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Body Mass Estimates in Dogs and North American Gray Wolves Using Limb Element Dimensions

R. J. LOSEY,[a,b]* K. MCLACHLIN,[a] T. NOMOKONOVA,[c] K. LATHAM[a] AND L. HARRINGTON[a]

[a] *Department of Anthropology, University of Alberta, Edmonton, AB Canada*
[b] *Centre for Advanced Study, Norwegian Academy of Science and Letters, Oslo, Norway*
[c] *Community, Culture and Global Studies, Irving K. Barber School of Arts and Science, University of British Columbia Okanagan, Kelowna, Canada*

ABSTRACT Body mass is a key biometric that is useful in interpreting many aspects of an animal's life history. For many species, including dogs and wolves, methods for estimating body mass are not well developed. This paper assesses the utility of using limb dimensions to predict body mass in dogs and North American wolves. Regression analyses are utilized here to explore the correlations between limb dimensions and body masses of modern dogs and wolves, all of known body mass at death. These analyses reveal that a number of limb end dimensions are correlated with body mass in both dogs and wolves. Regression formulae generated through the analyses appear to allow body masses to be predicted with relatively small margins of error, often less than 10%. Formulae are calculated for groups with and without juveniles. In some cases, the dimensions of the juvenile specimens plot distinctly from those of adults, indicating that regression formulae specifically for juvenile canids may be needed. The strength of the limb dimension correlations is then compared with that of regression formulae for dog and wolf cranio-mandibular dimensions. For the dogs, the cranio-mandibular dimensions appear to slightly out-perform the limb element dimensions in predicting body mass. The wolf limb dimensions, however, always appear to provide better predictions of body mass than do the skull dimensions. The newly developed regression formulae are applied to several Middle Holocene dog skeletons from Siberia for which previous body mass estimates are available, the latter based on cranial dimensions. These two sets of estimates are then compared. The overall results of our study indicate the need for further research, particularly with larger sample sizes, including more juvenile specimens. We also argue that work on body size estimation in single dog breeds may be warranted in some cases.

Key words: archaeology; body mass; canids; dogs; domestication; wolves

Introduction

Investigations of the roles of domesticated fauna in society are often hampered by the dearth of accurate methods for understanding key biometrics of such animals. This is particularly true for studies of archaeological dog remains, where the most commonly used methods for assessing an individual's basic characteristics, including its age, sex, and body mass, were mostly developed decades ago, often with small samples of modern comparative specimens. Some of these methods have seen little refinement in recent years, despite the fact that age, sex, and body mass are critical to more specific studies of animal life histories. Refinement of such methods is clearly needed and will help in understanding the complex and variable ways in which animals were interacting with humans and their environments.

In this study, we first develop regression formulae for estimating body mass in dogs. The same formulae are then developed for North American gray wolves. Body mass is a basic biometric that is critical for understanding many aspects of canids' life histories and interactions with people. For example, estimating a dog's body mass is informative about the caloric costs of maintaining it, as body mass maintenance is directly related to an individual's metabolic processes, including its nutrient intake (National Research Council, 2006). Body mass estimates also are useful for understanding the dietary contributions of taxa that are used as food items, and dogs and wolves were (and still are) clearly

* Correspondence to: Robert J. Losey, Department of Anthropology, University of Alberta, Edmonton, AB T6G 2H4 Canada. e-mail: robert.losey@ualberta.ca

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on the menu in various parts of the world (Schwartz, 1997; Podberscek, 2009). Further, trends in body mass variation through time, both within sites and across broad regions, are potentially informative about a suite of factors, ranging from the effects of ecological changes to shifts in how people managed dog and wolf populations (Manning *et al.*, 2015). Further, accurate methods for estimating body mass are critical in studies of habitual activity, such as sled pulling or burden carrying. Many studies of habitual activity in humans and other animals have focused on skeletal elements' structural changes related to recurrent strain, referred to as bone functional adaptation (Ruff, 2007a). Various techniques are used to measure the cross sectional properties of limb elements that reflect their strength in particular planes. Bone responds to repeated strain by adding bony tissue to the affected area. However, other factors cause differences in bone robusticity, particularly body mass. In other words, accurate body mass estimations are useful both as primary interpretive data and as aspects of other methodologies designed to study animal life histories.

Existing methods for estimating body masses of recent canids focus solely on cranial and mandibular dimensions (Wing, 1978; Legendre & Roth, 1988; Van Valkenburgh, 1990; Palmqvist *et al.*, 1999; Losey *et al.*, 2014). However, crania and mandibulars have no direct role in weight bearing and as such likely are not ideal elements for reconstructing body mass (Auerbach & Ruff, 2004; Yapuncich *et al.*, 2015). The dimensions of limb element articular surfaces are thought by many to provide more accurate indicators of body mass, as they are directly involved in load bearing, and are less influenced by activity patterns than cross sectional dimensions of element diaphyses (Ruff, 1988; Trinkaus *et al.*, 1994; Lieberman *et al.*, 2001). Two general methods for taking such dimensions are caliper measurements of articular ends of limb elements at defined landmarks, and surface area or cross-sectional measures of such element portions captured from digital models and radiographs, sometimes analysed using geometric morphometric methods. These latter approaches are far more technical and time-consuming processes and thus not likely to be used except in the most specialized studies.

Materials and methods

In this study, we employ caliper measurements, as these can be readily obtained by most researchers. Defined dimensions were measured on limb elements of 47 dog skeletons (Table S1). All of the specimens examined are of known sex, and many are of known age and breed. The body masses of these dogs ranged from 5.4 to 64.0 kg. Four specimens are osteological juveniles, having some unfused post-cranial epiphyses, and the remaining specimens are adults. The analysed sample consists of 21 specimens from museum collections, including nine Inuit sled dogs and 12 pet dogs of various breeds. An additional 26 pet dogs, all from Saskatchewan and Alberta, Canada, were skeletonized for the purposes of this study. All of these latter animals died of natural causes. The same dimensions were measured on the skeletons of 40 wolves from western Canada and Alaska, USA (Table S2). These specimens ranged in mass from 28.6 to 54.5 kg and included seven osteological juveniles.

