A new specimen-dependent method of estimating felid body mass

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ABSTRACT

Background. The estimation of body mass of long extinct species of the family *Felidae* has been a focus of paleontology. However, most utilized methods impose expected proportions on the fossil specimens being estimated, resulting in a high chance of underestimation or overestimation. This study proposes a new method of estimating felid body mass by accounting for osteological proportionality differences between the extinct taxa being estimated and the living species being used as comparisons.

Method. Using a manipulation of the cube law, 36 equations were formulated that estimate body mass based on certain humeral and femoral dimensions. The formulated equations were used to examine whether the mass of living comparison species, namely the tiger (*Panthera tigris*), the lion (*Panthera leo*), and the jaguar (*Panthera onca*), depends equally on a select set of long bone dimensions. The body mass of five extinct felids, namely *Panthera atrox*, *Panthera spelaea*, *Panthera tigris soloensis*, *Smilodon populator*, and *Smilodon fatalis*, was also estimated.

Results. Living comparisons species were found to somewhat incorrectly estimate other living comparison species. All five extinct taxa were found to weigh well over 300 kg, with the largest of the species weighing nearly 500 kg.

Discussion. The inability of one living comparison species to predict the mass of another with strong accuracy suggests that bone dimensions do not solely influence body mass. Discrepancies between the masses of *Smilodon populator* and *Smilodon fatalis* were likely the product of the difference in available niches in late Pleistocene North and South America. The masses of *Panthera spelaea* and *Panthera atrox* indicate a discrepancy in sociality between the two closely related species. Lastly, the extreme body mass of *Panthera tigris soloensis* points to great plasticity within the tiger lineage in terms of size, indicating that such variations among tiger populations may not warrant subspeciation.

INTRODUCTION

Body mass of prehistoric fauna has been a large focus within paleontology due to the great ecological and evolutionary implications body mass has for a species (LaBarbera, 1989). Moreover, long extinct species of the family *Felidae* have captivated and captured the attention of many (Antón, Turner & Howell, 2000). The combination of these two interests have led to quite a few attempts at reconstructing the body mass of such species. Some have used simple isometry to estimate fossil specimens (Sorkin, 2008; Christiansen & Harris, 2009). Others have developed regression equations that predict the body mass of extinct species based on allometric relationships between bone measurements and body masses of living felids (Anyonge, 1993; Christiansen & Harris, 2005; Volmer, Hertler & van der Geer, 2016). Today, usually the latter method of estimating body masses has been used to estimate not only the body mass of extinct felids, but also other large prehistoric mammals (Christiansen, 1999; Wheeler & Jefferson, 2009; Figueirido et al., 2010; Soibelzon & Schubert, 2011).

Despite the popularity of the regression method of estimating body mass, there are a few issues with such a method. For one, regression equations which are based off and targeted at the same group of animals produced by different studies rarely seem to result in allometric scaling factors that are even somewhat consistent across studies (Anyonge, 1993; Christiansen, 1999; Christiansen & Harris, 2005; Figueirido et al., 2010). The likely cause of such is difference in the combination of species used to develop the body mass estimating regression equations (Christiansen & Harris, 2005). This factor brings about the strong possibility that such regression equations have scale factors in which the proposed allometric trend is a product of the specific combination of data used rather than an actual reflection of allometric scaling in the given family. These equations and their corresponding scaling factors are then often applied indifferently to different species, imposing fixed allometric trends on species that may not share the same proportions as the dataset used to form the regression formulas (Larramendi, 2015).

This study proposes a new method of estimating body mass in *Felidae*. This method manipulates the cube law to produce scaling factors that take into account the specific osteological proportions of the fossil specimen being estimated relative to the living comparison species being used to estimate the fossil specimen. Using the weight-bearing humeri and femora of three extant felid species, namely the tiger (*Panthera tigris*), the lion (*Panthera leo*), and the jaguar (*Panthera onca*), equations were formulated to estimate the body mass of extinct species (Egi, 2001). The formulated equations were used to examine whether the mass of living comparison species, namely the tiger (*Panthera tigris*), the lion (*Panthera leo*), and the jaguar (*Panthera onca*), depends equally on a select set of long bone dimensions. The masses of the largest individuals of five cat species were subsequently estimated, namely *Panthera atrox* (Leidy, 1853), *Panthera spelaea* (Goldfuss, 1810), *Panthera tigris soloensis* (von Koenigswald, 1933), *Smilodon fatalis* (Leidy, 1869), and *Smilodon populator* (Lund, 1842). The resulting body masses were then used to investigate a range of key aspects of such extinct taxa.

MATERIALS AND METHODS

Acquisition of data

Data for the living comparison species and their corresponding bone measurements were borrowed from Christansen and Harris (2005). Average values of each species were used as the living comparison values for the appropriate equations (Table 1). However, unlike Christiansen and Harris (2005), data on *Panthera tigris tigris* and *Panthera tigris altaica* were pooled together as one based on new findings on tiger subspeciation (Wilting et al., 2015). Thus, a total of three species were used as living comparison species, namely the tiger (*Panthera tigris*), the lion (*Panthera leo*), and the jaguar (*Panthera onca*). The maximum body masses of the modern relatives of the extant taxa were collected from the following scientific sources: Smuts, Robinson, & Whyte (1980), Sunquist & Sunquist (2002), Dinerstein (2003), and Farhadinia et al. (2014).

The maximum body mass of five fossil species was determined by estimating only the largest of bones on record for each respective species. The species examined were *Panthera atrox* (Leidy, 1853), *Panthera spelaea* (Goldfuss, 1810), *Panthera tigris soloensis* (von Koenigswald, 1933), *Smilodon fatalis* (Leidy, 1869), and *Smilodon populator* (Lund, 1842). Data for these species was borrowed from the following literature: Merriam and Stock (1932), von Koenigswald (1933), Christiansen and Harris (2005), and Teschler-Nicola (2006). Where photographs were provided, digital measurements were taken by the author to ensure the best compatibility with the measurements of the living comparison species. Bone width measurements taken by the author are to the closest 0.1 mm. Bone lengths measured by the author are to the closest 0.5 mm.

