



# When and where do dogs improve hunting productivity? The empirical record and some implications for early Upper Paleolithic prey acquisition



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## ABSTRACT

Recent archeological finds of protodogs dating to 35,000 years ago have ignited controversy over the function of canids in early Upper Paleolithic societies. Reconstructions nominate the use of proto and early dogs in hunting and hauling as underwriting changes in subsistence technology, catalyzing human population growth and supporting the spread of modern humans at the expense of Neanderthals. These reconstructions assume that the use of canids in hunting will always have profound impacts on human subsistence. In this paper, I summarize existing quantitative data derived from the ethnographic record to evaluate productivity gains derived from the use of dogs in hunting. To augment this sparse information, I present some of the only data on the deployment of unspecialized Central African dogs (basenji's) by hunter-gatherers. These data show that while dogs can enhance hunting returns in certain circumstance, their overall impact on hunting productivity is highly variable and often restricted to specific prey types. Furthermore, the complex circumstances surrounding the emergence and spread of dogs globally precludes simple applications of these data to the archaeological record. These data invite a reexamination of when and how we expect dogs to have a significant impact on human subsistence and the circumstances that supported the emergence and spread of canids as effective hunting aids.

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## 1. Introduction: Early Upper Paleolithic dogs as collaborative hunting aids

It is widely accepted that dogs were derived from Pleistocene wolves (*Canis lupus*) and traditional reconstructions based on archaeological evidence from Central Russian place the earliest appearance of domesticated dogs some 16–17,000 years ago (Sablin and Khlopachev, 2002; Morey, 2014). But recent archaeological and biomolecular evidence suggest that dogs might have diverged some 15,000 years earlier (Freedman et al., 2014; Skoglund et al., 2015; Thalmann et al., 2013; Vilà et al., 1997; Wang et al., 2016). Biometric and morphological analyses of skeletal remains from early Upper Paleolithic sites in the Czech Republic, Belgium, the Ukraine and Siberia (Germonpré et al., 2009, 2012, 2015, 2017; Ovodov et al., 2011; Thalmann et al., 2013) identify incipient protodogs as early as 36,000–33,500 years ago (Germonpré et al., 2009, 2012; Ovodov et al., 2011). These analyses are bolstered by recent aMtDNA analysis of a fossil canid skull dating to 33,000 years BP from Razboinichya Cave, Altai Siberia that suggests it is more closely related to dogs than Pleistocene wolves (Druzhkova et al., 2013). Assemblage characteristics such as the co-

occurrence of high abundances of mammoth (*Mammuthus primigenius*) and carnivore remains, specialized treatment of certain canid skulls, and isotopic evidence indicating that at least some of the putative protodogs consumed special meat (Bocherens, 2015) suggest the early emergence of a commensal and potentially incipient domesticated canid population in northern Europe. Because of the rarity of these finds and temporal gap between these early protodogs and later domesticated dogs, the early Upper Paleolithic specimens are viewed as possible failed attempts at domestication (Ovodov et al., 2011) that failed because human populations were too mobile to create the anthropogenic niches (i.e., garbage middens) that attracted and tethered canids to human settlements (Coppinger and Coppinger, 2001). These finds have not only ignited intense controversy over the identity of the fossils (see Boudadi-Maligne and Escarguel, 2014; Crockford and Kuzmin, 2012; Germonpré et al., 2013, 2015), but also the roles that these early protodogs might have played in Upper Paleolithic societies (see Perri, 2016b; Perri et al., 2015; Shipman, 2015a, 2015b).

The conventional view has always been that early domesticated and/or protodogs served utilitarian functions, particularly as a means of transporting gear and food and/or as cooperative hunting partners (e.g., Clutton-Brock, 1981, 1995; Downs, 1960; Fiedel, 2005; Shipman, 2012; Shipman, 2015a; Speth et al., 2013; Turner, 2002). Based on taphonomic evidence and mammoth age

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profiles from Upper Paleolithic so-called mammoth megasites in Eurasia dating between 40 and 15,000 years ago, Shipman (2015a) argues that these wolf dogs (or semi-domesticated canids) transported meat to residential sites and collaboratively hunted mammoths with modern humans who possessed complex projectile technology (also see Germonpré et al., 2012). These purported collaborations led to increased prey acquisition rates and a growth in human population size that supported the spread of modern humans at the expense of the Neanderthals (Shipman, 2015a, 2015b) and the emergence of a cooperative interspecies communication system between canids and humans (Hare and Tomasello, 2005; Miklósi and Soproni, 2006). Germonpré et al. (2017) envision wider generalized roles with protodogs transporting gear and raw materials, guarding camps and carcasses, and assisting in the capture of large and dangerous carnivores, as well as mammoths.

