while Pit 91 is thought to be associated with rapid warmings, labeled Dansgaard-Oeschger events (Rahmstorf, 2003; Meachen et al., 2014; O’Keefe et al., 2014). However, more precise dating of all of these pits, especially Pits 61/67 and 13, will solidify these correlations. From these size changes it appears dire wolves did not follow a temporal Bergmann’s rule. Instead, body size in relation to climate is opposite to what Bergmann’s rule would have predicted; the colder pits (2051 and 13) display smaller body sizes and the warmer pits (91 and 61/67) show larger body sizes. This is particularly interesting because the gray wolf, our model species for the dire wolf, follows Bergmann’s rule (O’Keefe et al., 2013). Many carnivores do not follow Bergmann’s rule, including some canids, such as coyotes (Meiri and Dayan, 2003; Meachen and Samuels, 2012). This is thought to be related to levels of primary productivity and food availability rather than climate (Huston and Wolverton, 2011; Yom-Tov and Geffen, 2011). Huston and Wolverton (2011) suggest that carnivores may be indirectly affected by the amount of ecological and evolutionary net primary productivity (eNPP) during a given period of time. Higher outputs of eNPP, possibly due to warmer climatic conditions, may increase food availability for primary producers. With an increase of food for primary producers, larger populations of herbivores can be supported, which increases food availability for carnivores and allows for body size increases. Changing levels of primary productivity due to climate would have a cascading effect on carnivores, such as the dire wolf (Meachen et al., 2014).

Mandible shape also varies significantly from pit to pit. Fluctuating environmental pressures, such as changing nutrient stress, are a leading cause in changing the appearance and/or rate of development, or heterochrony, within a population (McNamara, 1990). Neoteny, decreased somatic growth relative to sexual maturation, in canids is recognizable through the identification of proportionally shorter snouts, smaller teeth, and a more steeply rising forehead region compared with the ancestral population (Gould, 1977; Paquet and Carbyn, 2003; O’Keefe et al., 2014). The largest amount of variance in shape is shown along PC1, representative of an allometric size vector, which displays evidence of neoteny in the dire wolf. A recent study on dire wolf cranial morphometrics found higher incidences of tooth breakage and wear (indicative of increased nutritional stress), along with neotenic characteristics in wolves of Pit 13. These specimens were also significantly smaller than those of other pits (O’Keefe et al., 2014). Our results are concurrent with this study; animals we examined are smallest in Pit 13. However, wolves of Pit 91 also had high tooth breakage and wear frequencies but were relatively large, using the centroid size of the entire skull as a metric (O’Keefe et al., 2014). These authors suggest nutrient stress for Pit 91 wolves was less severe than that for Pit 13 wolves or began after dental maturity was reached. Although wolves from Pit 91 were the second largest in this study, PC1 scores from our data suggest that Pit 91 wolves also show neotenic characteristics. These wolves have the smallest jaws relative to the size of their teeth. Since modern wolves reach dental maturity before they reach full somatic growth, it can be inferred that Pit 91 wolves experienced late-stage growth truncation (Kreeger, 2003; O’Keefe et al., 2014). This pattern was subtle but identifiable in the skull data.

The shape changes along PC1 primarily show allometric jaw growth but may contain some evolutionary effects as well. Pit positions along PC1 may also be in response to competition and prey availability. Taller coronoid processes allow increased area for the attachment of the temporalis muscle, which increases the speed and force of jaw closure (Anyonge and Baker, 2006; Wang and Tedford, 2008). Wolves of Pits 61/67 and 2051 have the largest jaws, including the coronoid process, relative to their teeth. Increased coronoid height suggests that these wolves are catching larger, faster prey, and tooth breakage and wear indicate that they are not under nutrient stress (O’Keefe et al., 2014). It follows that these wolves have a mechanical advantage in shearing when tooth breakage and wear indicates that they are not under nutrient stress. Wolves of Pits 91 and 13 have relatively the smallest jaws in comparison, including their coronoid processes. Having shorter coronoid processes decreases the mechanical advantage of the temporalis muscles in relation to the masseter muscle. Additionally,
shorter, broader jaws produce larger bite forces. These wolves are more masseter dominated, which is active in crushing at the molars. It follows that these wolves are probably consuming more bone, making crushing abilities necessary, or prey preference was different in comparison to pits 61/67 and 2051.