Formulation of equations

Here, a new method of producing scale factors is proposed that takes into account the specific animal being estimated rather than solely focusing on the scale factor produced by a given array of living species. In accord with the foundation of isometry, three measurements are required for this method to form a scale factor that rests within reasonable limits of allometry and isometry. The body mass estimates resultant from three scale factors will then be averaged to produce the estimated weight of the animal of interest. One length and two bone width measurements should be used to reconstruct a scale factor that has some resemblance to the formula of volume (height x width x length) that the cube law and isometry are founded upon (Froese, 2006). Ideally, one width measurement should be anteroposterior and the other lateromedial to again bear the strongest resemblance to the volume formula. However, often only lateromedial diameters are recorded for fossil specimens. Therefore, this study will use two lateromedial diameters alongside the measurement of the length of the respective bone. Furthermore, some species have evolved to have only certain parts of the bone thickened rather than consistent thickening of the entire bone, indicating such areas of the bone do not necessarily account for the mass they would be expected to (Viranta, 1994). Thus, it is recommended to not use two bone width measurements from the same part of the bone to prevent overestimation or underestimation of body mass.

The equation model revolves about adjusting the scale factor, and in turn the allometry, that will estimate the mass of the fossil specimen in a manner that takes into account the unique bone proportions of the specimen. In this manner, the scale factor in the following body mass estimation (Eq. BM) equation will be determined with specific regard to the relationship between the fossil animal and the living comparison:

Eq. BM:

Fossil body mass = (Fossil measurement/living comparison measurement)^scale factor x body mass of living comparison

For the sake of clearer communication, only the process of producing a scale factor for the relationship between bone length and body mass will be now be described in detail by itself first.

When the long bone of a fossil animal is for instance, 1.05 times the length of the living specimen used for comparison, the cube law dictates that the width measurements of the fossil animal should also be 1.05 times that of the living comparison. Such would result in both the volume and mass of the fossil animal being 1.05^3 greater than the corresponding values of the living comparison, and thus the scale factor would be considered to equal three ($\text{Scale Factor}_{\text{bone length}} = 3$).

However, usually this simple relationship between the fossil animal and living comparison species does not exist. Rather, the fossil specimen may have its bone widths be 1.10 times greater than the corresponding bone widths of the living comparison species. In such a case, it would be expected that the fossil animal is proportionately heavier for its bone length than the living comparison species. Thus, the scale factor relating the bone length of the fossil specimen to that of the living comparison would not be 3 but rather greater. To determine how much above 3 the scale factor is, the following equation is proposed:

Eq. 1:

Scale Factor = (fossil bone length/predicted bone length + fossil width #1/predicted width #1 + fossil width #2/predicted width #2)

Whereby,

Eq. 1a:

Predicted bone length = Fossil bone length x living comparison bone length/living comparison bone length

Eq. 1b:

Predicted width #1 = Fossil bone length x living comparison width #1/living comparison bone length

Eq. 1c:

Predicted width #2 = Fossil bone length x living comparison width #2/living comparison bone length

As the predicted bone length in this example is simply equal to the fossil bone length, the scale factor equation Eq. 1 can be simplified to:

Eq. 1:

Scale Factor = (1 + fossil width #1/predicted width #1 + fossil width #2/predicted width #2)

The ratios of fossil width #1/predicted width #1 and fossil width #2/predicted width #2 will, alongside the value of 1, sum to the scale factor that will then account for the proportion disparity between the fossil specimen and living comparison species.

A hypothetical, worked example will now be provided. Assume the fossil specimen of interest has a bone length of 1.05 mm, a bone width #1 of 1.10 mm, and a bone width #2 of 1.15 mm. The living comparison species has a bone length of 1.00 mm, a bone width #1 of 1.00 mm, and a bone width #2 of 1.00 mm. The living fossil specimen is known to weigh 1 kg. Substituting these values into the aforementioned equations results in the following (step in mathematical process denoted within parenthesis):

Eq. 1b: (1)

Predicted width #1 = Fossil bone length x living comparison width #1/living comparison bone length = 1.05 mm x 1.00 mm/1.00 mm = 1.05 mm

Eq. 1c: (2)

Predicted width #2 = Fossil bone length x living comparison width #2/living comparison bone length = 1.05 mm x 1.00 mm/1.00 mm = 1.05 mm

Eq. 1: (3)

Scale Factor = (1 + fossil width #1/predicted width #1 + fossil width #2/predicted width #2)

= (1 + 1.10 mm/1.05 mm + 1.15 mm/1.05 mm) = 3.14

Therefore, the equation that estimates the body mass of the fossil specimen based on the disparity between the length of the fossil specimen and the living comparison would be:

Eq. $\text{BM}_{\text{bone length}}$: (4)

Fossil body mass = (Fossil measurement/living comparison measurement)^scale factor x body mass of living comparison

Fossil body mass = (1.05 mm/1.00 mm)^3.14 x 1 kg

Fossil body mass = 1.17 kg

In this manner, the body mass estimate of the fossil has been established with regard to its own bone proportions rather than the theoretical proportions of isometry or a regression equation.