Central to these hypotheses is the idea that early canids work collaboratively with humans and will greatly enhance hunting productivity. Assuming these scenarios are correct invites a reconsideration of why protodogs and later early dogs were not immediately adopted by all groups, why it took so long for dogs to become widespread fixtures in human settlements, why dogs were never adopted or used by some populations, and the tradeoffs that hunter-gatherers made when dogs were deployed for other purposes such as haulage. One path towards explaining variation in dog deployment can be gained by understanding how and when dogs significantly impact hunting productivity, thereby allowing researchers to develop testable hypotheses for the archaeological record.

## 2. Evaluating changes in hunting productivity associated with dogs

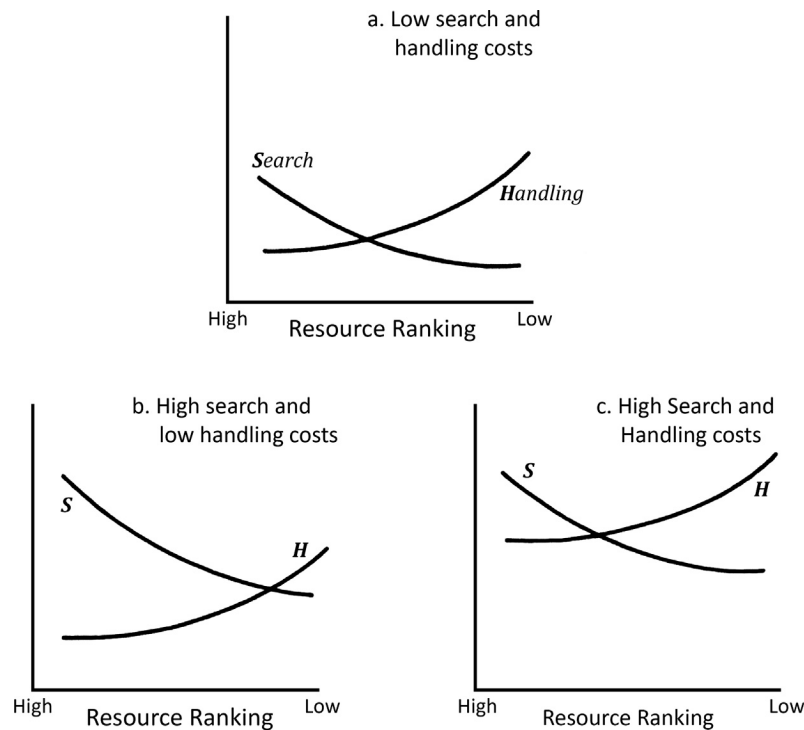
Increases in hunting productivity associated with the introduction of new technologies, such as dogs, are frequently cited as sources of change in the archaeological record but researchers often have difficulty identifying expectations about how these changes will be manifested in the material record. In this paper, I assume that hunting productivity or efficiency can be evaluated with rationale derived from the diet breadth model. The diet breadth model assumes that resources can be ranked along a single dimension of profitability (usually kcals obtained per unit of handling time or the post-encounter return rate). The basic assumption is that foragers attempt to maximize the long-term net rate of energy acquisition by adding resources into their diet in rank order from highest to lowest until the return rate per unit of time is maximized (e.g., MacArthur and Pianka, 1966; Pulliam, 1974; Smith, 1983). The costs of resource acquisition are usually partitioned into two opposing costs curves: search and handling. Since search is assumed to be randomized, the time devoted to searching for a resource is generalized across all the resources in the diet. Handling time includes the time spent pursuing, processing and consuming the prey after it has been encountered. Changes in the position of the two costs curves relative to one another resulting from technological change or other factors have important implications for the diet breadth (see Hawkes et al., 1982; Winterhalder, 1978, 1981). Winterhalder's (1978) analysis of how contemporary and historic technological changes influenced hunting and diet breadth among the Cree in Ontario is exemplary (Fig. 1, after Winterhalder, 1978:506). In this case, he showed how the advent of high-velocity motorized search technology in recent times (snowmobiles and motorized boats; Fig. 1a) lowered the search costs of high-ranking prey and narrowed the diet. One expectation is that under circumstances where introduced technology lowers the search costs of high ranking resources, the diet should become narrowly focused on those resources with an