In terms of shape, Pit 2051 wolves are interesting in that they discretely segregate from the other pits on the first two PC axes (Fig. 3). Pit 2051 wolves have anteroventrally oriented coronoid processes, while the anterior portion of the jaw orients posteriorly and dorsally. Additionally, these wolves do not display signs of neoteny, having the largest somatic jaws relative to their teeth. Wolves of Pit 13 score closest to Pit 2051 on the PC2 axis, which demonstrates reorientation of both ends of the jaw. Evidence of neoteny is present in Pit 13; further directional change of Pit 13 wolves toward the shape seen in Pit 2051 may have been hindered by nutritional stress or other factors. Because Pits 13 and 2051 were deposited during relatively colder climates than the other pits, it is possible that this anterior rotation of the terminal ends of the jaw may have been an adaptation for hunting in cold climates. The ecological drivers of the shape difference displayed in Pit 2051 are not clear, but our PCA analysis determined that shape evolution is evident.

Our results suggest that sexual dimorphism is present in the molars of C. dirus mandibles. PC3 seems to capture sexually dimorphic molar signals. This axis does not discriminate among the pits, and vectors are associated with movement and size fluctuations in the molars. PC3 is also significantly associated with size. Negative loadings (decrease in second molar size) on PC3 are associated with larger centroid size values; this would follow the trend we expected to see given the observed dimorphism seen in modern wolves. While PC3 represents sexual dimorphism, there is no clear evidence for dimorphism on PC4. PC4 is correlated with centroid size and captures shifts in the tooth row and slight fluctuations in jaw size. However, there is distinct segregation among the pits on this axis. We expect sexual dimorphism to remain constant through time, so variables indicating dimorphism should not differentiate between pits.

Regressions of molar interlandmark distances against centroid size also indicate sexual dimorphism. The length of the talonid basin, or grinding area, of the carnassial and the length of the second molar both decrease with increasing centroid size (Fig. 4). Small body sizes have relatively larger molars, which is consistent with patterns found in C. lupus. These trends are also evident in each individual pit, indicating this pattern did not change through time. Our molar interlandmark regressions agree with our interpretation of PC3.

Both PC3 and molar regressions display the same relationship between centroid size and molar size and are not time dependent, indicating a sexually dimorphic molar signal in the dire wolf. However, our results do not support a sexually dimorphic signal in the coronoid process, as seen in the gray wolf. Our global regression shows no correlation between coronoid height and centroid size (Fig. 4). There are several possibilities for not detecting this trend in the dire wolf specimens. First, the coronoid height signal was not as strong as the molar signal in gray wolves, so we may not have the power to detect this pattern. Second, the coronoid process is subject to evolutionary change in orientation, as seen in PC2, which may be masking the signal. Third, the dire wolf may not display this trend at all and is not sexually dimorphic in coronoid height like C. lupus.

In summary, C. dirus mandible shape and size, and therefore overall body size, do not remain constant throughout time. Size comparisons reveal that dire wolves were largest in pits with warmer climates and smaller in cooler pits, the opposite of what a temporal Bergmann’s rule would have predicted. Because the dire wolf does not seem to follow climate correlations similar to the gray wolf, its extant counterpart, it is appropriate to explore other environmental factors as possible causalities by examining shape change. Overall mandible shape shows certain microevolution, and nutrient stress and adaptions relating to food availability and competition are also influential factors. Because Pleistocene climate records reveal extreme variability, more precise dating of the La Brea tar pits would help more accurately define the existing environmental conditions of each deposit.

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LITERATURE CITED


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