However, despite the adjustment of the scale factor of bone length, the same mathematical process was conducted with bone widths to increase the accuracy of the final body mass estimate as adjustment of one scale factor may not be enough. The following derivations and worked examples will show how the bone widths were used in producing body mass estimates for the aforementioned hypothetical fossil specimen based on its comparison with the theoretical living species of known measurements. The process using bone width #1 process is signified by Eq. 2, Eq. 2a-c, and BM $_{\text{bone width \#1}}$ and the process using bone width #2 is signified by Eq. 3, Eq. 3a-c, and BM $_{\text{bone width \#2}}$:

Eq. 2:

Derivation:

Scale Factor = (fossil bone length/predicted bone length + fossil width #1/predicted width #1 + fossil width #2/predicted width #2)

Whereby,

Eq. 2a:

Predicted bone length = Fossil bone width #1 x living comparison bone length/living comparison bone width #1

Eq. 2b:

Predicted width #1 = Fossil bone width #1 x living comparison width #1/living comparison bone width #1

Eq. 2c:

Predicted width #2 = Fossil bone width #1 x living comparison width #2/living comparison bone width #1

As the predicted bone width #1 in this example is simply equal to the fossil bone width #1, the scale factor equation Eq. 2 can be simplified to:

Eq. 2:

Scale Factor $_{\text{bone width 1}}$ = (fossil bone length/predicted bone length + 1 + fossil width #2/predicted width #2)

Substitution of appropriate values:

Eq. 2a: (1)

Predicted bone length = Fossil bone width #1 x living comparison bone length/living comparison bone width #1 = 1.10 mm x 1.00 mm/1.00 mm = 1.10 mm

Eq. 2c: (2)

Predicted width #2 = Fossil bone width #1 x living comparison width #2/living comparison bone width #1 = 1.10 mm x 1.00 mm/1.00 mm = 1.10 mm

Eq. 2: (3)

Scale Factor = (fossil bone length/predicted bone length + fossil width #1/predicted width #1 + fossil width #2/predicted width #2) = (1.05/1.10 + 1 + 1.15/1.10 = 3.00

Eq. BM $_{\text{bone width \#1}}$: (4)

Fossil body mass = (Fossil measurement/living comparison measurement)^scale factor x body mass of living comparison

Fossil body mass = (1.10 mm/1.00 mm)^3.00 x 1 kg

Fossil body mass = 1.33 kg

Eq. 3:

Derivation:

Scale Factor = (fossil bone length/predicted bone length + fossil width #1/predicted width #1 + fossil width #2/predicted width #2)

Whereby,

Eq. 3a:

Predicted bone length = Fossil bone width #2 x living comparison bone length/living comparison bone width #2

Eq. 3b:

Predicted width #1 = Fossil bone width #2 x living comparison width #1/living comparison bone width #2

Eq. 3c:

Predicted width #2 = Fossil bone width #2 x living comparison width #2/living comparison bone width #2

As the predicted bone width #2 in this example is simply equal to the fossil bone width #2, the scale factor equation Eq. 3 can be simplified to:

Eq. 3:

Scale Factor $_{\text{bone width 2}}$ = (fossil bone length/predicted bone length + fossil width #1/predicted width #1 + 1)

Substitution of appropriate values:

Eq. 3a: (1)

Predicted bone length = Fossil bone width #2 x living comparison bone length/living comparison bone width #2 = 1.15 mm x 1.00 mm/1.00 mm = 1.15 mm

Eq. 3b: (2)

Predicted width #1 = Fossil bone width #2 x living comparison width #1/living comparison bone width #2 = 1.15 mm x 1.00 mm/1.00 mm = 1.15 mm

Eq. 3: (3)

Scale Factor $_{\text{bone width \#2}}$ = (fossil bone length/predicted bone length + fossil width #1/predicted width #1 + 1) = (1.05 mm/1.15 mm + 1.10 mm/1.15 mm + 1) = 2.87

Eq. BM $_{\text{bone width \#2}}$: (4)

Fossil body mass = (Fossil measurement/living comparison measurement)^scale factor x body mass of living comparison

Fossil body mass = (1.15 mm/1.00 mm)^2.87 x 1 kg

Fossil body mass = 1.49 kg

To produce the most realistic body mass, the body mass estimates produced by Eq. BM $_{\text{bone length,}}$ BM $_{\text{bone width \#}}$1, and BM $_{\text{bone width \#2}}$ are then averaged to produce the final estimate.

Body mass estimation

The aforementioned model equations were then applied to two types of long, namely the humerus and femur. The measurements of the femur were articular length (FL), distal articular width (FDAW), and the least lateromedial diameter of the shaft (FDLM) (Christiansen & Harris, 2005). The measurements of the humerus were articular length (HL), distal articular width (HDAW), and the least lateromedial diameter of the shaft (HDLM) (Christiansen & Harris, 2005). Equations were made using either tigers, lions, or jaguars as the living comparison species. Once the measurement values of living comparison species were substituted into the aforementioned model equations, the equations were simplified to produce single-step equations that calculated body mass for each type of bone measurement.

One modification had to be made to the aforementioned equations under a certain condition. Specifically, if a specimen being estimated by the living comparison species had a bone measurement less than that of the corresponding measurement of the living species, the following modified equations are used depending on the circumstance:

Eq. 1* (use only if bone length of fossil specimen is less than that of living comparison species):

Scale Factor = (1 + predicted width #1/fossil width #1 + predicted width #2/ fossil width #2)

Eq. 2* (use only if bone width #1 of fossil specimen is less than that of living comparison species):

Scale Factor $_{\text{bone width \#1}}$ = (predicted bone length/fossil bone length + 1 + predicted width #2/ fossil width #2)

Eq. 3* (use only if bone width #2 of fossil specimen is less than that of living comparison species):

Scale Factor $_{\text{bone width \#2}}$ = (predicted bone length/fossil bone length + predicted width #1/fossil width #1 + 1)

This change accounts for the intrinsic property of the scale factor that may result in the overestimation or underestimation of a specimen that is smaller than the living comparison species. For instance, a specimen whose long bone is proportionately thicker than the living comparison species will according to Eq. 1, produce a scale factor that is greater than 3. When a scale factor is greater than 3, the mathematics assume that the larger specimen is proportionately heavier than the smaller specimen with regard to the given bone measure. In this case where the opposite is occurring and the smaller specimen is proportionately heavier, a scale factor of greater than 3 would underestimate this smaller specimen. Therefore, using Eq. 1*, the scale factor would calculate as less than three and the allometric opposite of what would be resultant from the unmodified Eq. 1 would be produced. When applied to Eq. BM, the scale factor resulting from Eq. 1* would estimate a specimen that is correctly proportionately heavier than the larger living comparison species.