For each specimen, 29 element dimensions were measured (where possible), and all but two of these dimensions were taken from Von den Driesch (1976; Figure 1). For the long bones and scapula, these include element lengths [greatest lengths (GLs)], and various dimensions of the articular ends. Element lengths were included so that their utility for assessing body mass could be compared with that of articular end dimensions. Two new measures were developed, namely the breadth and depth of the femoral head, respectively abbreviated as Hbr and Hdt (Figure 1). Element lengths were taken with an osteometric board to nearest millimeter, and all other dimensions were obtained using a digital sliding caliper and recorded to the one-hundredth of a millimeter.

All biometric data were entered into SPSS version 22 (IBM corp.) and natural log-transformed. To begin the analyses, scatter plots of log-transformed element dimensions and body masses were produced and visually inspected to ensure that linear relationships were present. These plots were also examined to see if the juvenile specimens plotted as visual outliers, or if the results produced groupings by sex. Linear regression models were then calculated for individual element dimensions and body masses, with one set of regressions containing all specimens, the other with the juveniles excluded. For each regression, R and R^2 values, % prediction error (%PE), and % standard error (%SE) of estimate are presented, along with the coefficient and constant values.

To demonstrate the applicability of the limb dimension formulae on ancient specimens, we calculate body mass estimates for five Middle Holocene dog skeletons from the Lake Baikal region of Siberia, several of which were burials. These individuals are described in detail elsewhere (Losey *et al.*, 2013), and all have previous body mass estimations calculated on cranial dimensions (Losey *et al.*, 2014). Comparisons are made between

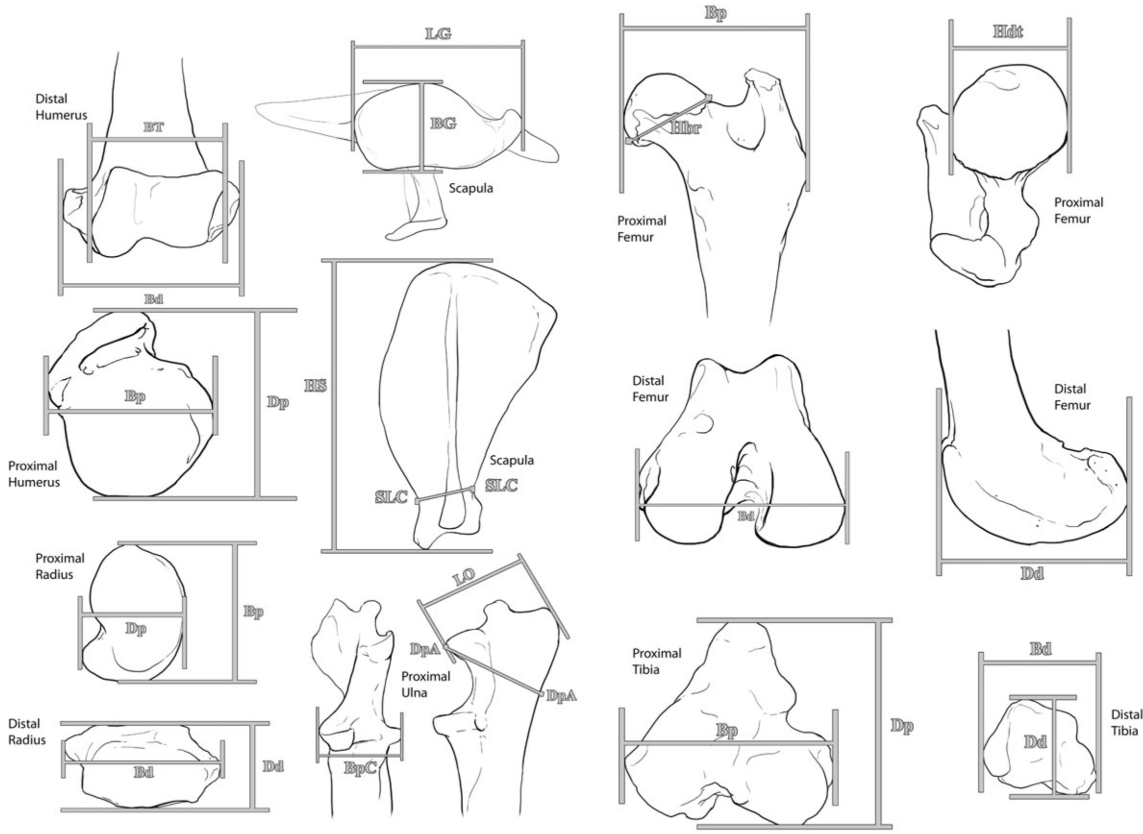

Figure 1. Dimensions taken on canid limb elements. Greatest lengths (GLs) are not pictured here. All dimensions pictured follow Von den Driesch (1976), except for Hbr and Hdt, which are defined in the text.

these previously calculated body mass estimates and those generated by using the limb dimension formulae developed here.

Results

Strong positive correlations were found between many limb bone dimensions and body mass (Tables 1–4). For the dogs, element lengths were more poorly correlated with body mass than were articular end dimensions (Tables 1 and 2). For example, %PE values for element lengths are at least 20%, while multiple articular end dimensions in the dogs had %PE values below 17%. Further, correlation coefficient factors were always higher for the epiphysis dimensions than the element lengths. A similar pattern is seen in the wolf data, where element lengths also are relatively poor predictors of body mass (Tables 3 and 4). Unlike in the dog data, however, wolf limb lengths sometimes performed slightly better in the regressions than articular end dimensions. In particular, femur length is more strongly correlated with body mass than any other dimension taken on this element.

Another pattern in the data is that while the correlations between element dimensions and body mass overall are stronger in the dogs than in the wolves, the %PE values are consistently lower in the wolf data, often falling below 10%. This pattern can be accounted for by differences in the two sample datasets. Specifically, the body masses of the dogs used in the study are far more variable than those of the wolves (59.6 kg range in the dogs; 25.9 kg in the wolves). The wider range of body masses in the dogs allows for stronger correlations, but the dogs' greater morphological variability compared with the wolves results in larger errors when predicting their body masses.

