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Estimating Body Mass in Dogs and Wolves Using Cranial and Mandibular Dimensions: Application to Siberian Canids

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ABSTRACT Previously developed regression formulae for estimating body mass in dogs and wolves based on cranial and mandibular dimensions are evaluated using modern canid specimens of known weight at death. Some of these equations proved reliable, but others have large standard errors of estimate and likely produce unreliable mass estimates. New sets of equations for estimating body mass in dogs and wolves are produced using our datasets, including a set of equations developed from combining the dog and wolf biometric data into a single population. The resulting regression equations allow body mass to be estimated from a series of cranial and mandibular dimensions with relatively low errors. Further, our datasets include larger numbers of specimens of larger ranges of body mass than in these previous studies. When the equations are applied to a suite of dogs and one wolf from Eastern Siberia, several patterns emerge. First, hunter–gatherers' dogs in this region vary widely in terms of body size, even within a limited geographic area and time period. Some were quite large, similar in size to modern Siberian huskies. Second, pastoralists' dogs are less variable in terms of body mass, but this may reflect the nature of our samples. In particular, pastoralists' dogs nearly all were sacrificed juvenile dogs, some of which appear to have been eaten. These dogs seem to have been approached adult body size when they were selected for sacrifice. Finally, our findings help to highlight the need for further refinement in methods used to study ancient canid remains. Copyright © 2013 John Wiley & Sons, Ltd.

Key words: dogs; wolves; body mass; canids; Siberia; Russia; domestication

Introduction

Archaeologists are asking increasingly complex questions about interactions between humans and domesticated animals. Such questions focus not just on the origins and dispersals of domesticates, but also on the various ways humans affected the life courses of their cohabitant species, and how these animals shaped human lives and societies. To address such questions, new and refined methodologies are being developed, many of which are designed to better document an animal's life history and basic physical characteristics. These approaches to the study of animal remains are borrowed in part from human osteology, which as a discipline has a suite of increasingly refined methods at its disposal. Such methods can generate details on a human's body size and form, diet, history of disease and trauma, and repetitive activities, and many of these methods have been in development for decades. Arguably, however, relatively few zooarchaeologists employ these types of methods when studying faunal remains, and for some species of interest, including dogs and wolves, life history methods remain underdeveloped and based on very small comparative datasets.

Our primary interests involve reconstructing the life histories and roles of dogs in past societies. Dogs were first domesticated among mobile hunter–gatherers in the Pleistocene (Morey, 2010) and subsequently have spread with humans to every continent. Further, these diverse and adaptive animals presently are integrated into societies in a wide variety of ways, ranging from being human food items to close co-workers. Generally speaking, this means that the range of relationships, societies, and environments dogs have participated in likely has been far broader than that of any other domesticated animal. Dogs' life histories then clearly

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are a rich area for archaeological investigation, and this can be undertaken with a variety of evidence, including that obtained through study of their skeletal remains.

One of the basic data points needed to interpret an animal's life history, including that of ancient canids, is an estimation of its body size or mass (Damuth & MacFadden, 1990). Such estimates can be used to better understand an individual's general appearance, metabolic needs, capacity for tasks such as burden carrying or load pulling, food yield, and even bite strength (c.f., Ellis *et al.*, 2008). Further, when such data is compiled for multiple specimens, population-level questions can be addressed, such as variability in body size within a region or site. In turn, these inferences can help provide insight on human activities related to such animals, including selective breeding practices, provisioning strategies, and human–animal co-participation in daily tasks such as hunting or transporting loads. Having reliable estimates of body mass for ancient dog remains would clearly help strengthen any such inferences.

For archaeological dog remains, the most commonly used approaches to reconstructing body size have focused on shoulder height (Harcourt, 1974; Von den Driesh & Boessneck, 1974) and body mass. While canid shoulder height estimates are useful for various purposes, the focus of this paper is body mass estimation. To our knowledge, archaeologists have relied exclusively on two sets of regression equations for estimating dog body mass. The first are those from Wing's (1978) study, which was based on only eight dogs ranging in mass from 5.4 to 25.9 kg. The second, by Van Valkenburgh (1990), is a more generalized approach designed for estimating body size across a suite of carnivores, with a dataset that included one male and one female individual from 72 different species, but no dogs and only two wolves. Wing's studies provide equations for mandibular body height, mandibular premolar row length, and mandibular molar row length, while Van Valkenburgh's equations are for cranial length, occipital-to-orbit length, and the length of the mandibular first molar. Neither study produced a means of estimating body mass from dog cranial dimensions actually using metric data from dogs.

Limb bone dimensions, particularly those of long bone cross sections and articular surfaces, are often considered more reliable predictors of body mass in mammals than cranial dimensions (Andersson, 2004; Christiansen, 1999a; Christiansen, 1999b; Christiansen, 2002; Damuth & MacFadden, 1990; Egi, 2001; Ruff, 1989), as these elements' dimensions are influenced by their role in weight bearing. Nonetheless, there remains a clear need for reliable canid body mass estimations based on cranial and mandibular dimensions because most efforts to morphologically identify archaeological and fossil canid remains focus exclusively on these elements (but see Pionnier-Capitan *et al.*, 2011). Further, many ancient canid remains consist only of crania or mandibles, which are relatively robust and commonly survive post-depositional fragmentation.

Correspondingly, this paper focuses on estimating body mass for dogs and wolves based on cranial and mandibular dimensions. To begin, we evaluate some of the established methods for estimating canid body mass introduced above using biometric data on multiple modern dog and North American wolf skeletons of known body mass at death. Second, we utilize our dataset to develop a series of new regression equations for estimating dog and wolf body masses. These equations are based on a far larger dataset of canids than used in previous studies, and on canids of a wider range of body sizes, both of which should increase the reliability of the resulting body mass estimates. The formulae developed in this paper then are used to explore the body masses of a set of archaeological canid remains from Eastern Siberia. The resulting data allow for a better understanding of the characteristics and potential of the dogs present in this region in the Holocene, including dogs that were living with both hunter–gatherers and pastoralists.

Materials

Modern canid materials and data collection

The modern dog skeletal collections used in this study consist of 36 individuals, including 22 Inuit sled dog specimens from Ellesmere Island, Nunavut, Canada; one house dog from Edmonton, Canada; three unspecified dogs from British Columbia, Canada; and eight mixed-breed dogs from an animal shelter in Florida, U.S.A. Seven of the eight Florida dogs were the same specimens used by Wing (1978); the eighth specimen used by Wing could not be relocated. Overall, the sample consists of 24 males, 11 females, and one individual of unknown sex. Within this sample were 30 adults, three juveniles and three newborns. The body masses of these specimens ranged from 1.9 to 49.0 kg.

