Dog body size in Siberia and the Russian Far East and its implications

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ABSTRACT

Body size is correlated with many critical behavioral and developmental patterns in carnivores, including domestic dogs. The body masses and bite forces of archaeological dog remains from Siberia and the Russian Far East were estimated to make inferences regarding their behaviors and capacitis. The dogs date from ~10,000−100 cal. BP and derive from archaeological sites spanning from steppe environments in the south to tundra regions of the northern Arctic. The dogs exhibit a four-fold difference in body mass, ranging from 7.6 to 32.5 kg, but have a mean body mass of only 16.4 kg. Bite forces are around only half those of modern wolves, indicating that the dogs had greatly reduced abilities to grasp and masticate prey and food items. The dogs exhibit a slight decrease in body size through time, perhaps due to human selection or greater survival rates for smaller individuals in human-dominated food environments. Dog body size variance within individual archaeological sites was as high as in a sample of modern wolves from throughout the study area, suggesting little strict human control over body size. No correlation was found between body size and site latitude, suggesting that Bergmann's rule does not hold for these canids. Human shelters may provide a buffer against low temperatures that might favour larger body sizes at high latitudes. About 90% of the analyzed dogs have estimated body masses less than 21.5 kg, suggesting most were best adapted for procuring prey smaller than themselves—the dogs were not capable of taking down larger prey without the assistance of humans. Estimated dog body masses cannot eliminate the possibility that many of the animals were used for pulling sleds, and nearly all were capable of packing modest loads on their backs. Livestock guarding dogs are not well-evidenced by the body mass data, but herding dogs are a possibility in all of the pastoral or agricultural settings analyzed.

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1. Introduction

Modern dogs are the most phenotypically diverse land mammal on earth, and their body sizes are no exception, with adults ranging in mass from ~1.4 kg to well over 100 kg (Speakman et al., 2003). Geneticists have been particularly fascinated by dog body size variation, making many efforts to understand its genetic underpinnings (Boyko et al., 2010; Chase et al., 2002; Rimbault et al., 2013; Sutter et al., 2007; Vaysse et al., 2011). Decreases in body size among early domestic dogs and other mammals are a continual concern in archaeology, particularly regarding the selective forces driving such trends (Clutton-Brock, 1999; Morey, 1992; Tchernov and Horwitz, 1991; Wilkins et al., 2014; Zeder and Hesse, 2000). Further, existing literature appears to show significant body size variation early in the domestication history of dogs—it is not solely a product of highly selective breeding for appearance practiced over the last few centuries (e.g., Benecke, 1987; Haag, 1948; Janssens et al., 2019; Welker and Byers, 2019; Welker and Dunham, 2019). Rarely discussed, however, are the consequences of this size variation for the evolution and lives of dogs, and their roles in past societies (but see Pitulko and Kasparov, 2017; Welker and Byers, 2019). Body size is correlated with many critical behavioral and developmental patterns in carnivores. Paleontology, in particular, has scrutinized size variation in canids, demonstrating that body mass is useful for assessing many aspects of these animals' behaviors (Carbone et al., 1999; Gittleman, 1985; Van Valkenburgh et al., 2004). Archaeology has mostly ignored these lines of inquiry, focusing instead on the challenges caused by size variation for taxonomically differentiating dogs from their closest relatives, grey wolves (Canis lupus). This is a missed opportunity, as body mass, a proxy for overall body size, can be readily estimated for dog skeletal remains.

Body size constrains and enables the essential performances of dogs and other mammals, particularly their locomotion (Fischer and Lilje, 2014; Heglund and Taylor, 1988; Taylor et al., 1982; Voss et al., 2010). Across a suite of mammals, long and gracile limbs allow for more rapid and economical running than shorter and heavier limbs (Hildebrand and Goslow, 2001). Canids are cursorial, with wolves being prime examples of mammals highly adapted for long-distance running (Ewer, 1973; Hildebrand, 1954). Large dogs have limb proportions similar to those of wolves (Wayne, 1986). The earliest domestic dogs probably had bodies functionally identical to wolves, meaning they were also very efficient long-distance runners. By at least the Early Holocene, domestication generated dogs considerably smaller than wolves, which correspondingly had shorter limbs, rendering them less rapid and efficient runners. However, some positive tradeoffs in locomotion are found with decreasing body size. Dogs with shorter and more robust limbs are often more agile than longer limbed animals (e.g., Kemp et al., 2005; Pasi and Carrier, 2003). Such differences in innate ability shape how dogs function in domestic settings, including in tasks such as hunting, sled pulling, pack carrying, or herding. For example, dogs inefficient at running long distances would be selected against if their primary role was to pull sleds, as seen historically among some northern Siberian Indigenous groups (Levin and Potapov, 1961). Large bodied dogs might not be favored in some types of hunting, particularly for pursuing small mammals that required high levels of agility and the ability to fit into small spaces. For example, hunting in many parts of Siberia for fur-bearers such as sable (Martes zibellina) often relies on working with relatively small and agile dogs (Oehler, 2018).

Body size is correlated with feeding behaviors in dogs and other carnivores (Carbone et al., 1999; Christiansen and Wroe, 2007; Flower, 2016; Gittleman, 1985; Herrel and Gibb, 2006). Carbone et al. (1999) found that among wild carnivores, those under ~21.5 kg tend to rely on prey less than half their body weights, while those over this amount often take prey larger than themselves. Grey wolves are an example of the latter, and even within this species, size influences predation abilities. Larger wolves are generally more effective than smaller individuals at holding and killing larger prey such as elk (Cervus elaphus) (MacNulty et al., 2009). However, very large wolves (>39 kg) show no improvement in hunting success over somewhat smaller individuals (MacNulty et al., 2009). Why performance levels-off with wolves over 39 kg may relate to limitations placed on locomotion by larger bodies—very large wolves might tire more quickly during pursuit (MacNulty et al., 2009). Larger body size in carnivores also correlates with larger foraging ranges (Eisenberg, 1990; Gittleman and Harvey, 1982). In addition, small carnivores feed on prey within a restricted size range because of the physical limits of their bodies—they are not fast enough nor strong enough to efficiently capture and process larger animals (Gittleman, 1985). Larger carnivores face fewer such limits, as they can take both larger and smaller prey, to some extent. This suggests that both the size and diversity of prey typically taken by most dogs in the past must differ significantly from those of wolves—they likely became too small to effectively take larger prey and forage over broad ranges on their own.

Bite strength and gape size also are closely connected to body size, and both affect feeding behaviors (Christiansen and Wroe, 2007; Damasceno et al., 2013; Therrien, 2005; Wroe et al., 2005). In wolves, the canine is primarily used for grasping food items and prey, while the post-carnassial molars are used for crushing bone and other food (Ewer, 1973). Bite forces are consistently higher at the molars than at the canines, as wolves typically use their canines for grasping and superficially slashing prey, rather than killing directly by biting with these teeth (Therrien, 2005). Ellis et al. (2008) measured bite forces in 20 dogs ranging in body mass from 7 to 40 kg. Again, bite forces were always greater at the molars than at the canines, and forces exerted at both increased with increases in body mass. Comparatively, Christiansen and Wroe (2007) estimated bite forces among dogs and wolves (and other carnivores), finding that a 25 kg dog produces ~29% less force at both the canine and carnassial than a 35.5 kg wolf. Finally, as body size decreases, so does gape size, meaning that progressively smaller food items can be accommodated in the mouth (Binder and Van Valkenburgh, 2000). A smaller dog, for example, would have difficulty extracting nutrients from the long bones of large mammals because these objects would not fit well in their mouths, and they lack the strength to break them open.