Excluding juveniles from the regressions tended to slightly increase correlation coefficients and reduce prediction errors for the wolves, and had mixed results for the dogs (Tables 3 and 4). Notably, the removal of the juvenile dogs and wolves from the samples resulted in no loss in overall size range in the sample—the juveniles in both groups were not the lightest canids in either group. For the dogs, the most marked

Table 1. Statistics for linear regression equations for dog limb dimensions and body mass, adult, and juvenile individuals combined

Dimension	No. of cases	*R*	R^2	%PE	SEE	Coefficent	Constant
Scapula							
LG	28	0.900	0.811	21.43	0.288	2.438	−5.339
BG	28	0.891	0.887	16.15	0.219	2.769	−5.151
SLC	28	0.941	0.886	16.43	0.223	2.339	−4.610
HS	28	0.877	0.770	23.79	0.318	2.663	−10.217
Humerus							
BP	46	0.911	0.830	17.96	0.236	2.401	−5.353
DP	47	0.922	0.843	17.88	0.222	2.645	−6.882
BD	46	0.920	0.846	16.89	0.225	2.547	−6.016
BT	46	0.897	0.804	19.61	0.253	2.564	−5.437
GL	47	0.873	0.762	20.91	0.277	2.339	−8.840
Radius							
BP	43	0.891	0.794	18.91	0.256	2.665	−4.831
DP	43	0.865	0.748	21.75	0.283	2.444	−3.149
BD	43	0.891	0.793	18.13	0.256	2.630	−5.528
DD	43	0.709	0.502	26.90	0.398	1.860	−1.909
GL	43	0.846	0.716	23.72	0.301	2.102	−7.577
Ulna							
LO	40	0.860	0.740	22.14	0.296	1.577	−2.327
DPA	41	0.925	0.855	15.84	0.219	2.351	−4.704
BPC	40	0.899	0.808	19.62	0.253	2.118	−3.134
GL	40	0.833	0.694	24.45	0.321	2.029	−7.571
Femur							
Hbr	46	0.925	0.856	17.68	0.217	2.631	−4.774
Hdp	46	0.913	0.834	19.43	0.233	2.563	−4.577
BP	46	0.921	0.849	15.45	0.222	2.607	−6.608
BD	47	0.896	0.803	19.13	0.252	2.634	−6.221
DD	46	0.895	0.801	18.95	0.239	2.320	−5.282
GL	47	0.881	0.775	20.23	0.269	2.327	−8.975
Tibia							
BP	42	0.920	0.846	16.09	0.215	2.740	−6.909
DP	41	0.905	0.818	19.26	0.237	2.667	−6.646
BD	42	0.926	0.858	16.86	0.208	2.775	−5.889
DD	42	0.879	0.773	20.98	0.264	2.720	−4.791
GL	41	0.849	0.721	22.40	0.283	2.038	−7.475

Dimensions are from Von den Driesch (1976). All data natural log transformed.

improvements were seen in the correlations for the distal radius. For example, the depth of the distal radius epiphysis in the dogs produced the weakest correlations ($R^2 = 0.502$, %PE = 26.90) with body mass when both adults and juveniles were included. When the juveniles were removed, the correlations greatly improved, with the R^2 value increasing to 0.825 and the prediction error decreasing to 14.78%. When the juveniles were removed from the wolf dataset, the most marked improvements also were observed in the distal radius correlations.

The diversity of dog breeds represented in our samples means that male dogs and female dogss overlap significantly in terms of body size (Figure 2a). This likely overrides any sexual dimorphic patterns that might be present if single breeds of dogs were under consideration. In the wolves some overlap in body mass by sex also occurs, but the females generally fall to the lower end of the scatter plots because of average smaller body masses (Figure 2b). Otherwise, the female and male data points fail to plot as two visually distinct clusters, suggesting that it is appropriate in this case to combine the two sexes for the regressions, a point we return to below.

Table 5 shows body mass estimates for the five archaeological Siberian dog specimens. Mass estimates are provided for each limb element (where possible) using the element dimension with the lowest %PE for that element. Only element lengths were available for the Shamanka dog and are utilized here. The right-hand column of the table displays the body mass estimates for these specimens calculated in Losey *et al*. (2014), all of which were based on a formula for Von den Driesch's (1976) cranial length two. The limb dimension predictions are generally within 2–3 kg of the cranial dimension estimates. The bolded mass estimates in the table are those generated by the equation with the lowest %PE, and these values are in all cases differed less than 2 kg from the cranial dimension estimates. The average difference in estimated body

Table 2. Statistics for linear regression equations for dog limb dimensions and body mass, adults only

