NEW BODY MASS ESTIMATES FOR CANIS DIRUS, THE EXTINCT PLEISTOCENE DIRE WOLF

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Over 200,000 specimens of the extinct Pleistocene dire wolf, *Canis dirus*, have been recovered from the Rancho La Brea Tar Pits in southern California (Merriam, 1912; Marcus, 1960; Nowak, 1979; Kurtén and Anderson, 1988; Stock and Harris, 1992; Dundas, 1999). A few specimens are known from San Josecito Cave in Mexico and several localities in South America (Churcher, 1959; Lemon and Churcher, 1961; Kisko, 1967). Unfortunately, limb bones are rare from the latter sites and this has limited the number of comparative studies. Numerous sites located east of the Rocky Mountains in North America have yielded additional material that indicates geographic differences between western and eastern populations of dire wolves (Galbreath, 1964; Hawksley et al., 1963; Nowak, 1979; Kurtén, 1984). Some of the major fossil-producing sites in this region include Friesenhahn Cave, Texas, Carroll Cave, Missouri, and Reddick, Florida.

The large body size and highly carnivorous dentition that is characteristic of *C. dirus* has stimulated much debate regarding preferred prey for the eastern population of dire wolves. These authors based their conclusions on size differences in skull and limb proportions between *C. dirus* and the modern gray wolf, *Canis lupus*. The overall consensus among most authors is that *C. dirus* was a large wolf that preferred large prey (Merriam, 1912; Stock and Harris, 1992; Kurtén and Anderson, 1980; Kurtén, 1984; Van Valkenburgh and Koepfli, 1993; Van Valkenburgh and Hertel, 1998).

Few quantitative studies of body mass estimation of *C. dirus* have been attempted. Van Valkenburgh and Koepfli (1993) listed a mass of 50 kg for *C. dirus* derived from regressions of skull length and head-body length against body weight for extant carnivores (Van Valkenburgh, 1987). A preliminary study using cross-sectional geometric properties of the femur predicted a body mass of 56 kg for *C. dirus* from Rancho La Brea (Anyonge et al., 2003). Here, we report new body mass estimates for *C. dirus* from the Rancho La Brea deposits in California and San Josecito Cave in Mexico. The body mass estimates are based on equations relating body mass to cross-sectional geometric properties and linear dimensions of the femur in extinct canids. In addition, we present preliminary body mass estimates for eastern populations of dire wolves based on linear measures (length and circumference) of the femur. Generally, long bone lengths are very poor body mass estimators and should not be used when cross-sectional geometric properties are available (Ruff, 2003). Femur length was used in this study only for comparative purposes and the body mass estimate based on this measure was excluded when computing the mean body mass for *C. dirus*.

MATERIAL AND METHODS

One hundred femora of the extinct Pleistocene dire wolf, *Canis dirus*, from the Rancho La Brea deposits in southern California were measured for this study. These fossils are housed at the George C. Page Museum in Los Angeles, California. The dire wolf material from San Josecito Cave in Mexico is stored at the Los Angeles County Museum of Natural History and included five well-preserved femora. The combined material from California and Mexico samples the population of dire wolves found west of the North American continental divide for which Kurtén (1984) erected the subspecies *Canis dirus guildayi*. Kurtén (1984) established the subspecies *Canis dirus dirus* for the eastern population of dire wolves. Femoral length measurements for *C. d. dirus* were obtained from Kurtén (1984) and Hawksley et al. (1963). Kurtén (1984) pooled data on femora of *C. d. dirus* from the larger fossil-bearing sites at Reddick, Florida, Friesenhahn Cave, Texas, and Bat Cave, Missouri (N = 6, range 256–278 mm, mean 266.3 ± 3.2 mm). Hawksley et al. (1963) figured a complete femur (MU 2817–CMS 14) from Carroll Cave, Missouri, which measured 278.5 mm long.

A total of 22 species of extant canids were used in this study (Table 1). Ten femora were measured for each species. Depending on availability, an equal number of males and females were used. This was achieved by pooling specimens from three museum collections (FMNH, UCLA, and USNM). The mean body weights of the extant canids were obtained from the literature (Table 1). Effort was made to match the weights published in the literature with known data that reflected the geographic variation in weight of each species. When mean weights for a species were not available, the mid-point of the minimum and maximum weights recorded in the literature was used as species means.

Linear measurements on the femur included maximum proximodistal length between articulating surfaces, circumference, and anteroposterior and mediolateral diameters at the mid-shafts. Digital calipers and a measuring tape were used to measure the length and circumference, respectively.

Biplanar radiographs were used to obtain cross-sectional geometric properties of the femur (cortical thickness and second moments of area). X-ray facilities at FMNH, UCLA, and USNM were used to produce the radiographs. For each species, four femora (2 males and 2 females when available) were x-rayed in the sagittal and frontal planes. The thickness of the cortical bone was measured on the radiographs using needle-point digital calipers to the nearest 0.1 mm. The femur was modeled as a hollow elliptical beam with symmetrical cross-sectional areas. This model allows the use of standard stress formulae (Table 1) to calculate the cortical area and second moments of area in the anteroposterior and mediolateral planes (Rook, 1965; Alexander, 1968; Biknevicius and Ruff, 1992; Anyonge, 1993). Cortical cross-sectional area is proportional to axial compressive and tensile rigidity, whereas the second moment of area is proportional to bending rigidity perpendicular to the axis about which it is measured. These parameters have been shown to be better predictors of body mass than linear measures in several vertebrate groups (Ruff et al., 1989; Scott, 1990; Anyonge, 1993; Egi, 2001; Ruff, 2003). This is because the forces acting on the limbs of an animal are proportional to the weight the limbs have to support and consequently to the stresses developed in the cross section of the bones (Alexander, 1991).

Least-squares regressions of \( \log_{10} \) transformed data were used to explore the relationship between body mass (the dependent variable) and five femoral measures (length, circumference, cortical area, and second moment of area in the anteroposterior and mediolateral axis) in the 22 species of extant canids. This sample comprised species with a mean body mass ranging from 1.7 kg (sand fox, *Vulpes rueppellii*) to 45 kg (gray wolf, *Canis lupus*). Least-squares and reduced-major-axis (RMA) regression models give similar results when the correlation coefficient between a pair of variables is high (Jungers, 1984); this also minimizes the error associated with slight extrapolation of data in body mass estimation. In addition to the correlation coefficient \( r \), the percent prediction error and the percent standard error of the estimate were used as indicators of...