Body size is related to bite force in several other ways. Both wolves and dogs are sexually size dimorphic, with males typically being larger than females. Dimorphism in grey wolves by body mass appears to range from ~18 to 28% (Hillis and Mallory, 1996; Moehlman and Hofer, 1997:112), a pattern thought to be due to enhanced selection for aggression and prey capture in males (Morris and Brandt, 2014). The wolf populations in Eurasia that gave rise to dogs may have had similar levels of sexual dimorphism, assuming they were of similar body size and under comparable selective forces. Within dogs, sexual dimorphism decreases with body size, following Rensch's rule (Frynta et al., 2012). Regarding ontogeny, wolves with deciduous dentition, or those with newly erupted adult dentition, are less efficient at processing bone than older adults (Therrien, 2005). Part of this is related to juveniles being smaller and having weaker adductor muscles than adults, but their mandibles also are not as robustly developed—they are not yet strong enough to accommodate high levels of force. A similar pattern should also be present in dogs, which appear to skeletally mature at much the same rate as wolves (Geiger et al., 2016).

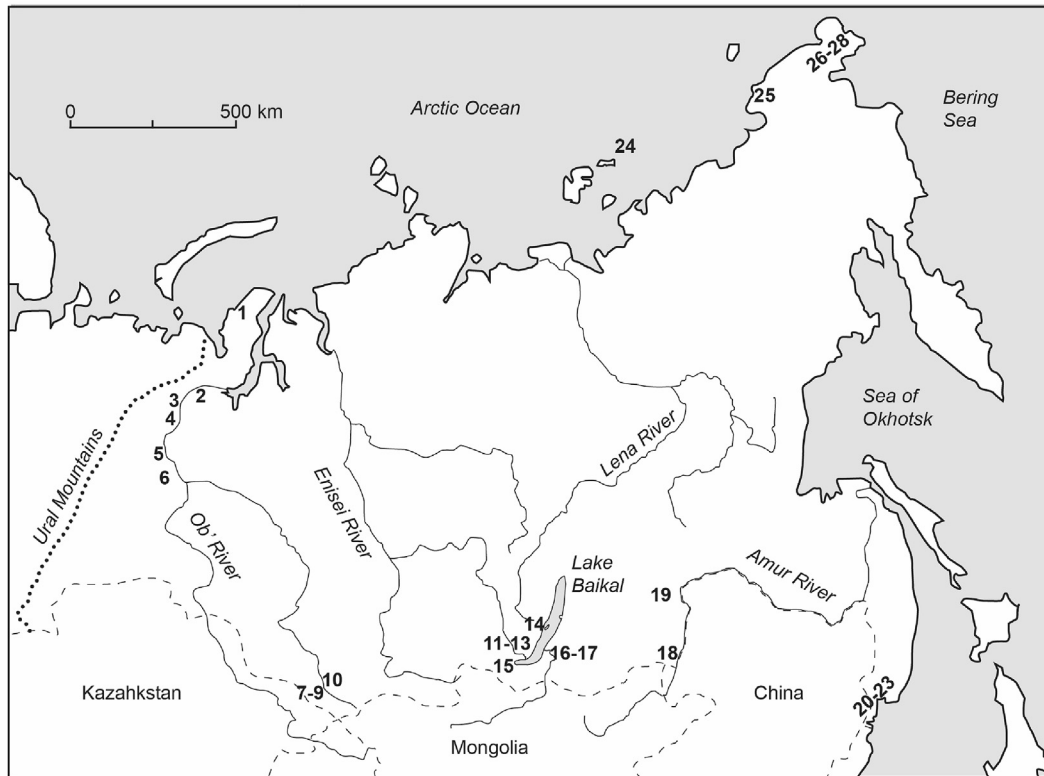Dog body size also is potentially linked to thermal regulation.

Fig. 1. Map of the study area, with archaeological sites indicated: 1) Tiutei-Sale I; 2) Ust'-Polui; 3) Katravozh I; 4) Ust'-Voikar; 5) Peregrebnoe I; 6) Endyrskoe I; 7) Berezovaia Luka; 8) Uspenovka II; 9) Zharkovo III; 10) Inia 1; 11) Ust'-Belaia; 12) Pad' Kalashnikova; 13) Maiakovskogo 2; 14) Uliarba II; 15) Shamanka II; 16) Nizhniaia Berezovka; 17) Ivolgin; 18) Bolshaia Kanga I; 19) Proezzhaia I; 20) Boisman II; 21) Pospelovo I; 22) Russki 1; 23) Cherniatino 2; 24) Zhokhov; 25) Aachim Mayak; 26) Ekven; 27) Kanisak; 28) Paipelghak.

Bergmann's rule states that within species of warm-blooded animals, those living in colder environments will be on average larger than those living in warmer environments (Bergmann, 1847; Mayr, 1942). The original explanation for such patterns was related to thermal regulation. An increase in body size involves a larger increase in volume than in surface area, and this volume to surface area ratio change allows for more heat to be generated and less to be lost. Lower ambient temperatures are in turn a selective force in body size clines. However, numerous other explanations for increasing body size with increasing latitude have been put forth, with no clear consensus emerging, and Bergmann's rule has many exceptions (Ashton et al., 2000; Blackburn et al., 1999; Meiri and Dayan, 2003). For example, Geist (1987) found that modern North American wolves exhibit a pattern of increasing body size, evidenced by longer crania, as latitude increases. However, this trend reversed after ~65° N, which Geist attributes to a decline in food availability, not decreasing ambient temperature. Other studies also have shown that wolf body size correlates with latitude or changes in climate, but only in select cases or regions (Meiri et al., 2004; Meachen and Samuels, 2012; Rosenzweig, 1968). Dogs are a particularly interesting case for exploring Bergmann's rule because they have inhabited a far wider range of latitudes than other mammalian carnivores, but have done so over a relatively short period.

Bigger dogs generally have higher basic caloric needs than smaller dogs, assuming all else is equal (Bermingham et al., 2014). This is pertinent when considering provisioning strategies with working animals such as sled dogs, which have very high daily caloric requirements (Hinchcliff et al., 1997; Loftus et al., 2014). Provisioning sled dogs is onerous, and efforts to reduce this are not trivial. For example, Chikachev (2004) reports that a team of ten

sled dogs in northern Siberia requires 3—4 tons of fish for food per year. Such provisioning costs would have influenced breeding decisions regarding body size—larger dogs might be preferred because they are stronger and faster, but this would be balanced against the costs of maintaining them. Archaeological studies across a wide range of environments show that dogs were intentionally provisioned with foods similar to those consumed by people, or that dogs were regularly accessing human food waste (Guiry, 2012; Losey et al., 2013). Dog and human diets are often so similar that dog stable carbon and nitrogen isotope ratios (δ^{13}C and δ^{15}N) are commonly used as proxies in assessments of human diets (Guiry, 2012). Clearly, dogs developed some level of dietary dependence on humans during their domestication.

Smaller dogs live longer on average than larger dogs, at least among the modern breeds tested (Egenvall et al., 2000; Li et al., 1996; Miller, 1999). Further, breeds of smaller dogs appear to reach near-complete adult body size a few months earlier in life than larger breeds (Hawthorne et al., 2004; Helmsmüller et al., 2013; von Pfeil and DeCamp, 2009). Greater longevity might be advantageous if the reproductive period was extended, which would allow individuals with desired traits to sire more offspring. Longer lives could also be correlated with extended working lives, as animals would have longer periods at full adult body size and with adult skills. More quickly attaining adult body size might also extend working lives by allowing individuals to begin these tasks when somewhat younger. Finally, achieving adult body size earlier would be preferred where people raised dogs primarily to eat them.