Dimension	No. of cases	R	R^2	%PE	SEE	Coefficent	Constant
Scapula							
LG	27	0.901	0.812	21.68	0.293	2.445	−5.357
BG	27	0.944	0.891	16.08	0.223	2.769	−5.151
SLC	27	0.941	0.886	16.85	0.228	2.341	−4.613
HS	27	0.877	0.770	24.41	0.324	2.665	−10.223
Humerus							
BP	43	0.910	0.829	18.60	0.243	2.420	−5.414
DP	43	0.923	0.852	17.91	0.227	2.668	−6.957
BD	43	0.919	0.845	17.41	0.232	2.551	−6.025
BT	43	0.896	0.803	20.47	0.261	2.573	−5.461
GL	43	0.872	0.760	22.12	0.288	2.358	−8.940
Radius							
BP	40	0.913	0.834	18.52	0.238	2.747	−5.056
DP	40	0.893	0.798	20.70	0.262	2.576	−3.467
BD	40	0.920	0.846	16.56	0.228	2.735	−5.845
DD	40	0.908	0.825	14.78	0.243	2.795	−4.362
GL	40	0.847	0.717	24.59	0.310	2.126	−7.698
Ulna							
LO	38	0.861	0.741	21.95	0.303	1.583	−2.344
DPA	39	0.925	0.856	15.68	0.223	2.357	−4.719
BPC	38	0.899	0.808	19.99	0.260	2.122	−3.145
GL	38	0.836	0.698	24.33	0.327	2.035	−7.606
Femur							
Hbr	43	0.927	0.860	18.11	0.220	2.645	−4.777
Hdp	43	0.913	0.834	20.10	0.239	2.568	−4.585
BP	43	0.922	0.850	13.94	0.228	2.647	−6.677
BD	43	0.906	0.821	19.05	0.249	2.682	−6.372
DD	42	0.901	0.812	18.30	0.240	2.359	−5.406
GL	43	0.872	0.772	21.62	0.281	2.332	−9.000
Tibia							
BP	39	0.926	0.858	17.20	0.214	2.766	−6.996
DP	39	0.907	0.823	19.27	0.239	2.688	−6.716
BD	40	0.931	0.866	16.55	0.207	2.790	−5.927
DD	40	0.903	0.815	20.14	0.243	2.812	−5.041
GL	39	0.849	0.720	23.02	0.290	2.041	−7.486

Dimensions are from Von den Driesch (1976). All data natural log transformed.

masses produced between these element equations and those for cranial dimensions is only 7.8%.

Comparing the performance of the limb element regressions with those for dog and wolf cranio-mandibular dimensions (Losey *et al.*, 2014) required re-analyses of our earlier datasets. The reason for this was that some juvenile animals were used in these earlier regressions, potentially biasing the results in unrecognized ways. For maximum comparability with this study, all juveniles were removed, leaving a sample of 30 dogs and 91 wolves (When originally analysed, mandibular dimensions were available for only 27 of the 36 dogs [Losey *et al.*, 2014]. Five juveniles were removed from this dataset here, and mandibular measurements were taken on eight other adult animals, added in here, bringing the total to 30). The dogs in this sample ranged in mass from 5 to 49 kg and the wolves from 28.6 to 58 kg. Both of these size ranges are similar to those of the specimens used in the limb dimension regressions presented earlier. To simplify the analyses, we selected those dimensions that had previously proven to be strongly correlated with body mass, all of which were length measures of the cranium and mandible (Tables 5 and 6). All data were natural log transformed, and regression analyses followed the procedures outlined for the specimens in the preceding texts.

Removal of the juvenile dogs only slightly changed the cranio-mandibular regressions, making nearly all of the cranial and mandibular correlations slightly weaker (R^2 values were only 1–2 hundredths difference; Table 6). The cranial R^2 values remain higher than those for the limb element correlations and %PE values slightly lower than those for the limbs. In other words, these skull dimensions seem to be relatively good predictors of dog's body masses, appearing to be even more reliable than the limb dimensions utilized in this study. As indicated in the introduction, this is counter to expectations, as one might expect the limbs to better track body mass, as they are directly involved

Table 3. Statistics for linear regression equations for wolf limb dimensions and body mass, adult, and juvenile individuals combined

Dimension	No. of cases	*R*	R^2	%PE	SEE	Coefficent	Constant
Scapula							
LG	39	0.833	0.694	8.03	0.101	2.209	−4.524
BG	39	0.820	0.672	8.63	0.104	2.379	−3.962
SLC	39	0.704	0.495	10.42	0.129	1.726	−2.467
HS	39	0.736	0.542	9.81	0.123	1.985	−6.610
Humerus							
BP	40	0.797	0.636	8.30	0.110	2.147	−4.389
DP	40	0.819	0.671	8.00	0.104	2.412	−6.077
BD	40	0.804	0.646	8.70	0.108	1.869	−3.453
BT	40	0.787	0.619	9.01	0.112	1.985	−3.402
GL	38	0.785	0.615	9.06	0.114	2.371	−9.208
Radius							
BP	40	0.829	0.687	8.00	0.102	2.023	−2.870
DP	40	0.687	0.472	10.21	0.132	1.039	0.720
BD	39	0.836	0.699	7.82	0.101	2.274	−4.360
DD	39	0.555	0.308	11.89	0.153	1.327	−0.229
GL	40	0.738	0.545	9.66	0.123	2.144	−7.938
Ulna							
LO	40	0.762	0.581	9.79	0.118	1.954	−3.798
DPA	40	0.737	0.544	10.24	0.123	2.043	−3.615
BPC	40	0.806	0.65	8.45	0.108	1.849	−2.271
GL	39	0.725	0.526	9.34	0.127	2.012	−7.562
Femur							
Hbr	40	0.806	0.640	8.39	0.108	2.504	−4.527
Hdp	40	0.815	0.664	8.36	0.106	2.537	−4.640
BP	40	0.795	0.633	9.17	0.110	1.807	−3.530
BD	38	0.783	0.613	9.07	0.116	2.267	−4.951
DD	39	0.611	0.373	11.87	0.146	1.813	−3.416
GL	40	0.976	0.625	8.20	0.110	2.597	−10.635
Tibia							
BP	39	0.818	0.670	7.37	0.105	2.020	−4.187
DP	40	0.774	0.599	8.21	0.115	1.851	−3.679
BD	40	0.703	0.494	9.85	0.129	1.897	−2.844
DD	40	0.673	0.453	9.53	0.135	1.201	−0.127
GL	40	0.808	0.654	8.43	0.107	2.321	−9.173

Dimensions are from Von den Driesch (1976). All data natural log transformed.

in weight bearing, unlike the skull. This may not necessarily always be the case (Elliot *et al.*, 2015) and is clearly worth investigating in future studies, particularly with larger numbers of comparative specimens, as sample sizes can have a significant effect on the strength of such correlations (Elliot *et al.*, 2015).