increase in productivity. Search often comprises the largest portion of the costs of acquisition, especially for game resources where acquisition is constrained by prey distribution and abundances, and reductions in search are one of the few ways that foragers can realize greater efficiency (e.g., Hawkes et al., 1982). But some larger-sized and potentially high value prey, such as mobile animals and some megafauna, also have very high handling costs rendering them low ranked options relative to other prey (Bird et al., 2009; Lupo and Schmitt, 2016). Expensive and sometimes dangerous prey are often associated with prolonged pursuits and/or have especially low rates of success (i.e., high rates of hunting failure where pursuits fail). Reductions in the search costs will not necessarily influence the abundance of expensive prey in the diet because acquisition of these animals is constrained by handling costs (Lupo and Schmitt, 2016). Novel technology that reduces the handling (but not search) costs of expensive prey may change the ranking of these resources relative to others in the diet, but the diet should remain relatively broad. Moreover, certain expensive resources that were previously rarely exploited may be better represented in the diet. Reduced handling costs of expensive prey will not necessarily narrow the diet if the search costs and encounter rates for those items remain unchanged. However, some of the most profound dietary impacts should result if the introduced technology reduces both the search and handling costs of highly valued and/or expensive prey. In this case, the diet should become narrowly focused on those resources with the latter becoming much more abundant in the diet and potentially greatly increase foraging efficiency.

Dogs can realize a decrease in search costs and an increase in prey encounter rates by flushing and finding animals. These characteristics may be especially important with pedestrian hunts where prey resources that are highly dispersed or have low densities, are cryptic or fossorial, and/or occupy biomes with heavy vegetation and rugged terrain. Reductions in search costs become less beneficial with prey that use habitual paths or runways or that are highly predictable in location and where hunting require stealth and ambush strategies and the use of some stationary technology (traps, snares). Dogs can also reduce the handling costs associated with prey acquisition by distracting or baying dangerous animals, pursuing wounded prey and finding carcasses of animals that have been killed. The latter characteristics are especially advantageous with the use of certain kinds of dispatch technology that do not always immediately kill the animals, such as poisoned arrows (Lupo and Schmitt, 2016) or in heavily vegetated areas and rugged terrain where locating dead animals is difficult. The ability of dogs to chase and locate a wounded and dying animal or the carcass of one that has died from its wounds is a crucial factor that reduces the chances of hunting failure and improves success (see Lupo and Schmitt, 2016). However, the benefits derived from deploying canids vary in response to the advent of other dispatch and transport technologies (i.e., horses, snowmobiles) (Osaki, 2005), prey characteristics, canid breed characteristics, and ecological contexts (i.e., vegetation types, terrain) (Koster and Noss, 2014; Perri, 2016a). Consequently, the advantages of hunting with dogs are not uniformly applicable to all circumstances and increases in productivity associated with the acquisition of particular species cannot be extended to all prey.

## 3. Hunting and dogs in the ethnographic and ethnohistoric record

While there is no doubt that dogs are frequently used as adjuncts to hunting in the ethnographic record, quantitative data demonstrating how and when the use of dogs improve productivity in small-scale societies are surprisingly limited (but see Koster,



**Fig. 1.** Changes in diet breadth as search and handling costs change as a function of new technologies; (a) recent, (b) protohistoric, (c) prehistoric (after Winterhalder (1978)).

2008, 2009; Koster and Noss, 2014; Lupo, 2011). Most sources that discuss the use of dogs are very limited in detail, do not provide comparable data on hunting returns when dogs are not used, and often fail to report if or how canids enhance productivity. Many ethnographic sources mention dogs accompanying hunters and it is often assumed *a priori* that the presence of canids had a positive impact on the outcome, even though other compounding factors such as group-size and enhanced dispatch technology (firearms) can also influence hunting success.