Estimation Errors

To determine whether the mass of different cat species depends equally on a given combination of long bone measurements, the equations formed using a certain living comparison species were used to estimate the other living comparison species used in this study. For instance, the simplified equation derived by from the data of tigers was used to estimate the body mass of lions and jaguars using the respective data of those species. Percent errors were then calculated for both femoral and humeral estimates. The humerus-based and femur-based percent errors were averaged. The ANOVA test was applied to determine if any of the percent errors associated with the three species estimates produced by a given living comparison species was significantly different from the other percent errors. Tukey's HSD test was subsequently applied to pinpoint which species in the set of living species was significantly misestimated by the living comparison species equation.

Due to disparities in body mass estimation between species, fossil taxa were estimated using only the most similar species as the living comparison species (Christiansen & Harris, 2009). Key aspects to examine when doing such include relative postcranial proportions as well as the habitat and subsequent locomotor behavior of the species. Data on postcranial proportions on the fossil lion-like species, *Panthera atrox* and *Panthera spelaea*, matches well with the corresponding proportions of the modern lion (*Panthera leo*) (Merriam & Stock, 1932; Antón, Turner & Howell, 2000; Diedrich, 2011; Meloro et al., 2013). Moreover, these species inhabited open, grassland landscapes and thus retained very cursorial properties similar to those of the modern lion, which also inhabits open areas (Wheeler & Jefferson, 2009; Bocherens et al., 2011; Meloro et al., 2013). Based on habitat and morphological similarities with the modern tiger, the ancient tiger, *Panthera tigris soloensis*, was estimated using only the modern tiger as the living comparison species (Koenigswald, 1933; Brongersma, 1935; van den Bergh, de Vos & Sondaar, 2001). Similar to the tiger and jaguar, both *Smilodon populator* and *Smilodon fatalis* lived in wooded, closed environments (Wheeler & Jefferson, 2009; Meloro et al., 2013). As such, only estimates from the equations based on the tiger and jaguar were averaged to estimate the mass of both *Smilodon* species.

Table 1. Average body masses and measurements of the humerus and femur of three cat species used as living comparisons. All body masses are in kilograms (kg) and all bone measurements are in millimeters (mm).

		Species		
Bone type	Measurement	*Panthera tigris*	*Panthera leo*	*Panthera onca*
Humerus	HL	335.5	343.3	226
	HDLM (width #1)	29.2	30.8	22.1
	HDAW (width #2)	61.4	66	44.2
Femur	FL	390.2	391.5	252
	FDLM (width #1)	31.8	33	24.4
	FDAW (width #2)	73.6	81.1	52
-	Mass	187.2	174.3	63.3

Abbreviations: HL – Humeral articular length, HDLM – Humeral least shaft diameter, HDAW – humoral distal articular width, FL – Femoral articular length, FDLM – Femoral least shaft diameter, FDAW – Femoral distal articular width. All measurements from Christiansen and Harris (2005).

RESULTS

Estimation Errors

The living comparison species values were substituted into the corresponding model equations and 36 equations were successfully produced and simplified to estimate felid body mass (Table 2). Body mass estimates founded on the lion-based equations were characterized by significantly different degrees of percent error between the species estimated (p=0.00264). Specifically, both the tiger (p=0.00262) and jaguar (p=0.00601) were significantly underestimated (Table 5). When the tiger was used as the living comparison species, there was again a significant difference in the degree of percent error between the mass estimates of the three species (p=0.0014). Namely, both the lion (p=0.00135) and jaguar (p=0.0388) were significantly overestimated (Table 5). The jaguar-based equations indicated a significant difference in the amount of percent error across the extant species estimated as well. However, the lion was just insignificantly overestimated (p=0.055) while the tiger was quite insignificantly underestimated (p=0.683) (Table 5). Thus, the difference suggested by the ANOVA test of the jaguar-based species estimates was only attributed to the significant discrepancy between the percent errors linked to the jaguar-based tiger and lion mass estimates (p=0.0326). Generally, the failure for a discrepancy between percent errors associated with a species to be considered significant may have been the result of the small sample size of estimates used (n=2), resulting in a false non-rejection of the null hypothesis. Nonetheless, the combination of such data indicates that the lion is usually significantly overestimated by the tiger and jaguar (Tables 3, 4, and 5). On the other hand, the tiger and jaguar produce relatively more accurate body masses for each other. Nonetheless, it seems that two species are still somewhat prone to misestimating one another to a lesser degree (Tables 3, 4, and 5).

Table 2. Body mass estimation equations for three taxa. All measurements must be in millimeters (mm) and masses in kilograms (kg).