The wolf cranio-mandibular data followed a similar pattern as the dogs when the juveniles were excluded from analyses. Removal of the juvenile wolves again weakened all cranio-mandibular correlations, with correlation coefficients falling below 0.5, but percent prediction errors dropped slightly, with all having values just above 10% (Table 7). The wolf limb regressions with juveniles removed appear to consistently outperform these formulae, as many have prediction errors of less than 10% and correlation coefficients above 0.8 (Table 4). To us, this indicates that limb regression formulae should be used when possible with the wolves, and the cranio-mandibular formulae employed only when limb elements are unavailable.

Discussion

It is important to recognize that body mass is an abstraction and not a permanent or fixed quality of an individual. For example, even a fully adult canid's body mass will vary over relatively short periods in relation to factors such as its health status and diet. Such short-term changes are unlikely to immediately manifest in the skeleton, which would almost certainly remodel at a slower rate than (lag-behind) the body's soft tissues. Little is known about the specifics of bone remodelling rates and processes in canids, and it remains unclear which element dimensions might be most sensitive to such short-term changes in body mass. Further, the body masses of the canids in this study were obtained immediately following their deaths, and this is the case with nearly all specimens in museum collections. The exact causes of death are mostly unknown for these specimens, but how the dogs and wolves died also could have introduced some

Table 4. Statistics for linear regression equations for wolf limb dimensions and body mass, adult individuals only

Dimension	No. of cases	*R*	R^2	%PE	SEE	Coefficent	Constant
Scapula							
LG	33	0.838	0.701	7.52	0.097	2.118	−4.174
BG	33	0.805	0.648	8.38	0.105	2.224	−3.453
SLC	33	0.718	0.515	9.66	0.124	1.620	−2.067
HS	33	0.757	0.573	8.88	0.116	2.426	−8.914
Humerus							
BP	33	0.808	0.653	7.54	0.104	2.062	−4.049
DP	33	0.812	0.659	7.32	0.104	2.263	−5.459
BD	33	0.819	0.670	7.77	0.102	1.781	−3.094
BT	33	0.760	0.578	9.20	0.115	1.871	−2.982
GL	31	0.789	0.622	8.94	0.111	2.303	−8.818
Radius							
BP	33	0.832	0.692	7.25	0.098	1.943	−2.601
DP	33	0.748	0.559	9.08	0.118	1.078	0.639
BD	33	0.840	0.706	7.26	0.096	2.269	−4.333
DD	33	0.685	0.469	9.68	0.129	1.603	−1.015
GL	33	0.743	0.553	9.07	0.119	2.035	−7.323
Ulna							
LO	33	0.791	0.626	8.80	0.108	1.884	−3.502
DPA	33	0.760	0.578	9.60	0.115	2.005	−3.455
BPC	33	0.788	0.620	8.44	0.109	1.795	−2.082
GL	32	0.725	0.526	8.98	0.124	1.863	−6.701
Femur							
Hbr	33	0.811	0.657	8.01	0.104	2.377	−4.090
Hdp	33	0.789	0.622	8.66	0.109	2.381	−4.115
BP	33	0.812	0.659	8.64	0.104	1.744	−3.263
BD	31	0.749	0.561	9.50	0.121	2.113	−4.349
DD	32	0.633	0.401	11.02	0.140	1.747	−3.128
GL	33	0.812	0.660	7.61	0.103	2.522	−10.203
Tibia							
BP	33	0.817	0.667	6.89	0.102	1.915	−3.765
DP	33	0.842	0.709	7.49	0.096	1.899	−3.843
BD	33	0.756	0.572	8.64	0.116	1.852	−2.700
DD	33	0.816	0.666	6.74	0.103	1.451	−0.883
GL	33	0.842	0.710	7.51	0.096	2.331	−9.213

Dimensions are from Von den Driesch (1976). All data natural log transformed.

variability in our data and potentially weakened the correlations that were documented. For instance, a healthy canid that died from acute trauma such as poisoning perhaps would have a body mass measurement relatively close to its average adult mass. On the other hand, an individual that perished from a long-term disease such as some forms of cancer might experience significant loss of body mass prior to our

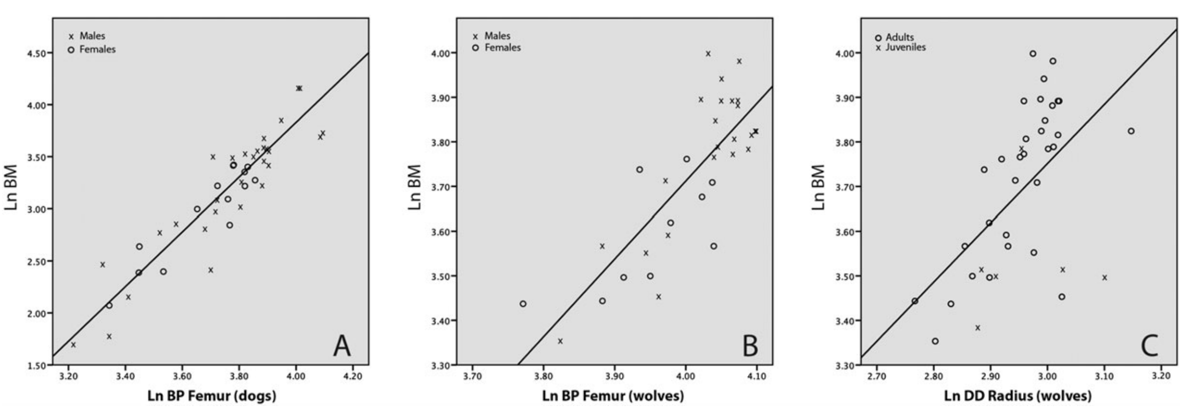

Figure 2. (a) Relationship between natural log of dog body mass and natural log femur BP (breadth of the proximal end), with male and female specimens indicated. Juvenile specimens excluded. (b) Relationship between natural log of wolf body mass and femur BP, with male and female specimens indicated. Juvenile specimens excluded. (c) Relationship between natural log of wolf body mass and radius DD (depth of the distal end), with adults and juveniles indicated.