The modern wolf skeletal collection includes: 108 specimens, all wild free-roaming individuals from Canada, including 34 from the Northwest Territories, 28 from Vancouver Island, British Columbia, 22 from Alberta, 17 from Nunavut, three from Ontario, and one each from the Yukon, Saskatchewan, Quebec and mainland British Columbia. Within the sample were

61 males, 46 females, and 1 individual of unknown sex; 91 individuals were adults and 17 were juveniles. The body masses of these specimens ranged from 9.2 to 50.8 kg. Note that for the Vancouver Island wolves, there is genetic evidence for some recent interbreeding with dogs (Muñoz-Fuentes *et al.*, 2010).

Some cautionary notes regarding the use of the wolf data and formulae are warranted. Our wolf specimens are from across much of Canada, including from three broad regions of the country that are home to different subspecies of wolves, which show some morphological differentiation (Nowak, 1985). While this suggests that the specimens in our sample likely present a considerable amount of morphological variability, it is unclear if this range of variability encompasses that seen in wolves from other regions, including more southerly portions of North America and Eurasia. In other words, the formulae based on this data are most accurate for wolves deriving from northern North America, and their accuracy for wolves from outside this region is unknown. Analysis of wolves from outside Canada is planned for a future study.

The cranial and mandibular dimensions (Figure 1) utilized in the study originally were collected for use in multivariate analyses, primarily for the purpose of identifying archaeological canid specimens of unknown taxonomy (see Losey *et al.*, 2011, 2013). The measurements included multiple dimensions described by Von den Driesch (1976; hereafter VDD, with VDDc indicating cranial measurements and VDDm indicating mandibular measurements) for canids, including 16 cranial measurements (numbers 1, 2, 3, 7–9, 13a, 15–18, 20 (length and breadth), 29, 30, 34, 35) and 19 on the mandible (numbers 1–14, 17–20; measurement 13 included length and breadth). Three additional cranial dimensions were collected, all from Morey (1992: 187; P3, OI, and IM2). All dimensions were taken using sliding calipers, with the exception of cranial lengths (VDDc1-3), which often required the use of a spreading caliper. All biometric data for the dogs and wolves were subsequently analysed using SPSS version 14 (IBM Corp., 2006).

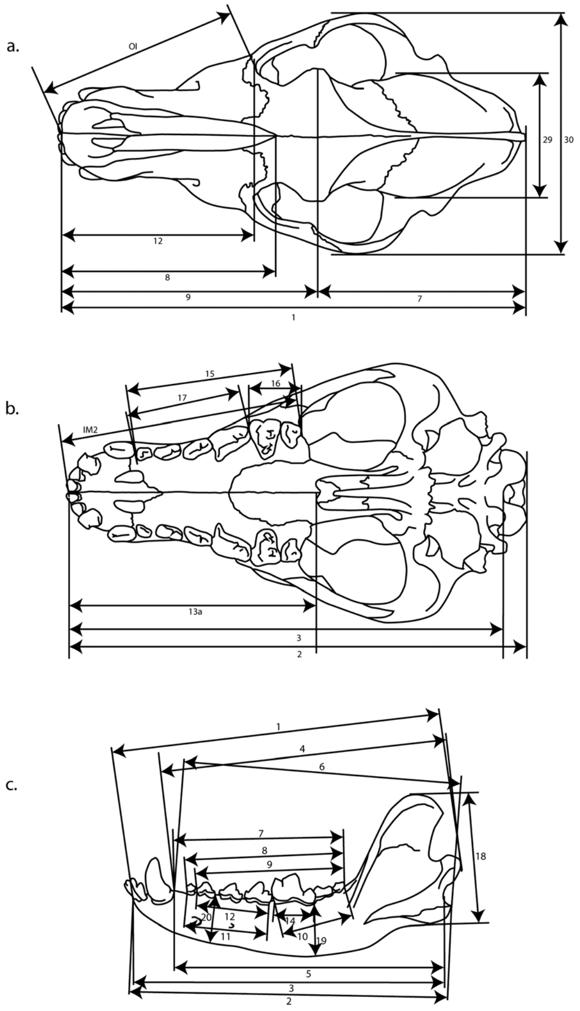

Figure 1. Canid cranial and mandibular dimensions taken in the study. Illustrations modified from Von den Driesch (1976) and Morey (1992); both citations provide written descriptions of the dimensions. Note that measurements taken on the teeth are not shown in these figures (Von den Driesch's cranial measurements 18 and 20 and mandibular measurement 13, and Morey's P3; Von den Driesch's mandibular measurement 17 also not shown. a) Dorsal view of cranium; b) ventral view of cranium; c) lateral view of mandible.

Eastern Siberia archaeological canids

The archaeological canids examined come from two regions of Eastern Siberia, namely Cis-Baikal and Eastern Trans-Baikal (Figure 2). All of these canid remains have been directly AMS radiocarbon dated (Table 1); all were calibrated using OxCal (v4.1) and the INTCAL09 dataset (Reimer *et al.*, 2009). Ageing of the specimens was done through study of dental eruption patterns and epiphysis fusion (Cahill & Marks, 1982; Evans & Christensen, 1979; Kremenak, 1967; Morgan & Miyabayashi, 1991; Shebestari *et al.*, 1967; Watson *et al.*, 1986). The presence of bacula was used to identify a few canids as males; otherwise, no sexing was attempted. The Cis-Baikal canids have been previously described (Losey *et al.*, 2011, 2013). These include a probable dog dating to the late Pleistocene, and one wolf and 10 dogs dating to the Siberian Neolithic and Early Bronze periods, all associated with hunter–gatherers. Several of these dogs were intentionally buried within cemeteries otherwise used for human burials. The two dogs dating to the Late Bronze and Late Iron ages appear to have been associated with pastoralists,