Studies of body size in canids and other carnivores are often carried out through the proxy of body mass. Most often, skeletal element dimensions of living animals with directly measured body masses are used to develop regression equations that are applied to

fossil or sub-fossil remains (Anyonge, 1993; Flower, 2016; Losey et al., 2017; Meloro et al., 2007, 2015; Van Valkenburgh, 1990). Fairly standard sets of skeletal dimensions are now taken on archaeological dog remains (e.g., Von den Driesch, 1976). Such measurements create the opportunity to evaluate body masses consistently across multiple studies, periods, and settings. Here we examine body size variation in archaeological dog remains from Siberia and the Russian Far East to explore how some of the long-term effects of domestication shaped these animals' behaviors and roles.

2. Methods and materials

2.1. Materials

Dog remains representing 199 individuals from 28 archaeological sites were assessed, with site locations spanning from 50° to 76° N, and 66° to 171° E (Table S1; Fig. 1). The dogs derive from archaeological sites in the steppe zone of the Altai region, the shores of Lake Baikal and its tributaries, steppe and forest-steppe areas of southern Trans-Baikal, coastal and interior areas of the maritime Primorye region, coastal areas of eastern Chukotka, and the boreal and tundra zones of Iamal. The specimens were identified as dogs using various techniques, including aDNA analyses (Ameen et al., 2019; Bergström et al., in review; Lee et al., 2015; Losey et al., 2011, 2013; Ollivier et al., 2013), traditional morphometrics (Losey et al., 2011, 2013, 2018c; Pitulko and Kasparov, 2017; Vasyukov and Savinetsky, 2016), and geometric morphometrics (Drake et al., 2015, 2017). Archaeological context information and culture history period are given in Table S1. The dog remains analyzed vary between intentionally buried whole skeletons to isolated and fragmented elements. For comparative purposes, metric data for 63 modern adult wild wolves from Siberia and the Russian Far East are analyzed. These specimens came from locations spanning 45° to 70° N, and 60° to 177° E (Table S2).

Only skeletal element dimensions from dogs with fully adult dentition were analyzed, and these were taken to the tenth of a millimeter using sliding or spreading calipers. Dogs develop adult dentition around six months of age, but their postcranial skeletons are not fully fused until around one year of age, by which time most dogs are sexually mature (Geiger et al., 2016). Among modern breeds, small and medium-sized dogs (Beagle-sized and smaller in the study) reach 99% of their adult weight around 9−10 months of age, while larger animals (Labrador Retriever and larger) reach this point at 11−15 months (Hawthorne et al., 2004). As such, some analyzed individuals potentially had not reached adulthood by the time of death (they were 6−11 months of age). This issue is not unique to this study. Most studies of fossil or sub-fossil canids do not utilize additional ageing methods on crania or mandibles that could demonstrate their status as fully-grown adults. Where whole or nearly whole skeletons were available for analysis in this study, individuals under one year of age (but with adult dentition) are noted (Table S1).

2.2. Dating

AMS radiocarbon dates are available for 25 of the analyzed dogs (Table S1). In most other cases, radiocarbon dates are available for associated archaeological materials. All dates were calibrated in Oxcal 4.2.4 using the IntCal-13 dataset and are presented at two sigma (Bronk Ramsey, 2014; Reimer et al., 2013). When only associated radiocarbon dates are available, the date ranges provided are the overall maximum and minimum ages for the sets of calibrated dates. When only typological age assessments exist, the broadest time estimates for the sites are provided. None of our analyses and

interpretations require precise chronologies but instead focus on broad trends through time. For graphical and analytical purposes, the midpoint of such ranges is utilized. Overall, the analyzed dogs date from ~10,500 to 100 cal. BP.

Radiocarbon dates on dog remains often carry old carbon offsets, particularly where their diets were heavily reliant on marine or freshwater fauna. This requires that relatively broad age estimates be used for many specimens analyzed, and that chronologies constructed using associated archaeological materials be utilized. For example, at the Arctic Ust'-Polui site on the lower Ob' River (case #s 54−105), the freshwater reservoir effect in the dated dogs was at least 500 years (Losey et al., 2017). For this site, a modeled age range based on associated dates on charcoal and reindeer bone is utilized to avoid this age bias. A freshwater old carbon offset is also evident or suspected with all of the Middle Holocene dog dates from the Lake Baikal shore and nearby portions of the Angara and Selenga rivers (case #s 1−11), where dog diets were dominated by freshwater fauna (Losey et al., 2011, 2013, 2018c). The extent of the old carbon offset with these dates is expected to be no more than two or three centuries (Losey et al., 2013). Finally, most of the Primorye and Chukotka dogs (case #s 32−35, 110−199) derive from coastal sites dominated by remains of marine fauna, suggesting that human and dog diets were rich in marine foods. The maximum marine reservoir effect in Primorye is suspected to be ~400 years (Kunikita et al., 2017), while in Chukotka, the maximum is ~750 years (Dumond and Griffin, 2002; Khasanov and Savinetsky, 2006). For these marine sites, the actual reservoir effect on dog radiocarbon dates is likely to be far less than these maximum values. Regardless, we utilize chronological information based on non-marine sources wherever possible.

2.3. Body mass estimation

Body mass estimates were made using regression equations in Losey et al. (2017), which were created using modern adult dogs and modern North American grey wolves with known body masses. Other body mass estimation methods (e.g., Van Valkenburgh, 1990; Wing, 1978) were developed using far smaller numbers of specimens, multiple carnivores where only species average body masses were known, or using element dimensions that correlate more poorly with body mass. In all but two cases, length measurements of the cranium or mandible following Von den Driesch (1976) were employed. In case #s 11 and 32, limb dimensions were utilized due to the fragmented nature of the associated skull elements. All skeletal element dimensions were natural log transformed. The log-transformed values were entered into regression equations and the results transformed back into real values, i.e., body mass estimates in kilograms (Table S1). Prediction errors for body mass estimations are also provided.

2.4. Bite force estimation

Estimated body masses were used to calculate bite forces (BF) for dogs and wolves using regression formulae developed by Ellis et al. (2008), which were built upon *in vivo* bite force measurements in dogs (Table S1). Ellis et al. (2008) found that lever models of bite force commonly used in studies of living and extinct carnivores substantially underestimate actual bite forces in dogs. Most importantly, they demonstrate that body mass correlates well with measured bite forces, and provide equations to convert body mass into an estimate of bite force (in Newtons) at both the canine and second mandibular molar.

For the mandibular second molar (M2), equation 11 in Ellis et al. (2008:775) was utilized to calculate bite force. Specifically:

$$BF = \text{body mass in kg}(80.3) + 258$$

For bite force at the canine (C), equation 18 in Ellis et al. (2008:775) was employed:

BF = body mass in kg(18.7) + 157

While it might be preferable to use skeletal element shapes and dimensions (rather than body mass estimates derived from them) to make bite force estimations, the equations developed by Ellis and colleagues do not utilize dimensions commonly taken in studies of archaeological dog remains. Estimating bite forces using calculated body masses allows for the maximum number of specimens to be compared in a consistent manner. In addition, bite forces are examined comparatively in this study, meaning that highly precise estimates are not needed to illustrate our points.

2.5. Subsistence economy groups

To assess the relationship between dog body mass and human subsistence economy, all specimens were assigned to categories encompassing the food production and acquisition practices of their archaeological context: 1) terrestrial hunter-gatherer (foragers who primarily rely on food from inland terrestrial environments); 2) aquatic (lake and river) and terrestrial hunter-gatherer; 3) marine coastal hunter-gatherer; and 4) pastoral-agricultural (Table S1). These categories are coarse, with each characterized by significant internal variability, but employing them here permits classification of all specimens. Assignments were made based on site location and faunal and floral remains recovered from associated archaeological deposits. For 16 of the specimens analyzed here, these assignments were further confirmed through dietary stable isotope (δ^{13}C and δ^{15}N) values for dog bone collagen (Fleming et al., 2018; Losey et al., 2011, 2013, 2018a).