Equation ID	Living Comparison Species	Measurement type	Equation	Notes
Eq. TFL	Tiger	FL	$BM = (FL/390.2\ mm)\wedge^{(1 + 12.27*DLM/FL + 5.30*DAW/FL)} * 187.2\ kg$	Use only if FL > 390.2 mm
Eq. TFL*	Tiger	FL	$BM = (FL/390.2\ mm)\wedge^{(1 + FL/12.27*DLM + FL/5.30*DAW)} * 187.2\ kg$	Use only if FL < 390.2 mm
Eq. TFDLM	Tiger	FDLM	$BM = (DLM/31.8mm)\wedge^{(1 + 0.0815*FL/DLM + 0.433*DAW/DLM)} * 187.2\ kg$	Use only if DLM > 31.8 mm
Eq. FDLM*	Tiger	FDLM	$BM = (DLM/31.8\ mm)\wedge^{(1 + DLM/(0.0815*FL) + DLM/(0.433*DAW))} * 187.2\ kg$	Use only if DLM < 31.8 mm
Eq. FDAW	Tiger	FDAW	$BM = (AW/73.6mm)\wedge^{(1 + 0.189*FL/DAW + 2.31*DLM/DAW)} * 187.2\ kg$	Use only if DAW > 73.6 mm
Eq. FDAW*	Tiger	FDAW	$BM = (AW/73.6\ mm)\wedge^{(1 + DAW/(0.189*FL) + DAW/(2.31*DLM))} * 187.2\ kg$	Use only if DAW < 73.6 mm
Eq. THL	Tiger	HL	$BM = (HL/335.5\ mm)\wedge^{(1 + 11.48*DLM/HL + 5.46*DAW/HL)} * 187.2\ kg$	Use only if HL > 335.5 mm
Eq. THL*	Tiger	HL	$BM = (HL/335.5\ mm)\wedge^{(1 + HL/11.48*DLM + HL/5.46*DAW)} * 187.2\ kg$	Use only if HL < 335.5 mm
Eq. HDLM	Tiger	HDLM	$BM = (DLM/29.2\ mm)\wedge^{(1 + 0.0871*HL/DLM + 0.476*DAW/DLM)} * 187.2\ kg$	Use only if DLM > 29.2 mm
Eq. HDLM*	Tiger	HDLM	$BM = (DLM/29.2\ mm)\wedge^{(1 + DLM/(0.0871*HL) + DLM/(0.476*DAW))} * 187.2\ kg$	Use only if DLM < 29.2 mm
Eq. HDAW	Tiger	HDAW	$BM = (AW/61.4\ mm)\wedge^{(1 + 0.183*HL/DAW + 2.10*DLM/DAW)} * 187.2\ kg$	Use only if DAW > 61.4 mm
Eq. HDAW*	Tiger	HDAW	$BM = (AW/61.4\ mm)\wedge^{(1 + DAW/(0.183*HL) + DAW/(2.10*DLM))} * 187.2\ kg$	Use only if DAW < 61.4 mm
Eq. LFL	Lion	FL	$BM = (FL/391.5\ mm)\wedge^{(1 + 11.86*DLM/FL + 4.83*DAW/FL)} * 174.3\ kg$	Use only if FL > 391.5 mm
Eq. LFL*	Lion	FL	$BM = (FL/391.5\ mm)\wedge^{(1 + FL/11.86*DLM + FL/4.83*DAW)} * 174.3\ kg$	Use only if FL < 391.5 mm
Eq. LFDLM	Lion	FDLM	$BM = (DLM/33.0mm)\wedge^{(1 + 0.0843*FL/DLM + 0.407*DAW/DLM)} * 174.3\ kg$	Use only if DLM > 33.0 mm
Eq. FDLM*	Lion	FDLM	$BM = (DLM/33.0\ mm)\wedge^{(1 + DLM/(0.0843*FL) + DLM/(0.407*DAW))} * 174.3\ kg$	Use only if DLM < 33.0 mm
Eq. LFDAW	Lion	FDAW	$BM = (AW/81.1\ mm)\wedge^{(1 + 0.207*FL/DAW + 2.46*DLM/DAW)} * 174.3\ kg$	Use only if DAW > 81.1 mm
Eq. FDAW*	Lion	FDAW	$BM = (AW/81.1\ mm)\wedge^{(1 + DAW/(0.207*FL) + DAW/(2.46*DLM))} * 174.3\ kg$	Use only if DAW < 81.1 mm
Eq. LHL	Lion	HL	$BM = (HL/343.3\ mm)\wedge^{(1 + 11.15*DLM/HL + 5.20*DAW/HL)} * 174.3\ kg$	Use only if HL > 343.3 mm
Eq. LHL*	Lion	HL	$BM = (HL/343.3\ mm)\wedge^{(1 + HL/11.15*DLM + HL/5.20*DAW)} * 174.3\ kg$	Use only if HL < 343.3 mm
Eq. LHDLM	Lion	HDLM	$BM = (DLM/30.8\ mm)\wedge^{(1 + 0.0897*HL/DLM + 0.467*DAW/DLM)} * 174.3\ kg$	Use only if DLM > 30.8 mm
Eq. HDLM*	Lion	HDLM	$BM = (DLM/30.8\ mm)\wedge^{(1 + DLM/(0.0897*HL) + DLM/(0.467*DAW))} * 174.3\ kg$	Use only if DLM < 30.8 mm
Eq. HDAW	Lion	HDAW	$BM = (AW/66.0\ mm)\wedge^{(1 + 0.192*HL/DAW + 2.14*DLM/DAW)} * 174.3\ kg$	Use only if DAW > 66.0 mm
Eq. HDAW*	Lion	HDAW	$BM = (AW/66.0\ mm)\wedge^{(1 + DAW/(0.192*HL) + DAW/(2.14*DLM))} * 174.3\ kg$	Use only if DAW < 66.0 mm
Eq. JFL	Jaguar	FL	$BM = (FL/252.0\ mm)\wedge^{(1 + 10.33*DLM/FL + 4.85*DAW/FL)} * 63.3\ kg$	Use only if FL > 252.0 mm
Eq. JFL*	Jaguar	FL	$BM = (FL/252.0\ mm)\wedge^{(1 + FL/10.33*DLM + FL/4.85*DAW)} * 63.3\ kg$	Use only if FL < 252.0 mm
Eq. JFDLM	Jaguar	FDLM	$BM = (DLM/24.4mm)\wedge^{(1 + 0.0968*FL/DLM + 0.469*DAW/DLM)} * 63.3\ kg$	Use only if DLM > 24.4 mm
Eq. JFDLM*	Jaguar	FDLM	$BM = (DLM/24.4\ mm)\wedge^{(1 + DLM/(0.0968*FL) + DLM/(0.469*DAW))} * 63.3\ kg$	Use only if DLM < 24.4 mm
Eq. JFDAW	Jaguar	FDAW	$BM = (AW/52.0\ mm)\wedge^{(1 + 0.206*FL/DAW + 2.13*DLM/DAW)} * 63.3\ kg$	Use only if DAW > 52.0 mm
Eq. FDAW*	Jaguar	FDAW	$BM = (AW/52.0\ mm)\wedge^{(1 + DAW/(0.206*FL) + DAW/(2.13*DLM))} * 63.3\ kg$	Use only if DAW < 52.0 mm
Eq. JHL	Jaguar	HL	$BM = (HL/226.0\ mm)\wedge^{(1 + 10.23*DLM/HL + 5.11*DAW/HL)} * 63.3\ kg$	Use only if HL > 226.0 mm
Eq. JHL*	Jaguar	HL	$BM = (HL/226.0\ mm)\wedge^{(1 + HL/10.23*DLM + HL/5.11*DAW)} * 63.3\ kg$	Use only if HL < 226.0 mm
Eq. JHDLM	Jaguar	HDLM	$BM = (DLM/22.1\ mm)\wedge^{(1 + 0.0978*HL/DLM + 0.500*DAW/DLM)} * 63.3\ kg$	Use only if DLM > 22.1 mm
Eq. HDLM*	Jaguar	HDLM	$BM = (DLM/22.1\ mm)\wedge^{(1 + DLM/(0.0978*HL) + DLM/(0.500*DAW))} * 63.3\ kg$	Use only if DLM < 22.1 mm
Eq. JHDAW	Jaguar	HDAW	$BM = (AW/44.2\ mm)\wedge^{(1 + 0.196*HL/DAW + 2.00*DLM/DAW)} * 63.3\ kg$	Use only if DAW > 44.2 mm
Eq. HDAW*	Jaguar	HDAW	$BM = (AW/44.2\ mm)\wedge^{(1 + DAW/(0.196*HL) + DAW/(2.00*DLM))} * 63.3\ kg$	Use only if DAW < 44.2 mm