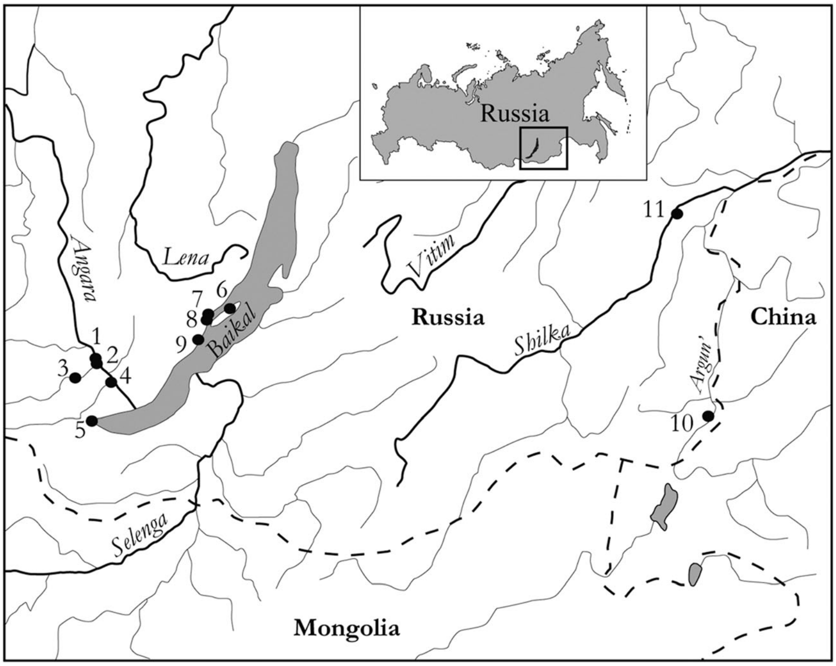

Figure 2. Map of Southeastern Siberia, with location of sites with canid remains analysed here indicated. 1. Pad' Kalashnikova, 2. Ust'-Belaia, 3. Ust'-Khaita, 4. Lokomotiv. 5. Shamanka II, 6. Todakta I, 7. Uliarba II, 8. Ulan-Khada, 9. Bugul'deika II, 10. Bol'shaia Kanga I, 11. Proezzhaia I.

as the layers or features where their remains were found also contained skeletal elements from cattle, horse, or sheep/goat. The Bronze Age Bugul'deika II dog is represented by a single mandible found within a habitation site deposit, while the Late Iron Age Todakta I dog is a complete skeleton from a sacrificed dog found within a human cemetery. All the canids were adults at the time of death, with three exceptions. First, the Late Pleistocene

Table 1. Archaeological wolf and dog specimens from Cis-Baikal and Eastern Transbaikal

Site	Specimen	Context	C14 lab number	Uncalibrated age BP	Calibrated age BP(1 sigma)	Culture history period
Cis-Baikal canids						
Lokomotiv	Wolf	Primary burial	GIN8841a	7230 ± 40	8150 to 7980	Late Mesolithic/
			TO11558	7320 ± 70	8185 to 8030	Early Neolithic
Ust'-Khaita	Probable dog	Non-burial	Ox23873	10375 ± 45	12380 to 12135	Early Mesolithic
Ust'-Belaia	Dog 1	Primary burial	Ox23874	5981 ± 34	6880 to 6755	Early/Middle Neolithic
	Dog 2	Non-burial	Ox23875	6213 ± 33	7175 to 7020	Early Neolithic
	Dog 4	Unknown	Ox23876	5946 ± 32	6845 to 6730	Early/Middle Neolithic
Pad' Kalashnikova	Dog 1	Primary burial	Ox23910	6122 ± 31	7150 to 6945	Early Neolithic
	Dog 2	Primary burial	Ox23911	6075 ± 32	6980 to 6890	Early Neolithic
Shamanka II	Dog 1	Primary burial	Ox20561	6430 ± 35	7420 to 7325	Early Neolithic
Ulan-Khada	Layer 1 dog 1	Non-burial	Ox23881	3995 ± 29	4515 to 4425	Early Bronze Age
Uliarba II	Dog 1	Secondary burial	Ox23879	3858 ± 29	4405 to 4185	Early Bronze Age
			Ox23880	3833 ± 28	4290 to 4155	
Bugul'dieka II	Dog 1	Non-burial	Ox23878	3002 ± 29	3260 to 3085	Late Bronze Age
Todakta I	Dog 1	Sacrifice	Ox23912	1062 ± 23	980 to 935	Late Iron Age
Eastern Transbaikal canids						
Bolshaia Kanga	Dog 1	Non-burial	Beta350520	6970 ± 30	7845 to 7750	Early Neolithic
	Dog 2	Non-burial	Beta350521	6670 ± 30	7580 to 7510	Early Neolithic
Proezzhaia I	Dwelling 28 dog 1	Sacrifice	Ua44177	1077 ± 30	1050 to 935	Late Iron Age
	Dwelling 32 dog 1	Sacrifice	Ua44179	1038 ± 30	965 to 930	Late Iron Age
	Dwelling 32 dog 2	Sacrifice	Ua44180	993 ± 30	955 to 805	Late Iron Age

probable dog, from the Ust′-Khaita site, is estimated to have been 5–8 months old at death, the Pad′ Kalashnikova dog #1 9–11 months old at death, and the Todakta I dog 4–5 months old at death.

The Trans-Baikal specimens are first reported here. The Bol′shaia Kanga site is located on the Argun′ River a few hundred meters from Russia–China border (Kirillov *et al.*, 2000, 2011), and all dog remains from this site appear to have been associated with hunter–gatherers. The specimens include remains of three adult dogs, each represented by a few elements only, and all of which were recovered from habitation site sediments in association with other fragmented faunal remains; only two are reported here, as the third was too fragmentary to permit body mass estimation. No other remains of domesticated fauna were present here, and none of the dog remains show cut marks or charring. All three specimens date to the Early Neolithic period. The Proezzhaia I specimens all are remains of dogs found within a Late Iron Age fortified settlement of multiple houses and other features located on a small peninsula along the Shilka River (Kovychev, 2009). All three dogs were found in their own pits below the floors of houses, and all were 6–10 months of age at death. The remains were completely disarticulated and some display cut marks, suggesting the dogs were butchered and consumed. The remains of the individual dogs were then placed within pits, with the crania and mandibles in all three cases carefully placed at one of end of the pits, sometimes in association with metal tools and river mussel shells. The dogs are interpreted as sacrificed animals that were placed below the floors of houses just prior to them being built. Remains of cattle and pigs dominate the faunal remains from these houses.