To control for age as a biasing factor in comparing the relationships between subsistence economy and body size, we included only those specimens with age midpoints less than 2500 cal. BP; body size outliers (n = 4) were also excluded to be as conservative as possible in these comparisons. For the total dog sample, the coastal hunter-gatherer, aquatic-terrestrial hunter-gatherer, and pastoral-agricultural groups each had over 50 specimens. Only six specimens could be assigned the terrestrial hunter-gatherer category, all dated to the Early or Middle Holocene. This latter category was eliminated from consideration, leaving a total of 175 specimens in the analyses, or 87.9% of the total sample. Importantly, the coastal group is almost entirely composed of specimens from eastern Chukotka (49 of 52 specimens), while the aquatic-terrestrial group is nearly entirely from a single site, Ust'-Polui in Iamal (52 of 54 specimens).
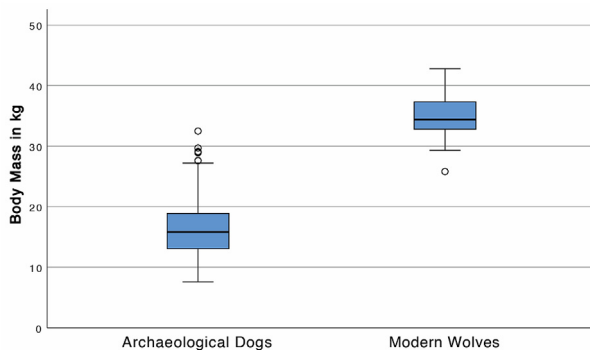
Fig. 2. Box plot of estimated body masses for archaeological dogs and modern wolves. The horizontal lines indicate the means, the box the interquartiles, and the whiskers the extent of values within 1.5 times the interquartile range. The circles indicate outliers in the two data sets.
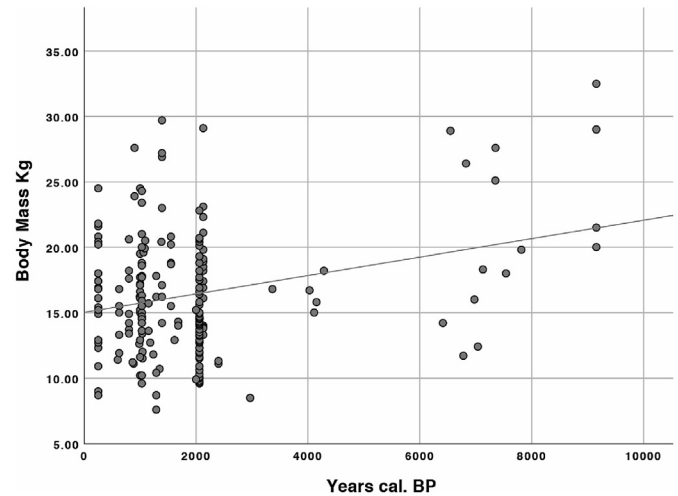
Fig. 3. Scatter plot of estimated dog body mass by specimen age, outliers included. Points indicate specimens, and the regression line is for illustrative purposes only.

3. Results

3.1. Dog and wolf body mass estimates

Estimated body masses for the archaeological dog remains range from 7.6 to 32.5 kg, with the mean being 16.4 kg (SD = 4.64) (Fig. 2). Dogs greater than 27.6 kg (seven specimens) are identified as outliers based on having body masses greater than 1.5 times the interquartile range. Of the 199 dogs, 176 (88.4%) have estimated body masses less than 21.5 kg, the proposed cutoff in carnivore body size at which individuals tend to pursue prey less than half their own body sizes (Carbone et al., 1999). For the modern Siberian wolves, body mass estimates range from 25.8 to 42.8 kg, with a mean of 35.0 kg (SD = 3.59), more than double the mean body mass of the dogs. The smallest wolf in the sample, however, is identified as an outlier. All wolves fall above the 21.5 kg threshold demarcating individuals that tend to pursue prey larger than themselves. Even including all outliers in both groups, the archaeological dogs and modern wolfs have significantly different body mass averages (t(260) = −29.102, p = <0.000).

3.2. Body mass and age

A Pearson's test revealed a moderately positive correlation between estimated body mass and specimen age, which is statistically significant (r = 0.276, n = 199, p = <0.000) (Fig. 3). This indicates a slight downward trend in dog body mass through time. When the body mass outliers are removed, however, this trend is not statistically significant (r = 0.114, n = 192, p = 0.116). By ~8−6000 cal. BP, body masses were already quite variable, from 11.7 to 29.9 kg, including multiple individuals under 20 kg. Two of the smallest individuals from this early period, case #3 from Ust'-Belaia and case #5 from Pad' Kalashnikova (both burials of whole skeletons), were juveniles at the time of death. However, two additional small individuals of this same period (case #s 4 and 6, both burials) are from adults, and have estimated body masses of 11.7 kg (SD = 1.6) and 16.0 kg (SD = 2.2). Finally, Fig. 3 indicates a significant temporal gap in the analyzed dogs extending from ~6400 to 4300 cal. BP.

3.3. Intrasite body mass variation

Five of the 28 sites have over 15 body mass estimations each,

Table 1
Comparison of body mass estimates for all archaeological sites from the last 2500 years with more than 15 individuals. Site locations are shown on Fig. 1.

	n	Mean (kg)	SD (kg)	Minimum (kg)	Maximum (kg)	Range (kg)
Ivolgin	17	18.5	4.01	13.3	29.1	15.8
Ust'-Polui	52	14.6	3.38	9.6	22.8	13.2
Ust'-Voikar	23	16.4	4.11	8.7	24.5	15.8
Kanisak	19	16.6	3.04	10.2	20.8	10.6
Paipelghak	22	17.3	4.56	9.6	27.6	18.0
Modern wolves	63	34.9	3.59	25.8	42.8	17.0

Table 2
Bartlett's tests of homogeneity of variance values for comparison of variance in individual archaeological sites from the last 2500 years with the variance in the modern wolf sample.

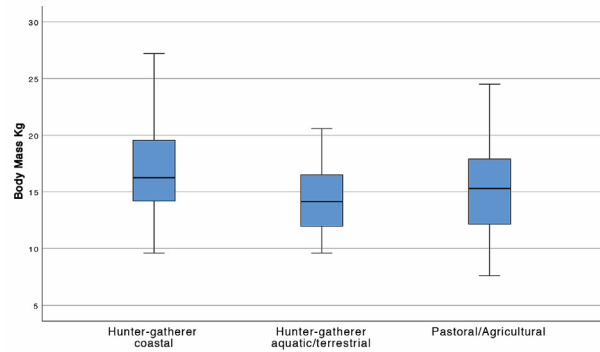|	n	Variance	X^2	P
Ivolgin dogs	17	16.078	0.3233	0.570
Ivolgin-no outliers	16	9.182	0.3345	0.563
Ust'-Polui	52	11.458	0.1908	0.662
Ust'-Polui-no outliers	52	11.458	0.0060	0.938
Ust'-Voikar	23	16.865	0.6101	0.435
Ust'-Voikar-no outliers	23	16.865	1.1403	0.286
Kanisak	19	9.212	0.7315	0.392
Kanisak-no outliers	19	9.212	0.3784	0.538
Paipelghak	22	20.783	1.9173	0.166
Paipelghak-no outliers	21	16.329	0.8821	0.348
Wolves	63	12.883		
Wolves-no outliers	62	11.699		

Fig. 4. Box plot of estimated body masses for archaeological dogs by subsistence economy group. The horizontal lines indicate the means, the box the interquartiles, and the whiskers the extent of values within 1.5 times the interquartile range.

and these were selected to explore body size variation within single archaeological communities (Table 1). All of the sites date to the Late Holocene, and include: 1) Ivolgin (case #s 12−28), a fortified agricultural and pastoral town; 2) Ust'-Polui (case #s 54−105), an inland Arctic hunter-gatherer ritual site with riverine fishing and hunting; 3) Ust'-Voikar (case #s 113−135), an inland Arctic site with hunting, riverine fishing, and domestic herd animals; 4) Kanisak (case #s 159−177), an Arctic marine hunter-gatherer site; and 5) Paipelghak (case #s 178−199), an Arctic marine hunter-gatherer site. The modern wolf sample was utilized for comparative purposes.