Table 5. Body mass estimation for Middle Holocene dog skeletons from the Lake Baikal region of Siberia, Russian Federation

Site/ Specimen	Specimen no.	Age	Scapula simension	Body mass estimate (kg)	Humerus dimension	Body mass estimate (kg)	Radius dimension	Body mass estimate (kg)	Ulna dimension	Body mass estimate (kg)	Femur dimension	Body mass estimate (kg)	Tibia dimension	Body mass estimate (kg)	Limb estimate range (kg)	Body mass estimate (kg) from cranial length
Ust'-Belaia Dog 2	2010-018	Juvenile	BG	16.4	BD	15.6	BD	17.2	**DPA**	**15.5**	DD	18.2	—	—	15.6–18.2	18.3
Ust'-Belaia Dog 4	2010-020	Adult	BG	14.2	DP	13.3	BD	14.0	DPA	11.8	**BP**	**13.2**	BD	13.2	11.8–14.2	12.5
Pad Kalashnikova Pit 1 Dog	2010-024	Juvenile	BG	13.0	BD	12.7	BD	12.5	**DPA**	**11.8**	—	—	BD	11.5	11.5–13.0	13.3
Pad Kalashnikova Pit 2 Dog	2010-026	Adult	BG	18.5	DP	17.9	BD	15.8	DPA	16.2	**BP**	**17.9**	BD	16.0	16.0–18.5	19.1
Shamanka Dog	E2008.175	Adult	—	—	GL	27.6	GL	28.6	GL	28.5	**GL**	**29.6**	GL	27.6	27.6–29.6	29.4

Bolded dimensions are those with the lowest percent prediction error for that element. The body mass estimates based on cranial length (cranial length 2 in Von den Driesch, 1976) are from Losey *et al.* (2014). Specimen descriptions can be found in Losey *et al.* (2013). Adult only regression formulae were used for the adults, and adult-juvenile regression formulae were employed in the juvenile body mass estimates.

Table 6. Statistics for linear regression equations for dog cranio-mandibular dimensions and body mass, adult individuals only

Dimension	No. of cases	*R*	R^2	%PE	SEE	Coefficent	Constant
VDD Cranial 1	30	0.942	0.888	13.88	0.173	3.260	−14.205
VDD Cranial 2	30	0.952	0.906	13.16	0.158	3.211	−13.742
VDD Cranial 3	28	0.957	0.915	12.60	0.154	3.212	−13.546
VDD Cranial 7	30	0.940	0.884	14.07	0.176	3.429	−12.602
VDD Mandible 1	28	0.962	0.923	11.11	0.144	3.219	−13.031
VDD Mandible 2	28	0.970	0.939	9.69	0.128	3.203	−12.935
VDD Mandible 3	28	0.966	0.934	10.50	0.136	3.216	−12.849
VDD Mandible 4	28	0.957	0.915	12.09	0.154	3.116	−12.067
VDD Mandible 5	28	0.963	0.927	10.98	0.143	3.129	−11.960
VDD Mandible 6	28	0.958	0.917	11.44	0.152	3.169	−12.323

Dimensions are from Von den Driesch (1976). Specimens described in Losey *et al.* (2014).

data being collected. In other words, body mass estimations should always be used cautiously.

With these caveats in mind, our results reveal that a number of limb dimensions can in fact be used to reasonably predict body mass in dogs and wolves, many with margins of error of less than 20% and correlation coefficients higher than 0.850. The canids' articular end dimensions typically provided better predictions of body mass than element lengths, a finding consistent with some previous studies on other mammals (Ruff *et al.*, 1991; Egi, 2001; Auerbach & Ruff, 2004; Anyonge & Roman, 2006; but refer to Puputti & Niskanen, 2008). Correspondingly, our recommendation is to avoid using the regression formulae for element lengths when possible and instead employ those for articular end dimensions, choosing those equations with the highest correlation coefficients and lowest % PE values.

Our second recommendation is to use adult-only regression equations when analysing fully fused archaeological specimens (Tables 2 and 4). Excluding the juveniles in both the wolf and dog groups improved results in many cases, indicating that some of these specimens' limb dimensions deviated from the overall trends. The lack of much change in some of the correlation coefficients after the removal of the juveniles was likely because of the fact that very few such specimens were present. A larger dataset of juveniles may have produced even more distinct patterned differences between adults and juveniles. When correlations did strengthen following the removal of the juveniles, they did not do so equally across all element dimensions. This is likely because of the fact that epiphyses form, grow, and fuse at different times and rates as an animal matures (Humphrey, 1998; Ruff, 2007b; Von Pfeil & DeCamp, 2009). In other words, consistently slower forming epiphyses will better track animal body mass during the process of maturation. More rapidly growing elements, such as the distal radius epiphyses of the dogs and wolves, appear to initially grow at a relatively fast rate, at least in some animals, nearly reaching adult size while the individual is still a juvenile and still below its adult body mass. Figure 2c plots the depth of the distal radius by body mass for the wolves, with the juvenile and adult specimens indicated. Note that most of the juveniles fall below the regression line, and several plot far to the right—they are longer than most other for their respective body masses.

Table 7. Statistics for linear regression equations for wolf cranio-mandibular dimensions and body mass, adult individuals only

Dimension	# cases	R	R2	%PE	SEE	Coefficent	Constant
VDD Cranial 1	89	0.666	0.444	10.62	0.138	2.286	−9.025
VDD Cranial 2	80	0.678	0.460	10.65	0.138	2.512	−10.088
VDD Cranial 3	59	0.555	0.308	11.32	0.141	2.129	−7.890
VDD Cranila 7	88	0.696	0.484	10.71	0.131	2.106	−6.412
VDD Mandible 1	84	0.576	0.332	11.68	0.148	1.936	−6.471
VDD Mandible 2	83	0.544	0.296	11.97	0.152	1.828	−5.920
VDD Mandible 3	84	0.558	0.312	12.02	0.150	1.982	−6.632
VDD Mandible 4	87	0.575	0.331	11.61	0.148	1.934	−6.193
VDD Mandible 5	87	0.571	0.326	11.72	0.149	2.047	−6.672
VDD Mandible 6	86	0.555	0.308	11.50	0.151	1.909	−6.099

Dimensions are from Von den Driesch (1976). Specimens described in Losey *et al.* (2014).