Evaluating existing body mass estimation methods

To assess the accuracy of the previously existing equations for estimating canid body mass, we conducted the following tests. Van Valkenburgh's (1990) cranial length and mandibular first molar equations were applied to the wolf and dog metric data we collected. We were unable to evaluate Van Valkenburgh's occipital-to-orbit length equation because this same measurement was not taken by us during data collection—the measurement is not included in Von den Driesch (1976), the standard measurement guide used for metric studies of canids in archaeology. For the two regression equations we could evaluate, the accuracies of the body mass estimates were evaluated by calculating the percent prediction error (PPE) for individual specimens, and the average value of this percentage error for the total sample. PPE was calculated as:

$$\text{PPE} = [(\text{observed body mass} - \text{predicted body mass}) / \text{predicted body mass}] * 100$$

Assessing the accuracy of Wing's (1978) equations involved several additional considerations. First, Wing recommended caution when using two of her equations, namely those on mandibular premolar and molar row lengths. In particular, she mentions that incidences of tooth crowding might bias body mass estimations using her formula. Regardless, she found the dimensions to be highly correlated with body mass in her samples, with both regressions having R values (R^2 values and PPE are not reported) greater than 0.930. Other issues to consider with these measurements (and others that rely on landmarks near teeth) not discussed in her study are antemortem tooth loss or hypodontia, both of which would prevent the measurements from being taken. Despite such limitations, we assessed Wing's two mandibular tooth row equations against our dog dataset using the same method outlined above.

Second, Wing's preferred formula for estimating body mass is based on the height of the mandible taken at the midpoint of the first molar, which is not listed in Von den Driesch (1976). Most studies of archaeological canid remains have not recorded this dimension, including us, preventing it from being tested here. Equally important is that this mandibular body height measurement is taken from the dorsal margin of the first molar alveolus (typically on the labial face at the midpoint of the alveolus; see Clutton-Brock & Hammond [1994]). Such regions can be affected by alveolar resorption in dogs of advanced age, as well as those afflicted with dental disease or trauma (Lobprise, 2007). Such bone loss clearly would introduce error into body mass estimates. The far more commonly taken mandibular body height dimension is VDD's measurement 19, which is observed immediately behind (caudally to) the first molar, an area also likely effected to some degree by these same agents of bone resorption.

Van Valkenburgh's (1990) general carnivore body mass regression equation for cranial length (VDDc2) produced good results for our wolf specimens, with a PPE of only 11.39% (Table 2). This prediction error percentage is nearly identical to our own most accurate equation for wolves (see Tables 5 and 6). When this equation was applied to our dog dataset, the prediction errors were generally larger, with a PPE for these

Table 2. Evaluation of previously existing regression formulas for estimating dog and wolf body mass based on cranium and mandible dimensions. Equations are from Van Valkenburgh (1990) and Wing (1978). PPE is percent prediction error

Regression equation	# cases	Test group	PPE
Van Valkenburgh cranial length (VDDc2)	94	wolf	11.39
Van Valkenburgh cranial length (VDDc2)	36	dog	18.41
Van Valkenburgh mandibular M1 length (VDDm13)	104	wolf	66.84
Van Valkenburgh mandibular M1 length (VDDm13)	27	dog	56.94
Wing mandibular premolar row length (VDDm11)	14	dog	43.39
Wing mandibular molar row length (VDDm10)	24	dog	63.04

specimens being 18.41%. While several of the equations on dog cranial dimensions we calculated for this study produce body mass prediction errors less than this Van Valkenburgh equation (see below), this percentage error is well within the range of other commonly used body mass estimation methods (see Damuth & MacFadden, 1990). In other words, this equation seems to produce reasonably accurate body mass estimates for both wolves and dogs. Van Valkenburgh's (1990) mandibular molar length (VDDm13) equation fared poorly with both of our canid datasets, producing a PPE of 66.84% for the wolves and 56.94% for the dogs (Table 2). Such poor results are expected given the broad taxonomic structure of the Van Valkenburgh's dataset, and the fact that tooth length does not increase through the development of an animal; for dogs, the mandibular first molar crown is calcified in the prenatal period (Williams & Evans, 1978). Given the lack of prediction accuracy in application of the molar length equation, we suggest it not be used for estimating body mass in dogs and wolves.

Wing's (1978) mandibular premolar (VDDm11) and molar (VDDm10) tooth row length equations also produced high errors on average when applied to our dog specimens, with the PPE for the two equations being 43.39% and 63.04%, respectively (Table 2). We thus second Wing's caution against using these equations. As previously mentioned, it was impossible to calculate the estimate errors for Wing's mandibular height equation using our dataset. However, it is worth nothing that the equation generated in our study for mandibular body height (VDDm19) produced a relatively low PPE of 20.83% (see Table 5). As this measurement of mandibular body height is similar to that taken by Wing, her formula perhaps would have had a similar degree of error in its prediction values. Regardless, we found several dimensions in our dog mandibles that more closely scale with body mass than body height; we suggest these equations be used for estimating body mass from dog mandibles, as their prediction errors appear in several cases to be over 50% less than those based on mandibular body height.

New regression equations for body mass estimation

To assess how the cranial and mandibular dimensions we collected scaled in accordance with body mass, the biometric data were first log-transformed, which renders it more convenient for interpretation and statistical manipulation. While log-transformation of data is not necessarily always needed or advisable (see Smith, 1984), this form of data manipulation is widely used in allometric scaling studies and was adopted here. All cranial and mandibular dimensions then were individually assessed against body mass using the 'curve estimation' feature in SPSS, with the dog and the wolf datasets first treated separately. Finally (explained below), the two groups were combined into one *Canis* spp. group, and the cranial and mandibular dimensions retested against the known body masses using the method just described. For each bone/tooth dimension and body mass equation produced, R and R^2 values, PPE values, and percent standard error of estimate (%SEE) also were calculated, and these were used to assess equations' predictive strengths. Overall, linear curves generated the best results, regardless of the group (dogs, wolves, or *Canis* spp.) examined, with results for each dimension and sample group shown in Tables 3–7.

For the dog crania, nine different dimensions in the dog sample had R^2 values greater than 0.850 (Table 3) and %SEE of 27.1 or less. For the wolf crania, the most strongly correlated dimension (VDDc2) had an R^2 value of 0.728, and three other dimensions in the wolf group fell just below this level, but all four resulting regression equations had %SEE of 16.51 or less (Table 4). For the dogs, strong correlations were seen with several different cranial total length (VDDc 1–3) and rostrum length dimensions (VDDc13a and Morey's OI), as well as neurocranium length (VDDc7), palate width (VDDc34), and zygomatic breadth (VDDc30; Figure 3a). Cranial tooth dimensions (VDDc 18 and 20 length and breadth, and Morey's P^3 length) and tooth row lengths (VDDc 15–17) were not as strongly correlated with body mass in our dog samples, having

Table 3. Statistics for linear regression equations between dog cranial and mandibular dimensions and body mass. VDD is Von den Driesch (1976), and Morey is Morey (1992)