Estimated dog body masses in these sites ranged from 10.6 to 18.0 kg when including all specimens identified as outliers (Table 1). The range in the wolves was 17.0 kg, with all outliers included. Bartlett's tests of homogeneity of variance show no statistically significant difference in the dog's body mass variances compared to those of the wolves (Table 2). This pattern held whether or not body mass outliers were included in the comparisons. In other words, the range of body mass variability within each site was not statistically different from that seen in the sample of modern wolves, the latter deriving from across Siberia and the Russian Far East.

3.4. Body mass and ambient temperature

Archaeological site latitude was used as a proxy for ambient temperature in assessing the applicability of Bergmann's rule. Dog body mass in the sample population is not significantly correlated

with latitude when examined through a Pearson's correlation (r = 0.107, n = 199, p = 0.133). Excluding the outliers further weakens the correlation (r = 0.103, n = 192, p = 0.155). This provides no support for Bergmann's rule, which postulates that body sizes should increase with decreases in ambient temperature.

3.5. Body mass and subsistence economy

A statistically significant difference was found between the subsistence economy groups, as demonstrated by a one-way ANOVA (F(2,172) = 4.9, p = 0.009) (Table 3; Fig. 4). A Tukey post hoc test showed that the coastal hunter-gatherer group had larger average body masses than the aquatic-terrestrial hunter-gatherer group (p = 0.006). No statistically significant difference was found between the coastal hunter-gatherer and pastoral-agricultural groups (p = 0.329), nor between the aquatic-terrestrial hunter-gatherer and the pastoral agricultural groups (p = 0.147). Recall that the comparison between the aquatic-terrestrial and coastal hunter-gatherer groups is largely one between a few coastal sites in Chukotka and the riverine-oriented Ust'-Polui site in Iamal. Including the four body mass outliers in these analyses produced no meaningful differences in these comparisons.

3.6. Bite force estimates

For the total sample of dogs, the mean estimated bite force at the M2 was 1572.9 N (st. dev. = 372.7), and when removing the outliers in the earlier body mass calculations, the mean bite force reduces to

Table 3
Comparison of body mass estimates by subsistence economy group from sites dating to the last 2500 years.

	n	Mean (kg)	SD (kg)	Min (kg)	Max (kg)	Range (kg)
Hunter-gatherer coastal	52	16.9	4.12	9.6	27.2	17.6
Hunter-gatherer aquatic-terrestrial	54	14.5	3.38	9.6	22.8	13.2
Pastoral-agricultural	69	15.9	4.03	7.6	24.5	16.9

Table 4
Comparison of estimated bite forces at the canine and second molar of archaeological dogs and modern wolves, in Newtons (N).

	n	Mean (N)	SD (N)	Min (N)	Max (N)	Range (N)
Canine bite fore						
Dogs	199	463.2	86.8	299.1	765.3	466.2
Dogs, no outliers	192	454.5	74.8	299.1	666.0	366.9
Modern wolves	69	810.6	67.2	638.8	956.9	318.1
Modern wolves, no outliers	62	813.3	64.0	704.3	956.9	252.6
Second molar bite force						
Dogs	199	1572.9	372.7	868.1	2870.1	2002.0
Dogs, no outliers	192	1535.4	321.1	868.1	2443.8	1575.7
Modern wolves	69	3064.5	288.7	2327.1	3693.0	1365.9
Modern wolves, no outliers	62	3076.4	275.0	2608.1	3693.0	1084.9

1535.4 N (SD = 321.1) (Tables S1 and S2; Table 4). For the canine, the mean estimated bite force for the total sample was 463.2 N (SD = 86.8), and removing the outliers reduces the mean to 454.5 N (SD = 74.8). For the total wolf sample, the mean M2 bite force is 3064.5 N (SD = 288.7), and excluding the single individual identified as an outlier by body mass, the mean increases to 3076.4 N (SD = 275.0). For the wolf canine, the overall mean is 810.57 N (SD = 67.2), and removing the outlier increases the mean to 813.3 N (SD 64.0). Overall, the dogs have average bite forces that around half those of modern wolves, and with or without outliers, the mean bite forces of the two groups are significantly different, with all T-tests returning significance values of <0.000. Estimated bite forces overlap between the dogs and modern wolves only when the outliers are included in comparisons, and then only marginally.

3.7. Bite force and age

Given that our methods involved calculating bite force directly from body mass estimates, trends in these estimations directly mirrored those in the body mass and age correlations. When all specimens are included, a Pearson's test revealed a moderately positive correlation between estimated second molar and canine bite force with specimen age, both of which are statistically significant (M2, r = 0.275, n = 199, p = <0.000; C, r = 0.275, n = 199, p = <0.000). Removing the body mass outliers, however, makes both correlations not statistically significant (M2 and C, r = 0.113, n = 192, p = 0.119).

3.8. Bite force and subsistence economy

As with the previous body mass and subsistence economy examination, we excluded the body mass estimate outliers, the six terrestrial hunter-gatherer specimens, and all dogs with age midpoints greater than 2500 cal. BP (Table 5). Using the remaining 175 specimens, a statistically significant difference was found between the groups as demonstrated by a one-way ANOVA (F(2,172) = 5.0, p = 0.008). A Tukey post hoc test indicates that the coastal hunter-gatherer group had higher average M2 bite forces than the aquatic-

terrestrial hunter-gatherer group (p = 0.006). No statistically significant difference was found between the coastal hunter-gatherer and pastoral-agricultural groups (p = 0.357), nor between the aquatic-terrestrial hunter-gatherer and the pastoral-agricultural groups (p = 0.123). The same statistical results were rendered when the C bite force data was analyzed. Note that including the four body mass outliers in these analyses produced no meaningful differences in the comparisons of bite force by subsistence economy group.

4. Discussion

4.1. Body mass patterns, variation

Nearly 90% of the analyzed archaeological dog remains have estimated body masses less than 21.5 kg. This suggests that the vast majority of these animals were most suitable for procuring prey less than half their body sizes and had much reduced caloric requirements compared to wolves (Carbone et al., 1999). These patterns are indicative of the dogs' adaptations to dietary niches dominated by humans, which likely involved intermittent human provisioning as well as scavenging and hunting small fauna. Reductions in body sizes had clearly produced domestic dogs with quite different physical capabilities and characteristics than their wild counterparts. Overall, most of the dogs had body masses less than half of those of modern wolves, which should correspond to them having reduced ability to grasp and masticate food items, less efficient long-distance running, reduced sexual size dimorphism, earlier age of sexual maturity and attainment of adult body size, and even extended life span. Late Pleistocene wolves in Siberia appear to have been somewhat larger than modern wolves from this same region (c.f., Germonpré et al., 2017). The dogs of the study area, even by the Early Holocene, were quite different from these large carnivores.