The task is further complicated by the fact that much of the existing data are derived from observations of specialized and trained hunting dog breeds that only emerged within the last 500–600 hundred years (Larson et al., 2012; Rimbault and Ostrander, 2012; Sundqvist et al., 2006; Vonholdt et al., 2010). Importantly, intense selective breeding has amplified certain traits in some breeds, but not others, resulting in so-called “mosaics” whereby any single dog population will display a subset of specialties (Galibert et al., 2011; Miklósi, 2014; Thalmann et al., 2013). This means that modern dog groups, such as scent and sight hounds, possess highly developed capabilities that are not similarly amplified in all dogs or in modern and probably ancestral canids (Gácsi et al., 2009; see especially Zimen, 1980). For example, the important findings of Ruusila and Pesonen (2004) are of special interest to researchers because this study is the only quantitative study involving moose (*Alces alces*), a highly mobile large-sized prey that closely approximates the natural prey of ancestral wolves and potentially early dogs. However, these data are derived from contemporary moose hunters in Finland using modern firearms who likely used specialized and trained dogs such as Norwegian elkhounds (Ericsson et al., 2015). The results show that searching and tracking by dogs increase hunter’s success rates by 56% with particularly marked effects in areas with low moose densities and among smaller-sized hunting groups. While these results demonstrate the value of specialized and trained dogs in hunting, the wide-ranging applicability to the prehistoric record and use as an analogue for unspecialized breeds remains questionable

and complicates identification of an appropriate canid ethogram for early protodogs.

Probably the most challenging problem constraining a clear understanding of how dogs influence hunting outcomes concerns the complex circumstances surrounding the spread of modern dogs. The introduction of European breeds (especially specialized hunting dogs) in Asia, Africa, Oceania, and the Americas beginning in the 15th century and during colonial expansion had profound consequences that led to inbreeding with and/or a reduction in, genetic diversity, and some cases the complete replacement of indigenous breeds (see Castroviejo-Fisher et al., 2011; Leonard et al., 2002; van Asch et al., 2013). Given the emergence and spread of specialized breeds, the influence of dogs on hunting productivity likely impacted different places in different ways at different times.

In some localities, especially islands, domesticated dogs were historically introduced as a novel predator and these places purportedly experienced some of the most dramatic influences on subsistence and technology (Table 1). Introduced canids were often highly desired by indigenous populations for their hunting abilities and, because of the expense and networks needed to acquire these animals, dogs conferred status on the individuals who possessed them. In some instances, introduced dogs became deeply embedded in societies with institutionalized systems of “dog culture” emerging that included rules about ownership, standards of care, feeding and breeding of dogs, and ranking system of animals (see Caldecott, 1988; Chan, 2007; Descada, 1994). One of the most dramatic examples of this process was documented in Tasmania where specialized hunting dogs were introduced by sealers and traders between CE 1798 and 1802 (Jones, 1970) to hunt kangaroos and became widespread among indigenous people by CE 1830 (Cummings, 2013; Meehan et al., 1999). Although prey in Tasmania were pre-exposed to an indigenous carnivorous marsupial (*Thylacine cynocephalus*) predator (Wroe et al., 2007), specialized hunting dogs represented a novel threat especially when deployed as packs and in concert with new dispatch technology (firearms). Jones (1970) argues that the high productivity of dog-assisted

**Table 1**

Examples of observed historic and recent subsistence, technological, and cultural changes associated with introduced dogs.

Location/date of introduction	Technological, economic and sociocultural change
Tasmania/1798–1830 <sup>a</sup>	Dogs associated with a change in hunting techniques with a shift towards the use of spears, clubs and dog packs to dispatch wallabies and kangaroos. Dogs become highly valued, are incorporated into exchange systems and used as bride wealth
Andaman Islands/1857–1858 <sup>b</sup>	Dogs associated with the increased use of hunting spears in wild pig hunts
Little Andaman Islands/1900 <sup>c</sup>	Introduction of dogs may have reduced consumption of shellfish and increased consumption of wild pigs

<sup>a</sup> Meehan et al. (1999) and Jones (1970).

<sup>b</sup> Radcliffe-Brown (1922):417. Despite the close geographic proximity to south-east Asia, there is no evidence that wild Asian dholes (*Cuon alpinus*) or indigenous domesticated dingoes (*Canis lupus dingo*) were ever present on the Andaman islands.