Dimension	# cases	R	R2	%PE	%SEE	Coefficient	Constant
Cranial							
VDDc1	36	0.964	0.929	14.80	18.57	3.140	−5.883
VDDc2	36	0.970	0.941	13.60	17.03	3.169	−5.867
VDDc3	34	0.973	0.947	13.21	16.61	3.152	−5.744
VDDc7	36	0.960	0.921	15.10	20.02	3.496	−5.601
VDDc8	36	0.929	0.864	20.46	27.10	2.604	−3.844
VDDc9	36	0.933	0.871	20.15	26.25	3.094	−5.014
VDDc13a	36	0.967	0.934	13.79	18.11	3.192	−5.026
VDDc15	32	0.897	0.805	16.73	22.65	4.039	−6.036
VDDc16	34	0.644	0.415	29.81	49.36	2.354	−1.599
VDDc17	31	0.677	0.459	26.79	41.24	2.414	−2.758
VDDc18 length	33	0.836	0.699	22.60	33.86	4.445	−4.382
VDDc18 breadth	31	0.892	0.795	16.94	28.00	3.180	−1.951
VDDc20 length	33	0.784	0.615	25.60	38.81	5.179	−4.402
VDDc20 breadth	33	0.849	0.721	22.91	32.22	3.538	−2.902
VDDc29	27	0.604	0.365	34.52	62.39	5.672	−8.466
VDDc30	27	0.955	0.913	13.92	19.66	3.312	−5.458
VDDc34	27	0.948	0.899	14.85	21.29	4.382	−6.791
Morey OI	36	0.948	0.899	17.86	22.97	2.578	−3.636
IM2	34	0.719	0.710	21.15	32.04	2.988	−4.615
P3 length	32	0.843	0.711	19.59	27.98	3.952	−3.028
Mandibular							
VDDm1	27	0.977	0.955	10.64	13.69	3.046	−5.259
VDDm2	27	0.981	0.962	9.30	12.43	2.877	−4.903
VDDm3	27	0.978	0.957	9.89	13.39	3.058	−5.218
VDDm4	26	0.965	0.932	9.61	13.92	2.474	−3.835
VDDm5	26	0.967	0.934	9.62	13.60	2.431	−3.688
VDDm6	26	0.954	0.911	10.88	16.06	2.398	−3.672
VDDm7	24	0.875	0.766	11.55	16.69	3.041	−4.437
VDDm8	15	0.864	0.746	11.55	18.63	3.794	−5.790
VDDm9	22	0.814	0.663	14.16	21.09	2.808	−3.801
VDDm10	24	0.713	0.508	17.04	25.06	4.265	−5.248
VDDm12	18	0.919	0.845	9.20	14.38	3.161	−3.579
VDDm13 length	21	0.691	0.477	17.60	25.94	4.063	−4.114
VDDm13 breadth	21	0.776	0.602	15.52	22.30	2.611	−1.143
VDDm14	21	0.611	0.374	18.86	28.71	3.048	−2.664
VDDm15 length	21	0.606	0.367	19.74	28.89	2.564	−1.057
VDDm15 breadth	21	$p > 0.05$					
VDDm17	23	0.843	0.710	24.46	40.97	3.226	−2.173
VDDm18	23	0.976	0.952	11.27	14.98	2.352	−2.826
VDDm19	23	0.908	0.825	20.83	30.57	3.086	−3.036
VDDm20	23	0.851	0.725	24.59	39.77	3.116	−2.819

R^2 values of 0.799 or less. For the wolf data, the strongest correlations are seen with cranial length (VDDc 1–3) and zygomatic breadth (VDDc30; Table 4).

For the dogs, several of the mandibular dimensions scaled more closely with body mass than did any of the cranial dimensions (compare Tables 3 and 4), having PPE and %SEE values of 11.27 and 16.06 or lower, respectively. These include several mandibular length dimensions (VDDm 1, 4, 5, 6) as well as height of the vertical ramus (VDDm18). Mandibular body height (VDDm19) had the sixth lowest %SEE among the mandibular dimensions tested (30.87%). Clearly, however, mandibular body height scales less closely with body mass in dogs than several of the length dimensions and should only be used when these latter dimensions cannot be accurately taken. Three wolf mandibular dimensions scaled closely with body mass in our samples, including two length dimensions (VDDm 1, 2) and height of the vertical ramus (VDDm 18; Table 4 and Figure 3b). As in the dog sample, the wolf mandibular regression equations have somewhat lower PPE and %SEE values than the equations for the cranial dimensions.

The combined dog and wolf (*Canis* spp.) dataset also produced a series of regression equations for crania and mandibular dimensions with relatively low PPE and % SEE values (Tables 5). These regression formulae might be best used for estimating body mass in very early dogs (Germonpré *et al.*, 2009, 2012; Ovodov *et al.*, 2011), or where wolf-dog hybrids are suspected (e.g.,

Table 4. Statistics for linear regression equations between wolf cranial and mandibular dimensions and body mass. VDD is Von den Driesch (1976), and Morey is Morey (1992)

Dimension	# cases	R	R2	%PE	%SEE	Coefficient	Constant
Cranial							
VDDc1	106	0.827	0.684	11.49	16.51	3.017	−5.683
VDDc2	94	0.853	0.728	11.72	15.78	3.349	−6.374
VDDc3	73	0.848	0.719	11.81	16.30	3.369	−6.335
VDDc7	103	0.833	0.694	11.09	16.00	2.602	−3.816
VDDc8	108	0.686	0.471	14.23	21.67	2.251	−3.174
VDDc9	107	0.662	0.439	15.29	22.39	2.626	−4.131
VDDc13a	106	0.813	0.660	12.62	17.09	3.258	−5.241
VDDc15	106	0.611	0.374	14.66	20.63	2.455	−3.175
VDDc16	106	0.305	0.093	16.79	23.87	1.268	−0.153
VDDc17	104	0.483	0.233	15.51	21.87	1.190	−0.599
VDDc18 length	106	0.548	0.300	14.85	20.69	2.138	−1.424
VDDc18 breadth	85	$p > 0.05$					
VDDc20 length	107	0.329	0.108	17.09	24.97	1.305	−0.042
VDDc20 breadth	106	0.334	0.112	17.48	25.04	1.071	+0.157
VDDc29	103	0.414	0.171	16.68	27.67	3.241	−4.315
VDDc30	104	0.848	0.719	11.32	15.47	2.547	−3.851
VDDc34	107	0.702	0.492	14.05	21.28	2.938	−4.024
Morey OI	108	0.773	0.598	13.14	18.64	2.769	−4.115
IM2	106	0.444	0.197	16.91	23.57	0.233	1.075
P3 length	105	0.406	0.165	15.35	22.03	1.255	−0.570
Mandibular							
VDDm1	103	0.799	0.639	12.68	17.71	2.945	−5.104
VDDm2	102	0.796	0.633	11.72	15.78	2.821	−4.832
VDDm3	103	0.791	0.626	13.00	18.06	3.090	−5.379
VDDm4	106	0.789	0.623	12.63	18.04	2.812	−4.633
VDDm5	106	0.790	0.624	12.78	17.99	3.032	−5.057
VDDm6	104	0.796	0.634	12.62	17.85	2.737	−4.484
VDDm7	100	0.696	0.485	13.08	17.51	2.920	−4.316
VDDm8	100	0.617	0.318	14.25	19.20	2.807	−4.014
VDDm9	101	0.641	0.410	13.74	18.73	2.855	−4.020
VDDm10	101	0.345	0.119	15.93	22.73	1.503	−0.949
VDDm11	102	0.598	0.358	14.35	19.67	2.277	−2.352
VDDm12	105	0.624	0.389	13.93	19.09	2.208	−2.099
VDDm13 length	104	0.351	0.123	15.95	23.29	1.265	−0.279
VDDm13 breadth	103	0.492	0.242	14.67	21.68	1.416	+0.066
VDDm14	105	0.474	0.224	14.85	21.76	1.823	−1.084
VDDm15 length	105	0.201	0.040	17.34	24.48	0.676	+0.831
VDDm15 breadth	105	$p > 0.05$					
VDDm17	105	0.490	0.240	14.43	22.83	1.426	−0.073
VDDm18	107	0.868	0.753	10.32	14.28	1.961	−2.100
VDDm19	106	0.661	0.437	13.63	19.27	1.644	−0.880
VDDm20	105	0.565	0.320	14.02	20.24	1.447	−0.463