The extent of dog body mass variation requires scrutiny. The seven largest individuals were recognized as outliers when their body masses were estimated. Possibly, these specimens were misidentified—they are small wolves or wolf-dog hybrids.

Table 5
Comparison of estimated bite forces at the canine and second molar of archaeological dogs by subsistence economy group, in Newtons (N).

	n	Mean (N)	SD (N)	Min (N)	Max (N)	Range (N)
Canine bite force						
Hunter-gatherer coastal	52	472.6	77.16	336.6	666.0	329.4
Hunter-gatherer aquatic-terrestrial	54	428.7	63.13	335.8	583.4	247.6
Pastoral-agricultural	69	454.4	74.16	299.1	615.8	316.7
Second molar bite force						
Hunter-gatherer coastal	52	1613.2	331.40	1029.4	2443.8	1414.4
Hunter-gatherer aquatic-terrestrial	54	1424.8	271.11	1025.8	2089.0	1063.2
Pastoral-agricultural	69	1535.3	318.44	868.1	2228.1	1360.0

Introgression between dogs and wolves in Eurasia occurred in the past, but this seemingly mostly involved gene flow from dogs into wolves (Bergström et al., in review; Pilot et al., 2019). Four of the seven largest individuals (case #s 1, 8, 107, and 109) have age midpoints of 6500 cal. BP or older, with the remaining three dating to the Late Holocene (case #s 152, 198, and 25, respectively). The best documented of former is case #1 from Shamanka II on Lake Baikal. The estimated body mass for this male (its *os penis* was present) is 27.6 ± 3.8 kg (Table S1). This individual was buried in a grave containing remains of several humans, had a diet rich in aquatic foods (similar to that of the humans buried there), and suffered from pre-mortem injuries to its spine, ribs, and dentition (Losey et al., 2011). Three studies have identified this specimen as a dog (Drake et al., 2015; Bergström et al., in review; Losey et al., 2011). Two of the other early specimens are from the Zhokhov site in the Arctic, where mtDNA and traditional morphometrics have identified multiple individuals as dogs (Lee et al., 2015; Pitulko and Kasparov, 2017). The largest Zhokhov specimens examined here, both mandibles, produced body mass estimates of 29.0 ± 4.0 kg and 32.5 ± 3.6 kg (Table S1). These studies indicate that at least some of the largest specimens in our dataset are dogs, and misidentification alone cannot account for the upper end of the body mass variation.

Some body mass variation in our estimates is due to sexual dimorphism and ontogenesis. Wolves are the most sexually size dimorphic canids, with males outweighing females ~1.28:1.0 (Moehlman and Hofer, 1997). Some modern large dog breeds exhibit similar levels of sexual size dimorphism (Frynta et al., 2012). Sexual size dimorphism effects should be most pronounced where average dog body masses are greatest, which here tends to be in the Early and Middle Holocene. Given that dogs follow Rensch's rule—that size dimorphism differences decrease with decreases in body size (Frynta et al., 2012)—such effects should be lower than 1.28:1.0 in nearly all of our dogs, as most are half the size of wolves. Currently, no means of morphologically sexing isolated dog skeletal remains are available, making it impossible to assess relationships between sex and body mass directly.

Dog age at death also results in some variability. The average body mass of the dogs in our sample is 16.4 kg (SD = 4.64), and dogs of this size reach 99% of their adult body masses at 39–52 weeks of age (~9–12 months) (Hawthorne et al., 2004). Given that this study included all individuals with fully adult dentition, which is present in dogs around six months of age (Geiger et al., 2016), some individuals could have been three to six months from reaching near-adult body size. Ontogenesis is expected to be a significant contributor to the relatively low average body mass observed at the Ust'-Polui site, where most of the dog remains were found as disarticulated elements, likely from being sacrificed and eaten (Losey et al., 2018b). Our body mass estimates for this site, like nearly all other samples in the study, are based on measurements on mandibles with adult dentition. Ageing based on fusion of the limb elements at Ust'-Polui indicates that 44.6% of the assessable individuals (n = 78) were less than 11–12 months of age at death, meaning that some portion of the animals with adult dentition at the site was not yet of full adult body size—they were 6–12 months of age at death. Further assessment of the effects of ontogenesis on our results will require the application of additional ageing methods (tooth wear, cementum annulation, or pulp cavity closure studies).

Regardless of the effects of these biases, substantial body size variation is present through the analyzed period. For example, the adult dogs from the Lake Baikal area dating to ~6500−7350 cal. BP (case #s 1−6, 8; all burials of articulated skeletons) have body masses ranging from 11.7 to 28.9 kg (Table S1, Fig. 3). Here the largest adult dogs are more than twice the size of the smallest

individuals. They are more variable in mass than the modern Russian wolves analyzed, and more variable than would be expected based on sexual dimorphism alone. Further, our analyses showed that variance in dog body mass within individual archaeological sites (all from the Late Holocene) is statistically indistinguishable from that of wild modern wolves collected across most of the entire study area, even when all outliers were removed from consideration. This suggests little strict control over dog body size by humans, even at individual archaeological communities. Perhaps control over breeding focused primarily on dog behavior rather than size or overall appearance, with a diversity of roles being available to dogs of varying abilities. To put this more directly, they were not bred to perform only one set of tasks exclusively, or dogs of various sizes could adequately accomplish those tasks, points we return to in section 4.6.

Overall, estimated adult dog body masses from Siberia and the Russian Far East range from 7.6 to 32.5 kg. This is just over a four-fold difference in body mass. These early dogs were nonetheless far less variable than modern dog breeds, where the largest types can be over fifty times the mass of the smallest (Speakman et al., 2003). Modern breeding practices have produced far more variability in dog size over the last few centuries than was present in Siberian and the Russian Far East over the preceding ~9000 years.

4.2. Diachronic size reduction and temporal gaps

A slight downward trend through time is present in the dog body mass data, but this trend was not statistically significant when the outliers were removed. As argued in section 4.1, some of the body mass outliers are dogs and thus should be considered in the analysis of diachronic body mass change. Arguably then, these data suggest at least some drift or selection for smaller dogs through time. One possible cause of this trend is human preference for smaller dogs. People might have favored smaller dogs for some roles, particularly the hunting of small fauna, where agile individuals might be more successful. Smaller dogs might also be preferred to reduce costs—all things being equal, they require less food to sustain themselves, and less food to reach full adult body mass. Adult body size could also be reached earlier in the lives of smaller dogs, a benefit if they were kept primarily as food sources. Within our dataset, no clear temporal trend toward increasing use of dogs for food is evident, but most collections have not been described with the level of detail necessary to make such evaluations. Consumption of dogs is well evidenced at some Late Holocene sites, including Ust'-Polui, described in section 4.1. Further, this practice is strongly suspected to have been common at Cherniatino 2 in Primorye (case #s 36−45), a medieval agricultural settlement where dog remains exhibited butchery marks and were discarded like those of other domestic animals (Nikitin and Chzhun, 2008). Notably, butchery marks are also found on some of the earliest dogs in our dataset, namely those from the Arctic Zhokhov site (Pitulko and Kasparov, 2017). It is difficult to discern whether any of this butchery evidence is indicative of dog consumption limited to occasions of ritual or food scarcity, or rather breeding of dogs primarily for use as food. Regardless, dogs seem to have been eaten over much of the study period, so it is difficult to link these practices to the gradual reduction in body size.