<sup>c</sup> Domesticated dogs were introduced as early as CE 1857 on the north and middle islands and about 30 years later to the little Andaman Island (Cipriani, 1966: 79–80).

hunting filled a subsistence vacuum created with the reduction in indigenous women, many of whom were abducted by sealers and sailors (Meehan et al., 1999). As a result, dogs quickly became a highly-valued commodity incorporated into ritual beliefs and embedded into the exchange system as bride wealth. However, the introduction of dogs also involved colonial occupations that were associated with dramatic sociopolitical, economic and ecological upheaval that profoundly impacted indigenous populations in a variety of ways, making the effects of dogs on hunting productivity difficult to discern.

Conversely, the impacts on hunting productivity resulting from dog hybridization or replacement where prey were previously exposed to canid predators likely differed from areas where dogs were introduced as novel predators. In the America's imported dogs introduced through colonization resulted in the hybridization with and/or extinction of many indigenous breeds (see Allen, 1920; Barsh et al., 2002; Clutton-Brock, 1999; Castroviejo-Fisher et al., 2011). Here largescale spatial incongruities in the distribution of indigenous dogs added to the complication. For example, in parts of the Neotropics indigenous domesticated dogs were never present (see Koster, 2009) or were rare (but see Prates et al., 2010). The first domesticated canids were introduced by the Spanish and some isolated Indian groups did not possess dogs until the middle of the 20th century (e.g., Forline, 1997; Koster, 2008).

Koster (2009:Table 2; also see Koster and Noss, 2014) provides an overview of the sparse existing quantitative data on dog use in the Neotropics and only those sources that report quantitative hunting outcomes are shown in Table 2. Probably the strongest of these studies is Koster's work with the Mayanga/Miskito of Nicaragua. In this study dogs increased the encounter rate with specific small-sized prey (<10 kg) especially agoutis (*Dasyprocta* spp.), pacas (*Cuniculus paca*) and nine-banded armadillo's (*Dasybus novemcinctus*), but the value of dogs in hunting varied as a function of the circumstance of capture. For example, dogs were not useful with tapirs and brocket deer unless the hunts involved driving the animals into water where they were easily shot with a firearm (Koster, 2009:583). Additional Neotropical observations suggest that dogs (often deployed with firearms) can improve hunting returns but not in all types of hunts (Table 2, Forline 1997; Romanoff, 1984). In Forline's (1997) and Romanoff's (1984) studies dogs enhanced hunting returns but were very rarely deployed. In contrast Lu's (1999) observations did not show an improvement in returns associated with dogs. As Koster and Noss (2014) con-

**Table 2**

Quantitative contexts for hunting with introduced dogs.

Cultural/geographic context	Dog introduction	Impact on hunting
<u>Hunter-gatherer/Horticulturalists</u>		
Matses, Peru	Post contact	Dogs used in one in 10 hunts with machetes, bows, and shotguns to pursue a wide range of prey. Use of dogs yielded more meat per hunt than hunting bouts without dogs (Romanoff, 1984)
Mayanga/Miskito, Nicaragua	18th Century	Dogs increased encounter rates with agoutis, pacas, and nine-banded armadillos. Dogs increased encounter rates with agoutis by 900% in comparison to hunters armed only with guns. Dogs do not increase encounters with tapirs, collared peccaries, or deer (Koster, 2007, 2008)
Guajá, Brazil	1980s	Dogs only used on 4.5% of hunting trips but dog-assisted hunts yielded the second highest return rate; dogs combined with shotguns yielded the highest return rates (Forline, 1997)
Hoarani, Ecuador	1970s	Dogs did not significantly influence hunting success or the amount of meat acquired by hunters (Lu, 1999) Dogs may have helped with the capture of tapirs, collared peccaries, and deer
<u>Hunter-gatherers</u>		
Jankuntjara, Australia	1950s	Dogs assisted in hunts of kangaroos and wallaroos and accounted for 3–5% of the kills over a 12-month period. Hunters without dogs brought in more kills than those with dogs (Hamilton, 1972)

clude, the evidence for increased hunting productivity associated with dogs is not unequivocal or universal (see Koster, 2009; Koster and Noss, 2014; Saffirio and Scaglione, 1982).

