



New body mass estimates of British Pleistocene wolves: Palaeoenvironmental implications and competitive interactions



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ABSTRACT

Body mass was reconstructed for early Middle Pleistocene *Canis mosbachensis* and late Middle to Late Pleistocene *Canis lupus* from key assemblages in Britain, to explore the presence of temporal size variability and whether size fluctuations were related to changes in climate and environment or to differences in Pleistocene carnivore community structure. Using the well-known body mass predictor of lower carnassial (m1) tooth length, combined with an extant canid dataset incorporating 25 species, least squares regression was used to assess allometric scaling prior to modelling the relationship between body mass and m1 length, producing a new predictive equation of Pleistocene canid body mass. The medium-sized *C. mosbachensis* had relatively stable body mass, with remarkable consistency in size compared to populations in the late Early Pleistocene of Europe. Periodical fluctuations in climatic conditions had a minimal effect on *C. mosbachensis* size over time, with the terrestrial connection between Britain and mainland Europe at this time key in promoting body mass stability by enabling movement away from less favourable conditions and to follow prey into refugia. Overall changes in carnivore guild structure were of minimal influence to *C. mosbachensis* in Britain, as the continued predominance of larger carnivores, in particular a larger canid, effectively constrained *C. mosbachensis*. In contrast, the body mass of larger-sized *C. lupus* was highly temporally varied, with an increasing size trend evident into the Devensian. Similar body size in the penultimate interglacial (MIS 7) and Middle Devensian (MIS 3) populations likely reflects palaeoenvironmental similarity and comparable carnivore community and prey spectrums, with larger predators effectively constraining *C. lupus*. However, the severely cold conditions of the Early Devensian (MIS 5a) may have caused a Bergmannian response in wolves, leading to their comparatively much larger size, with *C. lupus* further ecologically “liberated” by an absence of larger multiple larger predators at this time.

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1. Introduction

Body size dictates a range of well-known ecological characteristics in mammals, including life history traits, thermal biology and metabolic rate (McNab, 1988, 1990; Hayssen and Lacy, 1985), as well as population group size and home range extent (Gittleman and Harvey, 1982; Eisenberg, 1990). External factors such as latitude, and by proxy climatic conditions, can also influence body size in some homeotherms, as proposed by Bergmann's rule (Rensch, 1938; Mayr, 1963; Rosenweig, 1968). Whilst sexual selection may also promote male-biased size differences in some mammals (Clutton-Brock et al., 1977; Isaac, 2005), Rensch's rule infers the correlation between sexual size dimorphism and mean body size (Rensch, 1960).

For carnivorans, body size defines ecological niche by determining prey selectivity and prey size (Gittleman, 1985), as well as shaping behavioural adaptations relating to activity rate, locomotion and mode of predation (McNab, 1980, 1990). It also correlates with community structure as competition for resources varies with the body size of the predators present (Gittleman, 1985; Damuth and MacFadden, 1990). However, the interplay between body size, hunting and diet in carnivorans is complex, as exemplified by the presence of a “dietary shift” in body masses between 21.5 and 25 kg (Carbone et al., 1999). Thus, for carnivores below 21.5 kg, selected prey tends to be less than half the size of the predator, as well as their diet likely being more omnivorous. In contrast, when above this threshold, prey tends to be similar to or larger than the predator, with their diet being more carnivorous (Carbone et al., 1999). The factors responsible for this dietary shift are multiple and complex, with energetic constraints suggested to be the most

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influential factor (Carbone et al., 1999), although both metabolic rate and energy expenditure may also be involved (Andersson, 2004b).