When analysing a limb element with unfused or fusing epiphyses, we suggest using the regression formulae in which juveniles specimens are included. While these formulae will often result in estimates with larger average prediction errors, this level of uncertainty is necessary and more likely to encompass the true body mass of the animal. The use of these formulae is particularly warranted when analysing juvenile dog and wolf radii because of their sometimes distinct pattern of formation and growth. A far better solution to the issues of estimating body mass in juvenile dogs and wolves would be to develop regression formulae based solely on juvenile specimens of specifically known ages, but such specimens are very rare in most skeletal collections. Further, it is worth noting that body size itself appears to affect maturation rate and skeletal element fusion, with larger body-size breeds maturing more slowly than smaller breeds (Von Pfeil & DeCamp, 2009; Helmsmüller *et al.*, 2013). This suggests that the most accurate regression formulae for juveniles in future studies will be produced when analysing subsets of dogs of a limited range of body sizes.

Overall for the dogs, the breadth of glenoid of the scapula, depth of the proximal humerus, breadth of the distal (BD) radius, depth of the process anconaeus of the ulna, breadth of the proximal femur, and BD tibia had the strongest correlations with body mass for those particular elements (Figure 1; Tables 1 and 2). However, for each of these elements, other end dimensions also produced nearly as strong correlations and could alternatively be used if the best-performing dimension cannot be taken. The wolf elements displayed somewhat different patterns, in which element dimensions produced the strongest correlations: the length of the glenoid of the scapula, BD humerus, BD radius, length of the olecranon of the ulna, GL of the proximal femur, and GL of the tibia (Figure 1; Tables 3 and 4). Again, all wolf elements also had other dimensions with relatively strong correlations with body mass, providing useful alternatives.

Our choice to include both male dogs and female dogs in both sets of regression analyses was primarily because of the desire for larger sample sizes. Most archaeologists will encounter isolated canid remains and not complete skeletons, and presently, there is no reliable means for assessing sex in isolated limb bones, with the exception of the humerus (Ruscillo, 2006). In other words, non-sex specific regression equations are needed because we lack the ability to sex most limb elements. A further complication is that at least some of the dogs in our sample were almost certainly neutered (many were pets), and it is unknown what effects this might have on growth patterns and rates, and how any such changes might affect our correlations. Prehistoric neutering of males is also a possibility, but again cannot be identified with current methods. Until such methodological issues are resolved, non-sex specific body mass estimation methods will remain the norm, especially when dealing with isolated elements.

Finally, reassessment of the body masses of the Siberian archaeological dogs demonstrated that the newly developed limb dimension formulae produce estimates that correspond well (on average <8% difference) with those previously generated by cranial dimension formulae (Table 5). These five dogs, all associated with closely interacting hunter-gatherers groups dating to the Early Neolithic period (Middle Holocene) of the Lake Baikal region (Losey *et al.*, 2013), show a fairly wide range of body masses, even among the adult specimens, which appear to have weighed between ~12 and 30 kg at death. Interpreting the variation seen in Baikal dogs perhaps will only be possible when comparative data are generated for other prehistoric dog populations, and when our ability to accurately age and sex dog skeletons increases. At present, the significance of these dogs' body mass variation is unknown, but it could suggest that some range of dog types were present, and in turn that dogs of various sizes were engaging with their human counterparts here in numerous different ways.

Conclusion

This study has generated a number of useful regression formulae for estimating dog and North American wolf body masses from post-cranial remains. In some cases limb dimensions appear to out perform skull dimensions in predicting body mass, at least when tested against our samples. Some skull dimensions, particularly for the dogs, still appear to produce relatively accurate predictions of body mass and should not necessarily be abandoned in favour of the limb regression formulae produced in this study.

While we believe that these results constitute significant improvements in methodology, there remains room for improvement in several areas. First, increasing sample sizes of both dogs and wolves with known body masses is clearly needed. This will require skeletonization of animals, as most museum collections consist of largely of canid skulls and limited post-cranial skeletons, and relatively few of these have known body masses. A larger sample would allow some specimens to be excluded from the initial analyses and then used as independent data to evaluate the predictive strength of the resulting regression equations.

Second, if highly accurate body mass estimates are needed, it may prove useful to develop specific regressions for juvenile specimens, as has been performed for humans (Ruff, 2007b; Robbins *et al.*, 2010). Third, more accurate estimations might also be possible if one were to work with dogs of a limited size range, perhaps by working with a single breed. This would be particularly useful when the modern dogs available for analysis can be shown to very closely related (and within the same size range) to local archaeological populations. Such analyses may in fact be possible in places such as the North American Arctic, where some extant indigenous dog breeds have been shown to be directly descendant from earlier Thule dogs from the same general region (van Asch *et al.*, 2013; Brown *et al.*, 2015). Finally, while caliper measurement are very pragmatic, they clearly are not the most accurate means of assessing limb end surface areas, which presumably are highly correlated with body mass. Using digital models of limbs to calculate their end surface areas should allow for highly precise measurements, hopefully resulting in stronger predictive formulae for body mass in canids. Geometric morphometric approaches to calculating these surface areas should provide far better approximation of element portion sizes than possible through using linear measurements alone.

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References

Anyonge W, Roman C. 2006. New body mass estimates for Canis dirus, the extinct Pleistocene dire wolf. *Journal of Vertebrate Paleontology* **26**: 209–212.

Auerbach BM, Ruff CB. 2004. Human body mass estimation: a comparison of "morphometric" and "mechanical" methods. *American Journal of Physical Anthropology* **125**: 331–342.

Brown SK, Darwent CM, Wictum EJ, Sacks BN. 2015. Using multiple markers to elucidate the ancient, historical and modern relationships among North American Arctic dog breeds. *Heredity*. DOI:10.1038/hdy.2015.49.