A more complicated picture emerges in Southeast Asia and Oceania where domesticated indigenous dogs spread from mainland China with the dispersals of Austronesian-speaking peoples beginning 5000–4000 BP (Table 3). In Australia dingoes were introduced by ancient human populations some 3500 years ago (Gollan, 1985; but see Cairns and Wilton, 2016; Oskarsson et al., 2012) but imported dogs were introduced by British colonists in CE 1788.

Introduced dogs were widely adopted by aboriginal groups but did not reach the interior areas until the CE 1950–1960s. But the value of dingoes and introduced dogs as hunting aids among aboriginal populations is not unequivocal. Many of the historical records purportedly demonstrating the use of dingoes as hunting aids among aborigines are anecdotal or second-hand accounts, and others may be based on observations of dog-dingo hybrids (see Balme and O'Connor, 2016; Hayden, 1975; Smith, 2015; Spotte, 2012). Sparse, but credible, historic sources report that dingoes were used in hunting medium to small-sized marsupials. This evidence led Balme and O'Connor (2016; also, see Gould, 1969) to hypothesize that dingoes increased women's prey acquisition efforts and that this use was later transferred to introduced dogs. Even though historical evidence suggests that introduced European dogs had immediate impacts on Australian wildlife (see White, 1972, citing Darwin, 1839) that continues with feral and free-ranging dog populations today (May and Norton, 1996), many aboriginal groups, such as the Martu, keep large numbers of dogs and yet do not deploy them in hunting (D. Bird, personal communication 2017). There are several ethnographic descriptions of dogs

**Table 3**  
Quantitative Contexts for Hunting with Indigenous Dogs.

Cultural/geographic context	Dog introduction	Impact on hunting
<b>Hunter-gatherers</b>		
Agta, Philippines	≥Late Holocene <sup>a</sup>	Groups of women hunting wild boars with dogs had a 31% success rate compared to men (17%) who hunt alone without dogs (Estioko-Griffin, 1985; Estioko-Griffin and Griffin, 1981)
!Kung, Botswana	<5000 BP <sup>b</sup>	In a 4-week period tracking seven hunters who acquired 18 carcasses, Lee (1979) found that 75% of the meat was attributed to one hunter working with a pack of dogs
Aka/Bofi, Central African Republic	<5000 BP <sup>b</sup>	Use of dogs lowered handling times for fossorial pouched rats and increased hunt success rates. Dog-assisted spear hunts of porcupines are shorter in duration than those without dogs (Lupo, 2011)
<b>Hunter-gatherer/Horticulturalists</b>		
Penan, Borneo	Late Holocene <sup>c</sup>	Dogs associated with a transition in hunting practices from traditional use of blowpipes in arboreal prey acquisition to widespread use of spears in pig hunts. Hunters with dog packs had a 90% success rate depending on prey density (Brosius, 1986). Good hunting dogs highly esteemed and integrated into exchange relationships based on kin relationships
Seltaman, Papua	>2000 BP <sup>d</sup>	Dogs increased the success of wallaby hunts 15–34% and New Guinea and ground cuscus hunts 25%
<b>Horticulturalists</b>		
Rural hunters, Borneo	Late Holocene <sup>c</sup>	Dogs assisted with firearms in hunting ungulates (e.g., <i>Rusa unicolor</i> , <i>Muntiacus atherodes</i> , <i>Tragulus kanchil</i> ) and in 86.3% of the bearded pigs killed by hunters, compared to only 13.7% taken without dogs (Caldecot)

<sup>a</sup> The origins of dogs on the Philippines are obscure. Zooarchaeological evidence from Palawan Island (Piper et al., 2011) included foot bones from Terminal Pleistocene-early Holocene deposits and are identified as a dhole or extinct dingy-type dog. A handful of domesticated dog remains occur in Late Holocene levels. Askals or aspins, the so-called street dogs of the Philippines, are likely the result of interbreeding with indigenous and introduced dogs.

<sup>b</sup> The origin of African basenji-like dogs remains unclear due to a paucity of archaeological remains (Gifford-Gonzalez and Hanotte (2011)). Recent biomolecular analyses suggest ancestral African dogs may have originated in northern Europe and spread to northern and western Africa after 12,000 years ago (Adeola et al., 2016). Prehistoric dog remains are particularly sparse in Central Africa and it is assumed that dogs migrated with Bantu-speaking peoples beginning 5000 years ago.