Larger body size in carnivores facilitates the pursuit of larger and faster prey (Gittleman, 1985). As a consequence, increased mobility is required by these larger predators, which forms the basis of the “hunting mode threshold” (Andersson and Werdelin, 2003; Andersson, 2004b). As such, carnivores that tend to increase in body size retain the ability to supinate their forearms and are therefore able to grapple with prey. In contrast, those that have developed towards a pursuit hunting mode remain modestly sized, with cursors rarely reaching 100 kg (Andersson and Werdelin, 2003; Andersson, 2004b). Notably, carnivores of <20 kg in size remain intermediate between these hunting modes, whereas those above this threshold are committed to one or the other hunting pathways (Andersson and Werdelin, 2003). Beyond this hunting mode threshold, a strong pressure to increase body mass up to and above 40 kg exists in relation to the energetic costs of locomotion. Thus, at body masses of 40–80 kg a “cursorial window” occurs, whereby the longer strides of larger animals will be more energy efficient than those of smaller ones (Andersson, 2004b).

The modern grey wolf *Canis lupus* L. 1758 is an exemplar cursorial predator that is both highly social and hunts cooperatively, enabling them to capture and kill prey much larger than themselves (Macdonald, 1983). Based on an average body mass of 41.3 kg (mean female weight: 38.11 kg, mean male weight: 46.67 kg [data from Mech, 1974; Gittleman, 1986; Geffen et al., 1996; Flower, 2014]), modern wolves fit above Carbone et al.’s (1999) dietary threshold weight and can be categorised as within the cursorial window (Andersson and Werdelin, 2003; Andersson, 2004b).

Modern European wolf diet has been extensively documented, with red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) most frequently targeted in Europe, along with reindeer (*Rangifer tarandus*) at high latitudes (Kojola et al., 2004; Nowak et al., 2011). Nevertheless, the ability of wolves to adopt a more generalist diet is exemplified by the hunting of smaller mammals such as beaver (*Castor fiber*), brown hare (*Lepus europaeus*) and birds when availability of wild ungulates is permanently of seasonally low (Jędrzejewski et al., 2000). Dietary flexibility is however, not unique to modern wolves. Based on differences in cranio-dental morphology, Leonard et al. (2007) identified a specialised wolf ecomorph in Late Pleistocene eastern Beringia that predated on mega-herbivores such as bison. More recently, temporal variation in Pleistocene wolf palaeodiet has been identified between populations of Marine Isotope Stage 3 (50–25kya), 5a (80–70kya) and 7 (220–150kya) age in Britain (Flower, 2014; Flower and Schreve, 2014). Differences in the relative level of carnivory between these wolf populations reflected changes in carnivore community structure that were ultimately driven by environmental change and the dramatic climatic upheaval of the Late Pleistocene (Flower, 2014; Flower and Schreve, 2014).

The ability of Pleistocene wolves to flexibly adapt their diet to changes in their environment therefore raises the question of whether body mass was also flexible during the Pleistocene, and whether Bergmann’s rule was in operation during the colder climatic episodes. The aim of this paper is therefore to investigate body mass variation in early Middle Pleistocene *Canis mosbachensis* Soergel, 1925 and Middle to Late Pleistocene *Canis lupus* from Britain, and examine if variations in size relate to changes in competition and climate.

Reconstructions of extinct mammal body mass, used as a surrogate for body size, vary from comparisons of lower carnassial (m1) lengths and widths as a proxy for body size (Brugal and Boudadi-Maligne, 2011; Flower and Schreve, 2014), to statistical modelling of body mass based on tooth dimensions (e.g. Meloro

et al., 2007), post crania (e.g. Toledo et al., 2014), long bone cross-sections (e.g. Egi, 2003) and elbow joints (Andersson, 2004a). Notably, Van Valkenburgh (1990) created numerous well-known Family-based predictive equations using either lower carnassial length (m1L) or skull length that have been used extensively in carnivoran body mass reconstructions (e.g. Meloro et al., 2007). However, a common problem in palaeontological studies is the rarity of complete, unbroken fossil material, such as the cranium, and in some cases complete long bones. In contrast, the relative durability of the dentition often leads to teeth being frequently well preserved and abundant in faunal assemblages, resulting in the carnassials being a more accessible predictor of body mass.