Abbreviations: BM – Body mass, HL – Humeral articular length, HDLM – Humeral least shaft diameter, HDAW – humoral distal articular width, FL – Femoral articular length, FDLM – Femoral least shaft diameter, FDAW – Femoral distal articular width.
Any equations referenced in the text from hereon will be referenced by the equation ID.

Table 3. Percent errors for each species using femoral measurements.

Living Comparison Species	Species Estimated		
	Panthera tigris	*Panthera leo*	*Panthera onca*
Panthera tigris	0.0%[1]	+24.2%[1]	+5.53%[2]
Panthera leo	-16.4%[3]	0.0%[3]	-14.5%[3]
Panthera onca	-3.58%[4]	+37.8%[4]	0.0%[4]

(+) indicates overestimating, (-) indicates underestimations.

[1] Equations used were Eq. TFL, Eq. TFDLM, Eq. TFDAW

[2] Equations used were Eq. TFL*, Eq. TFDLM*, Eq. TFDAW*

[3] Equations used were Eq. LFL*, Eq. LFDLM*, Eq. LFDAW*

[4] Equations used were Eq. JFL, Eq. JFDLM, Eq. JFDAW

Table 4. Percent errors for each species using humoral measurements.

Living Comparison Species	Species Estimated		
	Panthera tigris	*Panthera leo*	*Panthera onca*
Panthera tigris	0.0%[1]	+24.8%[1]	+9.48%[2]
Panthera leo	-19.5%[3]	0.0%[3]	-12.5%[3]
Panthera onca	-9.35%[4]	+20.9%[4]	0.0%[4]

(+) indicates overestimation, (-) indicates underestimation.

[1] Equations used were Eq. THL, Eq. THDLM, Eq. THDAW

[2] Equations used were Eq. THL*, Eq. THDLM*, Eq. THDAW*

[3] Equations used were Eq. LHL*, Eq. LHDLM*, Eq. LHDAW*

[4] Equations used were Eq. JHL, Eq. JHDLM, Eq. JHDAW

Table 5. Average percent errors for each species.

Living Comparison Species	Species Estimated		
	Panthera tigris	*Panthera leo*	*Panthera onca*
Panthera tigris	0.0%	**+24.5%**	**+7.51%**
Panthera leo	**-18.0%**	0.0%	**-13.5%**
Panthera onca	-6.47%	+29.4%	0.0%

(+) indicates overestimation, (-) indicates underestimation.

Bold indicates that the species estimated was significantly misestimated by the living comparison species.

Extinct Species Masses

Panthera tigris solonesis was the heaviest species, with the largest specimen weighing 486 kg (Fig. 1; Appendix 1). *Panthera atrox* was slightly larger than *Panthera spelaea*, with the maximum masses being 363 kg and 339 kg, respectively (Fig.1; Appendix 1). The heaviest *Smilodon populator* specimen weighed 450 kg and the heaviest *Smilodon fatalis* specimen weighed 342 kg (Fig. 1; Appendix 1). All estimated fossil species well exceeded even the largest of modern felids in body mass (Fig. 1).

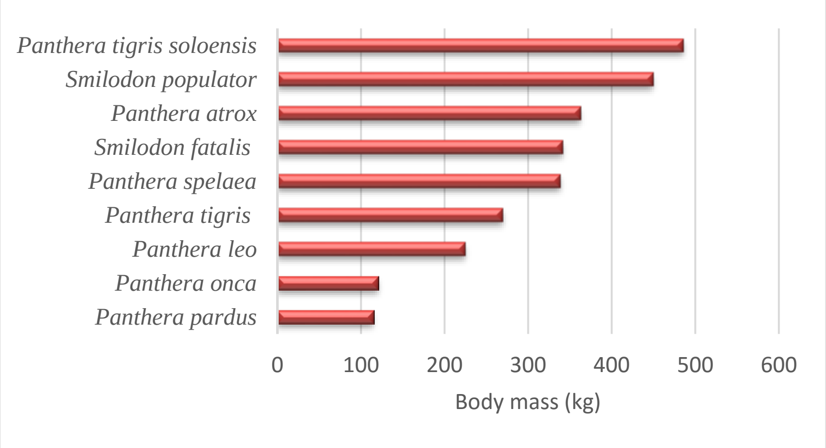

Figure 1. Body masses of nine of the largest felid species. All masses in kilograms (kg). The sources of the maximum extant species body mass are as follows: Smuts, Robinson, & Whyte (1980), Sunquist & Sunquist (2002), Dinerstein (2003), and Farhadinia et al. (2014).