<sup>c</sup> The origin of dogs on Borneo is not clear. Chan (2007) suggests domestic dogs only arrived within the last two centuries from the mainland. But there is evidence that the island supported a population of wild indigenous canids. Cranbrook (1988, 2010) identified possible dhole skeletal remains dating to 10,000 <sup>14</sup>C BP from archaeological contexts in Sabah, Borneo. Sparse zooarchaeological evidence from Niah Cave seems to support the presence of dogs by the Neolithic (Clutton-Brock, 1959; Piper and Rabett, 2009).

<sup>d</sup> Ancestral NGSD were likely transported to New Guinea by prehistoric populations by at least 2000 BP (Bulmer, 2001) and possibly as early as 6000 BP (Koler-Matznick et al., 2003; Bulmer, 1975). Recent hybridization with imported breeds was very rapid, especially in coastal areas, but the distribution of pure NGSD's and degree of introgression remains controversial (Dwyer and Minnegal, 2016).

<sup>e</sup> These data are based on interviews with nearly 5500 rural families and hunters using mostly firearms. Dogs were not traditionally used in hunting.

used in hunting (Gould, 1969; Hayden, 1975; Meehan et al., 1999; Smith and Litchfield, 2009; White, 1972), but the only quantitative

data is reported by Hamilton (1972), who observed dog assisted hunts of kangaroos and wallaroos among the Jankuntjara. But her sample shows that dogs only accounted for 3 to 5% of all kills over a 12-month period and that hunters without dogs actually brought in more kills.

A handful of accounts from Southeast Asia suggest that indigenous dogs enhance certain hunting opportunities (Table 3). According to Bulmer (1968), the New Guinea singing dog (NGSD) (*Canis hallstromi*) was important in the acquisition of certain prey including wallabies (Dorcopsids), tree-climbing kangaroos (*Dendrolagus* spp.), long-beaked echidnas (*Zaglossus* sp.) and spiny bandicoots (*Echymipera* sp.) (see Brass, 1956; Bulmer, 1968). Both Bulmer (1968) and Stillitoe (2003) note that while NGSD's were used in a variety of hunts, they were only essential for pig hunts. Whitehead (2000) (Table 3) provided the only quantitative data on NGSD's and she reported that they improved success in the procurement of wallaby's and ground cuscus (*Phalanger gymnotis*) and hunters who used dogs had catches dominated by these two prey in comparison to hunters who did not use NGSD's. Among the Agta dogs were used by groups of women to hunt wild pigs. These groups had a higher success rate than men who often hunted alone and did not use dogs (Griffin and Griffin, 2000). However, overall hunting success increased to 41% when men and women collaborated on hunts so it is not clear if the increase in success rates was related to hunting group-size or the use of dogs. In Borneo, Brosius (1986) noted changes in Penan Gang hunting technologies from traditional blowguns to the use of spears with dogs targeting wild bearded pigs (*Sus barbatus*) (Table 3). Hunters deploying dog packs of between 4 and 6 animals had an overall success rate of 90% depending on the density of prey (also see Brosius, 1986; Caldecott, 1988). But comparable data on hunting success without the use of dogs was never measured.

#### 4. Hunting with basal breeds: Central African dogs

Limited data are available for African basenji's, a so-called barkless dog that is widespread throughout parts of sub-Saharan Africa. Colonial occupation and sport big-game hunters brought specialized hunting breeds to different parts of Africa and, while disease limited the survivorship of European breeds in some places, introgression between introduced and African dogs occurred and was even encouraged in some areas (Boyko et al., 2009). Even so, Basenji's are considered by many to be a relatively ancient dog with little admixture from recent breeds (Brown et al., 2011; Fan et al., 2016; Parker et al., 2004; but see Adeola et al., 2016). Basenji's (or basenji-like dogs) were (and continue to be) used for hunting in many parts of Africa including hunter-gatherers such as the !Kung (Lee, 1979), G//ana and G//wi (Ikeya, 1994; Tanaka, 1980), Xo (Wilmsen and Durham, 1988), Kua (Bartram, 1993), Hadza (O'Connell personal communication) and Okiek. Among the San dogs were used as adjunctives in large-prey acquisition (e.g., Lee, 1979; Ikeya, 1994) but with the exception of Lee (1979) no sources report quantitative data on productivity. Lee (1979) reports that although most !Kung men in northern Botswana had owned or killed prey with a dog in their lifetime, dogs were uncommon in camps. Based on Lee's (1979) descriptions dogs were used to lower the handling costs of prey and were often deployed as packs. Small prey (bush duiker and steenbuck) were taken with one or two dogs but at least four or five dogs were required for large-sized, high-value species such as gemsbok. His quantitative observations were made over a one-month period where most of the kills were made by one hunter who owned an exceptionally successful hunting pack. Ikeya (1994), however, reported that the use of dogs in hunting by the San was of secondary importance in comparison to the use of bow and arrow, and that historically canids were uncommon