Walker and Frison, 1982), both of which might be expected to have body proportions intermediate between those of wolves and (more recent or non-hybrid) dogs. Application of these formulae to canid specimens tends to produce body mass estimates that are often intermediate between those produced through use of the dog and wolf equations. This occurs because some dimensions of the dog crania and mandible are often less than those of wolves of similar body mass. In our samples, for example, dog crania are shorter relative to the mass of the total body when compared to wolves (see Figure 3c). The regression lines for the combined dataset then tend to straddle the wolf and dog data points. However, because our *Canis* spp. dataset contains far more data points for wolves than dogs, the resulting body mass estimates are biased towards the wolf body form (mass estimates are often closer to those produced using the wolf formulae than the dog formulae). Clearly, the formulae must be used cautiously.

Finally, it is important to note that both of our canid datasets intentionally contained multiple juvenile individuals, in part because we wanted to have the ability to estimate body masses using elements from juvenile dogs and wolves in the archaeological record. The juvenile data points in all cases 'anchored' our regression lines, as these individuals had the lowest body masses and shortest element dimensions. Removing the juveniles from the datasets clearly would produce

Table 5. Statistics for linear regression equations between Canis spp. (combined wolf and dog dataset) cranium dimensions and body mass. VDD is Von den Driesch (1976), and Morey is Morey (1992)

Dimension	# cases	R	R2	%PE	%SEE	Coefficient	Constant
Cranial							
VDDc1	143	0.923	0.852	13.50	11.40	2.704	−4.919
VDDc2	130	0.935	0.874	13.15	11.56	2.849	−5.177
VDDc3	107	0.933	0.871	13.41	11.60	2.837	−5.075
VDDc7	139	0.930	0.864	12.93	11.30	2.998	−4.629
VDDc8	144	0.870	0.772	16.39	23.72	2.275	−3.216
VDDc9	143	0.863	0.745	17.67	25.36	2.444	−3.723
VDDc13a	142	0.925	0.856	14.04	12.65	2.869	−4.416
VDDc15	138	0.778	0.605	16.92	23.59	2.379	−3.017
VDDc16	139	0.702	0.492	19.72	29.34	2.528	−1.852
VDDc17	135	0.684	0.468	18.29	27.65	1.687	−1.502
VDDc18 length	139	0.747	0.558	19.10	27.49	2.269	−1.596
VDDc18 breadth	109	0.494	0.244	16.28	23.63	1.218	+0.164
VDDc20 length	134	0.468	0.219	18.47	26.70	1.144	+0.160
VDDc20 breadth	133	0.493	0.243	18.20	26.33	1.297	−0.138
VDDc29	130	0.564	0.318	34.34	37.63	2.751	−3.418
VDDc30	131	0.915	0.837	12.29	16.92	2.918	−4.639
VDDc34	134	0.846	0.716	15.23	22.66	3.804	−5.677
Morey OI	144	0.902	0.814	15.18	12.82	2.280	−3.101
IM2	140	0.426	0.181	21.94	39.55	0.389	+0.715
P3 length	137	0.700	0.489	17.30	26.12	2.101	−0.957
Mandibular							
VDDm1	137	0.930	0.864	13.08	12.46	2.840	−4.859
VDDm2	136	0.929	0.863	13.14	12.67	2.710	−4.570
VDDm3	137	0.925	0.855	13.56	12.81	2.815	−4.750
VDDm4	139	0.911	0.830	13.42	12.38	2.607	−4.174
VDDm5	139	0.908	0.825	13.68	12.55	2.586	−4.075
VDDm6	137	0.908	0.825	13.84	12.43	2.484	−3.917
VDDm7	130	0.825	0.681	15.50	20.49	2.600	−3.658
VDDm8	121	0.800	0.641	16.09	21.94	2.695	−3.782
VDDm9	129	0.780	0.608	16.46	22.95	2.444	−3.206
VDDm11	123	0.795	0.633	15.90	22.30	2.487	−2.707
VDDm12	129	0.827	0.685	34.76	20.37	2.590	−2.726
VDDm13 length	132	0.711	0.505	19.01	29.19	2.218	−1.659
VDDm13 breadth	131	0.775	0.600	17.29	25.95	2.373	−0.944
VDDm14	133	0.724	0.524	34.14	28.45	2.113	−1.495
VDDm15 length	126	0.416	0.173	18.20	25.67	1.008	+0.475
VDDm15 breadth	126	0.378	0.143	17.74	26.19	0.939	+0.663
VDDm17	135	0.811	0.658	33.72	29.30	2.588	−1.412
VDDm18	137	0.948	0.899	11.46	10.86	2.301	−2.738
VDDm19	137	0.878	0.771	15.28	23.34	2.406	−2.020
VDDm20	135	0.830	0.692	17.84	27.39	2.538	−2.000

regression equations with greater %SEEs. In other words, there would be more variation in body mass (which of course generally increases with age but also varies with other factors such as season) relative to variation in element length, the latter of which would largely be established at maturity.