DISCUSSION

Discrepancies with other literature estimations

The body masses of both *Smilodon populator* and *Smilodon fatalis* presented in this study of 450 kg and 342 kg, respectively, are quite greater than the masses provided in Christiansen and Harris (2005), in which the largest *Smilodon* did not exceed 360 kg (Fig. 1; Appendix 1). Christiansen and Harris (2005) used equations with very negatively allometric scale factors for bone widths, aspects for which both *Smilodon* species are exceptional in. As discussed earlier, the extreme negative allometry in such equations is more likely just a product of the combination of species used to formulate the regression equations rather than an actual trend. Thus the body mass of the extremely robust *Smilodon* species would be underestimated by such equations.

Estimation Errors and Habitat

The hefty and significant percent errors in estimation of one species using another as the living comparison species indicates that bone measurements may not on their own be enough to accurately estimate a specimen. However, it is interesting to note that the forest-dwelling species, the tiger and the jaguar, estimated one another more accurately than they did the lion, which occurs in open landscapes (Sunquist & Sunquist, 2002; Meloro et al., 2013). This may suggest that the postcranial anatomy of the jaguar and tiger convergently evolved to some degree to better deal with the tighter spaces offered by forests. Moreover, the trend of the mass of the lion being overestimated by the other two living comparison species suggests that lions carry less mass relative to their bone dimensions than the tiger and jaguar. Such may be an adaptation to cursorial living on the savannah, whereby the body mass to limb size ratio of the lion would result in sturdier bones, longer stride lengths, and decreased stresses on limb bones due to relatively decreased mass. Overall, the sample examined provides an indication that habitat should be considered when choosing a living comparison species to estimate an extinct species, as done in this study.

General Species Discussion

Panthera atrox has often been reported to greatly outsize *Smilodon fatalis* (Anyonge, 1993). The mass estimates here show that even though *Panthera atrox* may have been significantly longer and taller than *Smilodon fatalis*, it was not much heavier when accounting for its cursorial, lion-like characteristics (Fig. 1; Appendix 1). In agreeance with isotopic data on the diets of these two species, this finding suggests some niche overlap and direct competition between *Panthera atrox* and *Smilodon fatalis*, as both would have had the size to take down similarly sized prey (Coltrain et al., 2004). This niche overlap may have played a role in the mutual extinction of these two megafauna at the end of the Pleistocene, whereby the niche overlap could not be maintained once late Pleistocene prey populations collapsed in North America (Faith & Surovell, 2009).

The ability for *Smilodon populator* to far exceed its smaller North American relative in body mass may have been a result of the lack of competition at the high end of the food chain in Pleistocene South America. In South America, *Smilodon populator* emerged after the extinction of possibly the largest carnivore ever, *Arctotherium angustidens* (Castro, 2008; Soibelzon & Schubert, 2011). This likely allowed *Smilodon populator* to easily assume the niche of a mega-carnivore to displace itself from competition with smaller carnivores present at the time (Prevosti & Vizcaino, 2006). In the case of *Smilodon fatalis*, the combination of the aforementioned niche overlap with *Panthera atrox* and the presence of the enormous North American giant short-faced bear (*Arctodus simus*) in North America may have played a role in not permitting *Smilodon fatalis* to reach the massive size of its South American cousin (Coltrain et al., 2004; Figueirido et al., 2010).

The largest of *Panthera spelaea* was estimated to weigh 339 kg (Fig. 1; Appendix 1). This weight may imply a lack of sociality in this large lion-like cat due to isotopic data which indicate that this species preyed most often on the reindeer (*Rangifer tarandus*), occasionally on cave bear (*Ursus spelaeus*) young, and essentially never on mammoths (*Mammuthus*) (Bocherens et al., 2011). The largest of modern reindeer are reported to weigh around 200 kg (Finstad & Prichard, 2000; Puputti & Niskanen, 2008). Thus, even if Pleistocene gigantism was to be assumed for the reindeer of that time period, it would seem that *Panthera spelaea* strongly preferred to hunt species smaller than itself. In light of such, the predatory style of *Panthera spelaea* would have been more like solitary *Panthera* species than social *Panthera* species. Specifically, the tiger, leopard, and jaguar have been found to prey most regularly on species smaller than themselves while the lion prefers prey larger than itself (Karanth & Sunquist, 1995; Hayward & Kerley, 2005; Hayward et al., 2006, 2016). Therefore, the size disparity within the predator-prey relationship of *Panthera spelaea* and the reindeer supports the conclusion of

Bocherens et al. (2011) that *Panthera spelaea* was solitary as if it lived in prides, its prey preference would be expected to mirror that of modern lions. The conclusions regarding the diet of *Panthera spelaea* make the extinction of the species quite complicated as well, considering that many relatively smaller prey species that could have sustained the cat have survived through the Holocene.