Egi N. 2001. Body mass estimates in extinct mammals from limb bone dimensions: The case of North American hyaenodontids. *Palaeontology* **44**: 497–528.

Elliot M, Kurki H, Weston DA, Collard M. 2015. Estimating body mass from skeletal material: New predictive equations and methodological insights from analyses of a known-mass sample of humans. *Archaeological and Anthropological Sciences*. DOI:10.1007/s12520-015-0252-5.

Helmsmüller D, Wefstaedt P, Nolte I, Schilling N. 2013. Ontogenetic allometry of the beagle. *BMC Veterinary Research* **9**: 203.

Humphrey LT. 1998. Growth patterns in the modern human skeleton. *American Journal of Physical Anthropology* **105**: 57–72.

Legendre S, Roth C. 1988. Correlation of carnassial tooth size and body weight in recent carnivores (Mammalia). *Historical Biology* **1**: 85–98.

Lieberman DE, Devlin MJ, Pearson OM. 2001. Articular area responses to mechanical loading: Effects of exercise, age, and skeletal location. *American Journal of Physical Anthropology* **116**: 266–277.

Losey RJ, Garvie-Lok S, Leonard JA, Katzenberg MA, Germonpre M, Nomokonova T, Sablin MV, Goriunova OI, Berdnikova NE, Savel'ev NA. 2013. Burying bogs in Ancient Cis-Baikal, Siberia: Temporal trends and relationships with human diet and subsistence practices. *PLoS One* **8**(5): e63740.

Losey RJ, Osipov B, Sivakumaran R, Nomokonova T, Kovychev EV, Diatchina NG. 2014. Estimating body mass in dogs and wolves using cranial and mandibular dimensions: Application to Siberian canids. *International Journal of Osteoarchaeology*. DOI:10.1002/oa.2386.

Manning K, Timpson A, Shennan S, Crema E. 2015. Size reduction in early European domestic cattle relates to intensification of Neolithic herding strategies. *PLoS One* **10**(12e0141873). DOI:10.1371/journal.pone.0141873.

National Research Council. 2006. Nutritional Requirements of Dogs and Cats. National Academies Press: Washington D.C.

Palmqvist P, Arribas A, Martinez-Navarro B. 1999. Ecomorphological study of large canids from the lower Pleistocene of southeastern Spain. *Lethaia* **32**: 75–88.

Podberscek AL. 2009. Good to pet and eat: The keeping and consuming of dogs and cats in South Korea. *Journal of Social Issues* **65**: 615–632.

Puputti A, Niskanen M. 2008. The estimation of body weight of the reindeer (Rangifer tarandus L.) from skeletal measurements: Preliminary analyses and application to archaeological material from 17th- and 18th-century northern Finland. *Environmental Archaeology* **13**(2): 153–164.

Robbins G, Sciulli PW, Blatt SH. 2010. Estimating body mass in subadult human skeletons. *American Journal of Physical Anthropology* **143**: 146–150.

Ruff CB. 1988. Hindlimb articular surface allometry in Hominoidea and Macaca, with comparisons to diaphyseal scaling. *Journal of Human Evolution* **17**: 687–714.

Ruff CB. 2007a. Biomechanical analyses of archaeological human skeletons. Biological Anthropology of the Human Skeleton, MA Katzenberg, SR Saunders (eds.), 2nd edn. Wiley-Liss Inc.: Hoboken; 183–206.

Ruff C. 2007b. Body size prediction from juvenile skeletal remains. *American Journal of Physical Anthropology* **133**: 698–716.

Ruff CB, Scott WW, Liu AYC. 1991. Articular and diaphyseal remodeling of the proximal femur with changes in body mass in adults. *American Journal of Physical Anthropology* **86**: 397–413.

Ruscillo D. 2006. The table test: A simple technique for sexing canid humerii. Recent Advances in Ageing and Sexing Animal Bones, D Ruscillo (ed.). Oxbow Books: Oxford, United Kingdom; 62–67.

Schwartz M. 1997. A History of Dogs in the Early Americas. Yale University Press: Ann Arbor, MI.

Trinkaus E, Churchill SE, Ruff CB. 1994. Postcranial robusticity in Homo, II: Humeral bilateral asymmetry and bone plasticity. *American Journal of Physical Anthropology* **93**: 1–34.

Van Asch B, Zhang AB, Oskarsson MC, Klütsch CF, Amorim A, Savolainen P. 2013. Pre-Columbian origins of Native American dog breeds, with only limited replacement by European dogs, confirmed by mtDNA analysis. *Proceedings of the Royal Society B* **280** 20131142.

Van Valkenburgh B. 1990. Skeletal and dental predictors of body mass in carnivores. Body Size in Mammalian Paleobiology, J Damuth, BJ MacFadden (eds.). Cambridge University Press: Cambridge; 181–205.

Von den Driesch A. 1976. A Guide to the Measurement of Animal Bones from Archaeological Sites. Harvard University Press: Cambridge, MA.

Von Pfeil DJF, DeCamp CE. 2009. The epiphyseal plate: Physiology, anatomy, and trauma. *Compendium: Continuing Education for Veterinarians* **31**: e1–11.

Wing ES. 1978. Use of dogs for food: An adaptation to the coastal environment. Prehistoric Coastal Adaptations, BL Stark, B Voorhies (eds.). Academic Press: New York; 29–35.

Yapuncich GS, Gladman JT, Boyer DM. 2015. Predicting Euarchontan body mass: A comparison of tarsal and dental variables. *American Journal of Physical Anthropology* **157**: 472–506.

Supporting information

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Table S1: Dog specimens analysed in this study. CMN, Canadian Museum of Nature; RMBC, Royal Museum of British Columbia; SI-NMNH, Smithsonian Institution National Museum of Natural History; UFM, University of Florida Museum; CAS, California Academy of Science; UA Anthro, University of Alberta Department of Anthropology.

Table S2: Wolf specimens analysed in this study. RAM, Royal Alberta Museum; RMBC, Royal Museum of British Columbia; CAS, California Academy of Sciences; UAMF, University of Alaska Museum Fairbanks.