Body mass estimation for Eastern Siberian canids

To apply the regression equations in Tables 3–7 to ancient specimens, one first measures the specimens, recording the results in millimeters. Second, a regression formula is chosen, preferably one with the smallest PEE and %SEE that can be applied to the specimen, producing a single mass estimate. Alternatively, one could apply a suite of regression equations to a specimen and then report a range of mass estimates. Regardless, to begin, the dimension under consideration must first be $\log_{10}$ transformed, and then multiplied by the coefficient and the constant subtracted from this amount. The inverse log of this result renders the specimen's estimated body mass in kilograms.

For example, for the Lokomotiv wolf, we estimated its body mass using the VDDm18 wolf mandibular regression equation. The raw measurement of this dimension on the wolf mandible was 80.62 mm, which can be entered into Microsoft Excel and then $\log_{10}$

Table 6. Body mass estimates for archaeological canid remains from Eastern Siberia

Site	Specimen	Formula	Body mass (kg)
Cis-Baikal canids			
Lokomotiv	Wolf	VDDm18 (wolf)	43.50
Ust'-Belaia	Dog 1	VDDc2 (dog)	26.23
	Dog 2	VDDc2 (dog)	18.32
	Dog 4	VDDc2 (dog)	12.53
Pad' Kalashnikova	Dog 1	VDDc2 (dog)	13.27
	Dog 2	VDDc2 (dog)	19.12
Shamanka II	Dog 1	VDDm5 (dog)	29.44
Ulan-Khada	Layer 1 dog 1	VDDm18 (dog)	23.82
Uliarba II	Dog 1	VDDm18 (dog)	17.84
Bugul'deika II	Dog 1	VDDm19 (dog)	16.36
Todakta I	Dog 1	VDDm5 (dog)	14.61
Eastern Transbaikal canids			
Bolshaia Kanga	Dog 1	VDDm5 (dog)	24.66
	Dog 2	VDDm5 (dog)	20.26
Proezzhaia I	Dwelling 28 dog 1	VDDM5 (dog)	19.33
	Dwelling 32 dog 1	VDDM5 (dog)	16.72
	Dwelling 32 dog 2	VDDM5 (dog)	14.95

transformed using the '=log10(80.62)' function, producing a result of 1.9064. This number was then multiplied by the constant value of 1.961, and 2.1000 was then subtracted from this result, which rendered a value of 1.6385. The inverse log of this number was then obtained using Excel function '=10^1.6385', producing an estimated body mass value of 43.50 kg (Table 6). More formally, this equation is as follows, with y being the dependent variable (weight), α the constant, β the regression coefficient, and x the element measurement:

$$\mathrm{Log}(y) = \alpha + \beta \log(x)$$

Note that this wolf was a male (Losey *et al.*, 2011), and the body mass estimated for this specimen is near the average for male wolves in taiga regions of Siberia (Heptner *et al.*, 1974).

For the Ust'-Khaita canid, which was previously identified as a probable dog (Losey *et al.*, 2013), we take the broader approach, estimating its body mass based on several dimension, and using regression equations made from the wolf, dog, and *Canis* spp. datasets (Table 7). The equations indicate the canid weighed somewhere between 15.4 and 19.4 kg, with the average of the estimations being 17.9 kg. While this mass is well within the range of that estimated for the Holocene dogs from this region (Table 6), the Ust'-Khaita canid was only 5–8 months old at death and thus had not reached adult body size. Studies of modern dogs indicate they rapidly increase in body mass for the first three months or so of their lives, with the rate body mass increase markedly slowing after this point, with many breeds reaching mature body weights at roughly one year of age (Allard *et al.*, 1988; Hawthorne *et al.*, 2004; Helmink *et al.*, 2000; Tangerud *et al.*, 2007; Voorhout *et al.*, 1994); both dogs and wolves can of course increase in body mass after first reaching adulthood (c.f., Mech, 2006). If this canid were to have lived to adulthood (~1 year of age), it is likely it would have weighed somewhat more than its current estimated mass. At adulthood, this canid likely would have had a body mass similar to that of the largest dogs in our sample (which reach nearly 30 kg; Table 6), which is also within the lower end of the size range of modern Siberian wolves (Heptner *et al.*, 1974). If the canid's growth profile was more similar to wolves, which reach adult size only slightly later in life than dogs (at 12–14 months; Kreeger, 2003), its body mass likely would have been slightly greater at one year.

Table 7. Body mass estimates for the Ust'-Khaita canid, which was identified as a probable dog, that was 5–8 months old at the time of death

Formula	Body Mass (kg)
VDDc2 (dog)	19.39
VDDc2 (wolf)	15.38
VDDc2 (*Canis* spp.)	17.99
VDDm18 (dog)	17.66
VDDm18 (wolf)	19.76
VDDm18 (*Canis* spp.)	17.64
VDDm1 (dog)	19.18
VDDm1 (wolf)	16.63
VDDm1 (*Canis* spp.)	17.40

Body mass estimates for all of the Eastern Siberian dog specimens are far smaller than that of the Lokomotiv wolf, with the largest dog (from the Early Neolithic Shamanka II cemetery), weighing ~14 kg less