The largest of *Panthera spelaea* examined in this study also approached the size of *Panthera atrox* (Fig. 1; Appendix 1). Therefore, it is very likely *Panthera atrox* and *Panthera spelaea* were not significantly different in size. Despite this lack of size difference, it seems the prey available to *Panthera atrox*, such as the 1,000 kg *Bison antiquus* and *Camelops hesternus*, would have weighed much more than the reindeer preyed upon by *Panthera spelaea* (Lambert & Holling; Finstad & Prichard, 2000; Coltrain et al., 2004; Puputti & Niskanen, 2008; Bocherens et al., 2011). In turn, *Panthera atrox* would have been quite smaller than its prey targets. As mentioned earlier, the only *Panthera* species that prefers to hunt prey larger than itself is the pride-living, social lion (Karanth & Sunquist, 1995; Hayward & Kerley, 2005; Hayward et al., 2006, 2016). Thus, the predator size to prey size ratio in the relationship between *Panthera atrox* and its prey suggests that this cat was social in at least some capacity, agreeing with conclusions of sociality based on sexual dimorphism (Wheeler & Jefferson, 2009; Meachen-Samuels & Binder, 2010).

The extreme mass of the tiger that lived in Java before the last interglacial, *Panthera tigris solonesis*, has its most major implications on the evolution and subspeciation of the tiger as a whole (Westaway et al., 2007) (Fig. 1, Appendix 1). The 500,000 year old direct ancestor of this giant cat, *Panthera tigris trinilensis*, seems to not have been much larger than the smallest of the modern tiger subspecies (Koenigswald, 1933; Brongersma, 1935; Groves, 1992; Joordens et al., 2015). Similarly, the direct ancestor of *Panthera tigris soloensis*, the Javan tiger (*Panthera tigris sondaica*), is also only a third of the mass of *Panthera tigris soloensis* (Mazak, 1981; Groves, 1992). To make this rapid evolution of size more striking, the possibility of *Panthera tigris soloensis* being a separate sister species from the tiger is made quite unlikely by the fact that the cranial and postcranial morphology of this giant tiger are essentially identical to that of the Javan tiger (Koenigswald, 1933; Brongersma, 1935; Groves, 1992). This would indicate that the lineage of tiger inhabiting the Sunda shelf underwent a dramatic increase in size in a relatively short time span, and then reverted back to its former size in another very short time span. Such plasticity in body mass of the tiger lineage indicates that discrepancies in body mass may not be enough to declare subspeciation within tigers, as such a trait seems to be very volatile. This conclusion somewhat supports propositions that suggest that only two subspecies of tiger exist, the mainland tiger (*Panthera tigris tigris*) and island tigers (*Panthera tigris sondaica*), with discrepancies within populations being simply clinal (Kitchener & Dugmore, 2000; Wilting et al., 2015).

CONCLUSIONS

A new method of estimating felid body mass that gives regard to unique osteological properties of the specimen being estimated was successfully derived. The discrepancy in the relative body mass accounted for by proximal long bones between lions, jaguars, and tigers was also demonstrated. The body mass of *Panthera atrox*, *Panthera spelaea*, *Panthera tigris soloensis*, *Smilodon fatalis*, and *Smilodon populator* were successfully estimated, showing that these extinct cats outsized all modern felids. Implications of these new body mass estimates were widespread. *Smilodon fatalis* seemed to overlaps its niche with *Panthera atrox* more than previously thought due to a decreased discrepancy in size between the two species. *Smilodon populator* was likely the product of an opening at the high end of the food chain in its region. Predator size to prey size ratios suggest *Panthera spelaea* may have been solitary while *Panthera atrox* was a more social cat. The sudden increase in size within the tiger lineage to produce *Panthera tigris soloensis* seems to support the notion that variations in size between modern tiger populations are too volatile to justify subspeciation.

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Appendix 1. The osteological measurements and corresponding mass estimates for specimens examined in this study. All measurements in millimeters (mm) and all masses in kilograms (kg).

		Measurement						Mass estimate based on…						Final
Specimen ID	Species	FL	FDLM	FDAW	HL	HDLM	HDAW	FL	FDLM	FDAW	HL	HDLM	HDAW	Mass
Nr. 2641[1]	*Panthera tigris soloensis*	480	42.8	110.0	-	-	-	372	460	626	-	-	-	486
Nr. 9554[1]	*Panthera tigris soloensis*	-	-	-	373	35.8	74.2	-	-	-	263	337	330	310
Nr. 1933[1]	*Panthera tigris soloensis*	-	-	-	348	37.0	77.5	-	-	-	212	364	376	317
72.190[2]	*Panthera spelaea*	470	44	99	-	-	-	309	392	317	-	-	-	339
2907-R-3[3]	*Panthera atrox*	460	41	95.5	-	-	-	286	327	285	-	-	-	299
2907-R-2[3]	*Panthera atrox*	455	45.3	105.4	-	-	-	286	422	382	-	-	-	363
MLP10-13[4a]	*Smilodon populator*	-	-	-	387.5	44.7	82.1	-	-	-	339	508	427	425
CN11[4b]	*Smilodon populator*	-	-	-	374.5	43.4	88.8	-	-	-	316	494	540	450
K3592[4a]	*Smilodon fatalis*	423.5	39.1	83.9	-	-	-	265	301	272	-	-	-	279
K807[4a]	*Smilodon fatalis*	-	-	-	381.1	35.8	81.1	-	-	-	297	319	411	342

Abbreviations: HL – Humeral articular length, HDLM – Humeral least shaft diameter, HDAW – humoral distal articular width, FL – Femoral articular length, FDLM – Femoral least shaft diameter, FDAW – Femoral distal articular width.

[1] From von Koenigswald (1933). Measured digitally by author. Located in Geological Museum of Bandung, Indonesia per Volmer, Hertler, & van der Geer (2016).

[2] From Teschler-Nicola (2006). Located in Naturhistorisches Museum Wien in Vienna, Austria.

[3] From Merriam and Stock (1932). Located in Natural History Museum of Los Angeles County in California, United States.

[4] From Christiansen and Harris (2005).

a) Located in Museo de La Plata of Buenos Aires, Argentina.

b) Located in University of Copenhagen Zoological Museum of Copenhagen, Denmark.

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