As this paper focuses exclusively on the body size of British Pleistocene canids, the history of the wolf lineage in mainland Europe will be summarised here only (see Sardella and Palombo, 2007; Sotnikova and Rook, 2010; Croitor and Brugal, 2010 for a review). The classic wolf evolutionary lineage of *Canis etruscus*, *C. mosbachensis* and *C. lupus* is widely supported (Torre, 1979; Rook and Torre, 1996b; Sotnikova, 2001; Cherin et al., 2013a), based on the Early Pleistocene *Canis etruscus* Forsyth-Major, 1877 evolving into *C. mosbachensis*, before increasing in size and becoming *C. lupus* during the Middle Pleistocene. This lineage is also considered by Brugal and Boudadi-Maligne (2011) as representing three chronospecies. However, arguments exist over the phylogenetic position of *C. mosbachensis* (Palombo and Valli, 2003–2004; Garrido and Arribas, 2008; Martinez Navarro et al., 2009), as well as its status as a separate species or as a subspecies of *C. lupus* (i.e. *Canis lupus mosbachensis* Thenius, 1954 [see Kurtén, 1968; Kurtén and Poulianos, 1977, 1981; Lumley et al., 1988; Argant, 2009; later]). In the present study, *C. mosbachensis* is regarded as a separate species to avoid presumptive linkage to *C. lupus*.

The Early Pleistocene fossil record of *Canis* in Europe contains considerable hiatuses, nevertheless, the oldest remains attributed to *Canis* are from the Late Pliocene early Villafranchian site of Vialatte, France, dated to 3.1 Ma (Lacombat et al., 2008). Furthermore, the earliest remains attributed to *Canis* cf. *Etruscus* are from Coste San Giacomo, Italy, dated to 2.1–2.2 Ma (Rook and Torre, 1996a; Sardella and Palombo, 2007; Rook and Martinez-Navarro, 2010; Bellucci et al., 2012). Thus, the so called ‘Wolf Event’ (Azzaroli, 1983) that was typified by the abundant remains of *C. etruscus* at the late Villafranchian typesite of the Olivola Faunal Unit at Val di Magra, Italy (Azzaroli et al., 1988) and thought to mark the expansion of this species into Europe, likely occurred much earlier. Other members of the genus *Canis* joined *C. etruscus* in mainland Europe during the Early Pleistocene, such as *Canis armensis* Del Campna, 1913 (Sardella and Palombo, 2007; Sotnikova and Rook, 2010) and *Canis falconeri* Forsyth-Major, 1877 (Rook, 1994) that typically characterised sites of the Upper Valdarno Basin, Italy (Tasso Faunal Unit, late Villafranchian). However, complex issues remain regarding the systematics and phylogenetic relationships of both these canids that are beyond the scope of this study (see Rook and Torre, 1996a; Martinez-Navarro and Rook, 2003; Werdelin and Lewis, 2005 for a review).

Following *C. etruscus* in the classic Pleistocene wolf lineage, the earliest known occurrences of *C. mosbachensis* are at Pirro Nord, Italy (Pirro Nord Faunal Unit), dated between 1.3 and 1.7 Ma (Arzarello et al., 2009) and 1.3–1.5 Ma (Bertini et al., 2010), and at Venta Micena, Spain, which has been correlated to between the Jaramillo and Olduvai subchrons (1.22–1.77 Ma) and dated to 1.37 ± 0.24 Ma (Duval et al., 2011). In Britain however, the earliest known occurrence of *C. mosbachensis* is much later, with remains originally recognised as “small” *C. lupus* by Stuart (1995) and later as *C. mosbachensis* by Lewis et al. (2010) in the Cromer Forest-bed Formation (CF-bF) at West Runton (Norfolk) (Fig. 1.). West Runton is assigned to the ‘Cromerian Complex’ of interglacials, which can

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