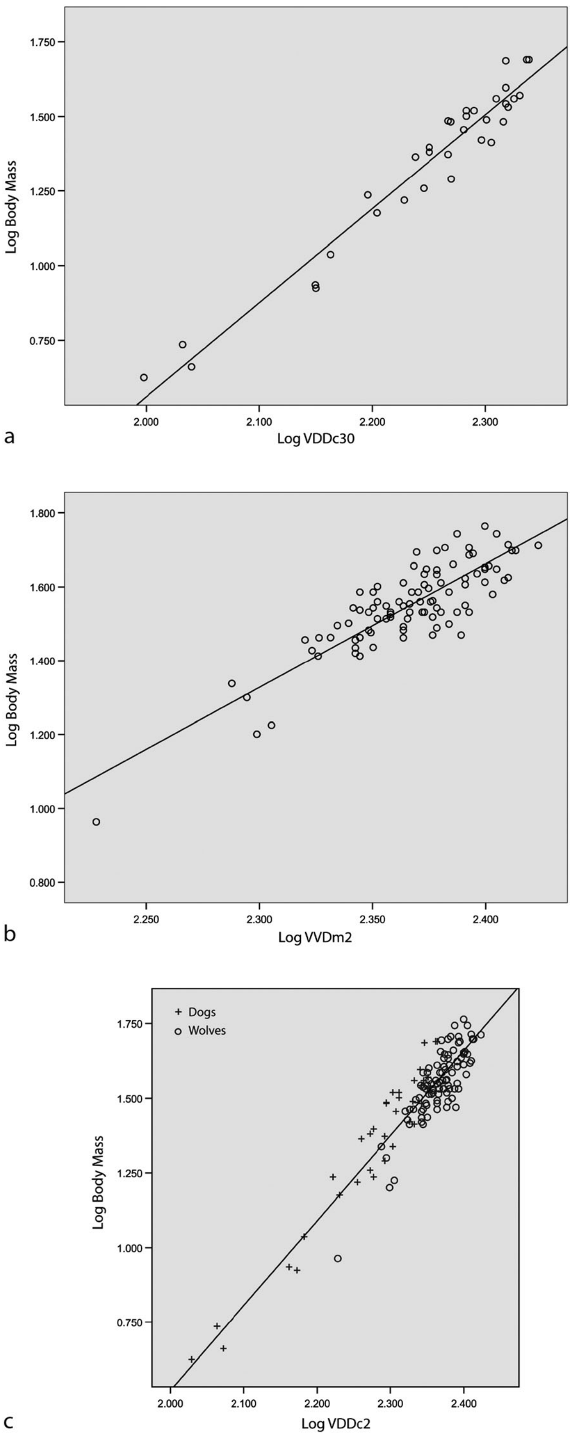

Figure 3. a) Relationship between dog $\log_{10}$ body mass and $\log_{10}$ of Von den Driesch's (1976) cranial measurement 30. b) Relationship between wolf $\log_{10}$ body mass and $\log_{10}$ of Von den Driesch's (1976) mandibular measurement 2. c) Relationship between Canis spp. (combined wolf and dog dataset) $\log_{10}$ body mass and $\log_{10}$ of Von den Driesch's (1976) cranial measurement 2, with dog and wolf data points indicated. Statistics for regression lines are in Tables 3, 4, and 5.

than this wolf (Table 6). The dogs associated with hunter–gatherers (all dogs except for those from Bugul'deika II, Todakta I, and Proezzhaia I) varied widely in terms of body mass, with estimations ranging from 12.53 to 29.44 kg (Table 6). This variability is present even within limited geographic space and time. For example, the Ust'-Belaia and Pad' Kalashnikova adult dogs all date within a few centuries of one another (~6880 to 7175 cal. BP) and the two sites are only ~25 km apart, yet some of the dogs there are more than twice the mass of others. To better visualize this size range, these dogs can be compared with common modern breeds—the largest of the ancient hunter–gatherer dogs were roughly the same size as modern Labrador retrievers, while the smallest were in the same size range as spaniels (American Kennel Club, 1975). Notably, modern Siberian huskies overlap in body size with all of these early dogs (American Kennel Club 1975) and are today used for a wide array of tasks, from pulling sleds to hunting. Finally, there seems to be little correlation between body mass and whether or not dogs were buried, as at least one smaller dog was buried (dog 1 at Pad' Kalashnikova, a juvenile), as were several of the largest ones (dog 2 at Pad' Kalashnikova, dog 1 at Ust'-Belaia, and the Shamanka II dog); none of the larger dogs from Bol'shaia Kanga were interred.

The dogs associated with pastoralists were less variable in mass, ranging from 14.61 to 19.33 kg, overlapping in size with the smaller hunter–gatherer dogs. However, this may be misleading, because among this group only the dog from Bugul'deika II was an adult at death; many of the pastoralists' dogs had not reached adult body mass (most of the earlier hunter–gatherer dogs were adults). The other four pastoralist dogs were 4–10 months old at death, and all were sacrificed, with the three dogs from Proezzhaia I also being butchered and likely eaten. This pattern suggests some selectivity in choosing dogs for sacrifice—juvenile animals approaching adult body size seem to have been preferred. Such selection might be a matter of appearance, taste, and economics. These animals would have at least superficially appeared to be young adults (in modern terms, they would have the mass of medium-sized dogs), and perhaps thus capable of adult dog behaviors. Further, perhaps younger animals would be considered more palatable than older individuals, a possible consideration for dogs being selected for eating. Further, feeding and caring for a dog well into adulthood would have relatively little advantage in terms of increases in edible body mass, as these late-juvenile aged animals were approaching adult size—the butchered dogs at Proezzhaia I were already ~15 kg or larger. Sacrificing an older dog, particularly one that had been trained and cared for, would be a far more costly sacrifice.

Conclusions

Our analyses demonstrated that some previously used regression formulae for estimating body mass in dogs and wolves work reasonably well, while others fair poorly when tested against canids of known body mass. The newly developed formulae presented above allow body mass to be estimated in wolves and dogs using a far broader set of cranial and mandibular dimensions than previously was possible. These means of body mass estimation have fairly low margins of error, but should be used cautiously, particularly when being applied to canids suspected to be outside the size range of the animals used in this study. Further, the application of the formula to the dogs and one wolf from Eastern Siberia revealed a number of interesting patterns that previously had been unrecognized, including substantial size variability in the early hunter–gatherer dogs, and pastoralist selection of dogs of certain body sizes (and ages) for sacrifices.

While the body mass estimations made possible through the regression formula developed here are useful and informative, they point to the need for additional refinement of various methods used to study ancient dogs and wolves. First, several sets of dog remains from Eastern Siberia were excluded from discussion here because they consisted solely of post-cranial remains. This points to the need to develop methods for estimating body mass in dogs and wolves from limb elements. Second, the lack of reliable methods (well tested, and based on a large and diverse comparative dataset) for sexing dog remains, beyond the mere presence or absence of bacula, also is an issue, as male dogs typically have greater body mass than females, particularly among larger breeds, and in some breeds males can be nearly double the body mass of females (Frynta *et al.*, 2012). Some of the variability seen in our body mass estimates may be the result of sexual size dimorphism rather than the overall variability of dog body sizes within these early Siberian communities. Third, more accurate means of ageing adult dogs also is needed, as tooth eruption and skeletal fusion essentially cease to be useful after dogs reach one year of age. Body mass ranges in a community of ancient dogs might relate in part to animals' ages at death, not simply their genetic potential or nutritional history. Finally, estimates of body mass are informative about the potential capabilities of ancient dogs, but they are not direct assessments of activity patterns in these animals. Careful study of the shapes and sizes of the postcranial skeleton is needed for this, and models for such studies are already available in the literature on activity patterns in humans and other animals. When these issues are more fully addressed, the study of the life histories of dogs and their interactions with humans will be a much richer and scientifically secure endeavor. We hope this paper is one step in that direction.

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