An additional set of factors that might account for some decline in dog body size is greater survival rates for smaller dogs in human-dominated food environments. Reduced food quantity and quality could be selective forces, but the extent of such stresses across the archaeological communities is mostly unknown. Some evidence for recurrent human food stress has been found in at least one study setting, namely the lands just west of Lake Baikal (Cis-Baikal). Many Middle Holocene humans buried in this region, including at

cemeteries where several of our buried dogs were found, show relatively high incidences of enamel hypoplasia, probably the results of seasonal food stress (Lieverse et al., 2007). Further, across the North, 20th century working dogs experienced far higher rates of tooth fracture and premortem tooth loss than contemporary wolves from these same regions (Losey et al., 2014). This may relate to the dogs inhabiting food-poor environments where they had to extract nutrients from hard foods such as bone and frozen flesh. The dogs were intentionally fed such foods, or resorted to scavenging on them when higher quality and more easily handled foods were not available. These studies provide reasons to expect that the archaeological dogs occupied niches where food stresses occurred, at least on an intermittent basis. This would seemingly favour animals with lower caloric requirements—those with smaller body sizes.

However, just the opposite has been proposed for some mammals. Larger body sizes potentially afforded greater abilities to withstand food shortages by providing increased fat stores (Boyce, 1979; Millar and Hickling, 1990). Not just the quantity and quality of food changed with domestication, however, but also how this food was obtained. If dogs obtained most of their food by being provisioned by people and through scavenging, perhaps they would no longer require large and strong bodies to run down, kill, and process large prey. Maintaining larger body sizes might be a costly disadvantage. Conversely, intragroup competition for human food scraps might be high, particularly in situations where food stress is common, benefitting larger, stronger individuals who could outcompete smaller individuals for these resources. Regardless, all of these proposed selective forces would have been in play early in the domestication process, long before the time of our earliest specimens. Our data may show the continuing effects of such selective forces through the Holocene, the body size outcomes of which were moderate.

One additional note regarding temporal patterns is the dearth of specimens dating from ~6400 to 4300 cal. BP (Fig. 3). The near-absence of dogs in this general period was previously noted in surveys of Cis- and Trans-Baikal dog remains (Losey et al., 2013, 2018c). While the current study is not a comprehensive review of all dog remains in Siberia and the Russia Far East, it is the broadest examination of dogs in these regions to date. Our data suggest a decline in dog abundances across a far broader area than the southern portions of Siberia flanking Lake Baikal, including the Pacific Coast regions of Primorye to the east and portions of the Arctic to the north. At present, it is unknown if this pattern can be attributed to uneven archaeological sampling or broader cultural or environmental factors. Human and dog population movements could be related to this temporal gap (Bergström et al., in review). Migrations of new populations also could be complicating factors in the body mass temporal trends (c.f., Welker and Dunham, 2019).

4.3. Dogs and Bergmann's rule

Dog body mass showed no statistically significant relation to latitude, used here as a proxy for ambient temperature. In many ways, this is not surprising. First, not all mammals follow Bergmann's rule (Ashton et al., 2000), and even grey wolves follow the patterns predicted by rule in select cases only (Geist, 1987; Meachen and Samuels, 2012; Meiri et al., 2004; Rosenzweig, 1968). Second, thermal regulation, the original explanation for Bergmann's rule (Bergmann, 1847; Mayr, 1942), can be achieved through other biological and even cultural means. For example, human homes might buffer the effects of low ambient temperatures on dogs by providing them with shelter during severe conditions. Biological adaptations beyond changes in body size can also help in thermal regulation. With canids, the most obvious of these

would be increased pelage length or density in cold environments. Increased fat stores would also assist in conservation of heat. Neither of these adaptations would manifest in the skeleton, meaning they are undetectable in archaeological settings.

4.4. Subsistence economy effects?

For the dogs from the last ~2500 years, the only significant difference in body mass by subsistence economy occurred between the coastal hunter-gatherer group and the aquatic-terrestrial hunter-gatherer group, the former having a mean body mass 2.4 kg greater than the latter. Neither of these hunter-gatherer groups differed significantly from the pastoral-agricultural dogs in body mass. The same pattern was observed in the bite force data, with significant differences only found between the coastal and aquatic-terrestrial groups. We suspect the nature of these two samples exacerbated both sets of differences. The dogs from Ust'-Polui account for nearly all of the aquatic-terrestrial group, and their average body mass is likely reduced because of the presence of many juvenile dogs at the site (see section 4.1). Juveniles appear to constitute far smaller parts of the coastal assemblages, nearly all of which are from Chukotka.

Beyond these biases, it is unclear why coastal subsistence economies might afford larger dogs than aquatic-terrestrial settings. Perhaps the former provided a more productive and reliable food environment for dogs, including more calorie-rich food waste (from sea mammals, for example) and opportunities for scavenging, including in intertidal areas. Stable isotope analysis of dogs at Ust'-Polui, by contrast, reveals these individuals had diets primarily composed of riverine fish, which are relatively lean (Losey et al., 2018a). Other factors seem just as likely to account for the observed body size differences, including genetic-based size differences between the two groups, or even different dog roles between the two areas. The latter point is returned to in section 4.6 below. Overall, this general area of inquiry may be more fruitful in the future when comparisons can be made with other dog populations, particularly urban street dogs, which might mostly scavenge, or dogs living with hunters of large terrestrial mammals, who might regularly feed on very dense bone.

4.5. Bite force comparison implications

The average archaeological dog bite force was around half of those of the average modern wolves (Table 4), and dog bite forces appear to have declined slightly over the Holocene. Overlap in estimated bite forces occurs between only the very largest dogs and the smallest wolves. This indicates that the size reduction associated with domestication had produced dogs with far lesser abilities than most wolves to grasp prey and food items, and reduced abilities to crush hard food items. As with the effects of overall body size reduction, this would have affected dogs' predatory capabilities, namely by limiting them to pursuing prey smaller than themselves. These reduced bite forces also placed restrictions on what foods could have been effectively given to dogs, and likely also shaped dog food preparation methods. Bones of larger mammals might need to be fractured before being given to dogs, or even cooked to reduce their resistance to fracture (Outram, 2002). Because most dogs have far less jaw strength than wolves to masticate hard foods, they would have had to extend the time spent gnawing on them to extract nutrients, increasing both tooth wear and opportunities for fractures. This might help explain the relatively high rates of tooth fracture and loss in historic northern dogs relative to wolves, mentioned in section 4.2. Regardless, foods other than bone likely were far more economically used in feeding dogs, particularly fish flesh and bone. Provisioning dogs with fish in

Siberia and the Russian Far East is widely reported historically, particularly in regions with productive freshwater or anadromous fisheries (c.f., Losey et al., 2018a). These foods were not time or cost-prohibitive to procure and process for dogs, particularly in the North where they could be frozen for storage. Further, dogs could effectively masticate them because of their far less dense skeletal structures. Offal, blubber, and general human food waste are other likely candidates. Extensive use of carbohydrate-rich foods as dog food would require dogs to have the capacity to digest these foods, which seems to have primarily emerged in Eurasia several thousand years after dependence on starch-rich foods developed with increasing reliance on agriculture (Bergström et al., in review).

To estimated bite forces, we utilized regression formulae created using data derived from directly measured bite forces in modern dogs. The regression formulae require the estimated body masses for the specimens, the latter obtained through regressions on skeletal dimensions. This approach likely provides reliable indication of the scale of bite forces differences between the dogs and wolves, but could be improved upon with additional study. One improvement would be to calculate bite forces directly from skeletal element dimensions, avoiding the additional step of first estimating body mass. A second improvement would be to take into account differences in skull shape, not just element size, when estimating bite forces. Even Late Holocene archaeological dogs seem to differ in skull shape from most modern dogs (Drake et al., 2017), and such differences likely affect bite forces (Brassard et al., 2020).

4.6. Body mass and dogs' roles

One of the dog's most important roles in the past was surely hunting (c.f., Guagnin et al., 2018; Lupo, 2017; Yeomans et al., 2019). Body mass estimates for the Siberian and Russian Far East dogs indicate that most of these individuals lacked the necessary body sizes and strength to be hunters of prey larger than themselves, at least without the assistance of humans. However, the dogs could have been active in such hunts through locating, tracking, cornering, or driving large-bodied prey. Hunting smaller animals such as hares, sables, marmots, ground squirrels, and some birds was well within their range of their own capabilities, and they could readily join people in procuring these resources. While many of the dogs analyzed came from subsistence economies where freshwater fish or marine mammals were staples, most of these potential prey were beyond their reach and were obtained for them by their human companions. Notably, dogs historically were involved in hunting of some pinnipeds in the study area, primarily by sniffing out locations of their breathing holes and dens in the ice (Nomokonova et al., 2013).

A second major role for dogs is transport, including sled pulling and pack carrying. The issue of dogs' participation in transport has been approached recently in archaeology using body mass estimates. Pitulko and Kasparov (2017) argued that some of the dogs at the Zhokhov site dogs pulled sleds based on their estimated masses. They drew on the Coppingers' (2001) arguments regarding the ideal body size for modern racing sled dogs, which they assert is 20−25 kg. These arguments relate primarily to thermal regulation, caloric costs, and strength. Dogs larger than the ideal mass tend to over-heat when running and require more food to sustain, while those below this threshold are not strong enough to rapidly propel a sled over long distances. While this body mass range may be ideal for racing, traditional Arctic sled dogs had far different lives than today's racing animals. Speed of travel would be lower than in most race settings, rests more frequent, and loads pulled would often be far greater. In other words, ideal racing bodies might differ significantly from working sled dog bodies.

Further, the limited quantitative information on early historic period working sled dogs (from Chukotka, Ellesmere Island (Canada), and Greenland; n = 46) shows widely ranging body masses, from 12 to 49 kg, with a mean of 25.8 kg (SD = 8.80) (Losey et al., 2018b). Within a single community on Ellesmere Island in 1966-7, adult sled dogs ranged from 23.1 to 49 kg, with the mean body mass being 33.8 kg (SD = 7.10), far above the so-called ideal. This mean body size is greater than the maximum estimated body mass for any dog in our sample. At the opposite end of the size spectrum, the estimated body masses for 14 sled dogs from eastern Chukotka, collected in 1901, range from only 12.1−20.2 kg, with a mean of 16.8 kg (SD = 2.48).

Dog sledding is said to have been practiced within the study area at Zhokhov by ~9000 cal. BP, at Ust'-Polui by ~2200 cal. BP, and in eastern coastal Chukotka by at least 1300 cal. BP (Losey et al., 2018b; Pitulko and Kasparov, 2017; Vasyukov and Savinetsky, 2016). The average body mass of the archaeological dogs in this study (16.4 kg) is just under 4 kg lower than the smaller end of Coppinger's ideal range for racing sled dogs, but within the range of historic working sled dogs, and nearly identical to that of the historic sled dogs from Chukotka. In other words, our body mass estimations allow for all but the very smallest dogs in the study to have been sled dogs, regardless of period.

Welker and Byers (2019), building on Henderson (1994) and US War Department (1994), estimated body masses of archaeological dogs from the American west to explore these animals' capacities in transport. They summarize historical, experimental, and recreational data on load sizes transported by dogs. The study shows that sled dogs, working as a team, can pull up to 300% of their body masses in ideal conditions, but that loads of ~115% of body mass were ideal where frequent rests could be taken. For rapid sled transport, loads were further reduced to about 60% of a dog's body mass. Loads carried as packs on the backs of dogs were lower, ranging from ~65 to 25% of body mass.

The Welker and Byers approach to utilizing dog body masses allows for the capacities of the study dogs to be explored. At 16.4 kg, our mean dog size, the pack loads carried by the dogs would range from 4.1 to 10.7 kg. While these are seemingly small loads, if a household or small community had access to even five dogs, they could pack around 54 kg, equivalent to the total edible body mass of a large adult reindeer (Ashley, 2002). This is a significant contribution, potentially extending the foraging radius of the group by reducing the burden carried by humans, freeing up individuals to transport other items or engage in other tasks. Assessing the size of loads carried on sleds is more complex, as this would depend on how many dogs were pulling each load. Using the proportion of 115% of body mass, a team of just four of our average dogs could pull ~75 kg. Again, this is a significant mass of gear or food, but if the sled were designed for hauling people, probably only a single adult individual could be accommodated. Using the 300% pulling capacity, the load could be as high as 300 kg with just four dogs. At this level, the sled would accommodate an adult human and much gear, or even significant portions of some of the largest prey animals in the study area (except Cetacea) such as muskox, walrus, or elk. Perhaps more likely, sleds were mostly for more modest loads of gear and food, and just a few dogs pulled these loads with people running or walking alongside. Regardless, such practices would reduce the number of trips required in transporting loads.

The final dog role considered here is guarding and herding livestock. We identified 69 dogs from settings where domestic herd animals were present, and their mean body mass was 15.9 kg (SD = 4.03) (Table 5). Modern livestock guarding dogs tend to be large-bodied animals, with body masses of 30−55 kg, while herding dogs are far lighter, from 10 to 20 kg (Coppinger and Coppinger, 2007). Guarding dogs need larger bodies to fend of predators such

as wolves, while herding dogs require high levels of agility, favouring a smaller body sizes. If these modern body size patterns apply to earlier dogs, our body mass reconstructions indicate the absence of guarding dogs in Siberia and the Russian Far East prior to the modern period. Herding dogs, however, remain a strong possibility.

5. Conclusion

This macro-scale analysis of archaeological dog body size revealed several key characteristics of these Holocene animals. Body size variation was significant, even within individual communities, indicating limited human control over dog body size. Breeding for ability and disposition seems far more likely than strict breeding for appearance, the latter more characteristic of modern dog-keeping practices. Most dogs were relatively moderately sized, meaning they were best suited to pursuing small prey, and they likely depended on humans for much of their caloric intake. Bite forces were around half those of modern wolves, indicating they had reduced abilities to hold prey and masticate dense food items—they physically could not feed in the same way as their wild counterparts. The dogs also declined slightly in body size over the Holocene, potentially the result of factors such as human preference for smaller dogs or environments that favored smaller individuals who could survive on lower quality and quantities of food.

Some information on dog roles can also be gleaned from the body mass data. Most dogs were at the small end of the range expected for sled dogs, but well within the modern range of variation for these working animals, even by the Early Holocene. Nearly all could pack modest loads on their backs. Both of these forms of transport were likely valuable for people, particularly where other transport animals were not available. The body mass estimates suggest that livestock guarding dogs were absent, while herding dogs are possible. Participation in hunting is also highly likely, although most dogs lacked the physical abilities to take down larger prey on their own. Overall, a diverse array of dog roles is allowed for in the body mass data.

Future work on dog body mass variation will require improved methodologies, including those for ageing and sexing. Bone functional adaptation research to assess the habitual activities of dogs also needs to be developed. Integration of genetic research with studies of dog body size is also warranted, particularly for disentangling causes of regional variation and temporal shifts in body size. Expanding body size comparisons to adjacent regions should also prove interesting for assessing the application of Bergmann's rule and the effects of subsistence economy variation on dog body size.

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Data availability

All data for this project is presented in Tables S1 and S2.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2020.106430.

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