the northern Kalahari and only became important as aids to spear hunts for large game during the 1980s with the increased market value of antelope hides.

To expand the quantitative information on how unspecialized dogs influence hunting, here I present data derived from an ethnoarchaeological study of Bofi and Aka forest foragers occupying the Ngotto forest in northern Congo Basin (Table 4) (Lupo, 2011; Lupo et al., 2014; Lupo and Schmitt, 2002, 2005). The Bofi and Aka are forest foragers who rely on hunting and gathering and domesticated crops. Hunting is conducted with a variety of traditional tools including metal-tipped spears, poisoned arrows, fiber hand-woven nets, snares and traps. About one-half of all hunters used one or more dogs as adjunctives to their hunting efforts. This area is characterized by low levels of introgression with specialized or introduced breeds because colonization was relatively late (~CE 1889) and the Ngotto forest is an isolated area.

Data presented here are augmented by analysis of published data collected by other researchers working with forest populations elsewhere in Central Africa (Table 4; Harako, 1976; Sato, 1983). Prior research shows that while Central African dogs are useful in some hunting situations, they are not particularly effective in others (Harako, 1976; Lupo, 2011; Noss). Harako (1976) found that dogs were not used to hunt extremely large-sized prey such as elephants (*Loxodonta africana*), forest buffalo (*Syncerus caffer*) and giant forest hogs (*Hylochoerus meinertzhageni*) because these animals require hunting by stealth. Even though the dogs are barkless, they can be difficult to control and often frighten animals before the hunter approaches. Even so, Central African dogs can lower the handling costs and increase the success rates of certain kinds of prey. Hunts using dogs to hand capture fossorial giant pouched rats (*Cricetomys gambianus*) are shorter in duration than those that are not dog assisted, but the differences in time are only marginally significant (Lupo, 2011). However, hand capture dog-

assisted rat hunts are more successful than those without dogs largely because the dogs excel at capturing rats flushed from their burrows by hunters (Table 4). Dog-assisted spear hunts targeting porcupine (*Atherurus africanus*) had significantly reduced handling times in comparison to hunts without dogs, but there are no appreciable differences in the success rates of these hunts. In both types of hunts, hunters who had dogs were more persistent (i.e., had longer giving up thresholds) than hunters who did not have dogs. Conversely, the use of dogs had no impact on the productivity of net-hunts, the most common type of communal hunts practiced in the Congo Basin. In fact, while dogs frequently accompanied hunters on these hunts they sometimes negatively impacted the outcome by chasing the prey away from the nets.

Table 4 presents additional analyses derived from observations of forest foragers and farmers hunting with thrusting spears and projectiles in the Congo Basin. These data show that dog-assisted thrusting spear hunts targeting a variety of prey such as porcupine, blue duiker (*Cephalophus monticola*), medium-sized duikers and giant forest hog are shorter on average than hunts without dogs, albeit the differences are not significant. In this sample dogs had no appreciable influence on hunting success; hunters without dogs have a higher proportion of successful hunts than bouts that were dog assisted. With thrusting spears, most of small to medium-sized prey were either immediately killed by the weapon or fled before becoming wounded. In these cases, the dogs failed to find or successfully track the animals after they were encountered by the hunters. Table 4 shows analyses of data collected by Harako (1976) who observed Mbuti bow and poisoned arrow hunters in the Ituri Forest. In his sample, dog-assisted hunts were longer and had higher success rates than those hunts without dogs. Data on communal bow and poisoned arrow hunts among Boyela agriculturalists using dogs to target duikers, small carnivores, and bush pigs were reported by Sato (1983). Because the number of dogs used in a hunt can influence hunting outcome (Fiorello et al., 2006), these data are segregated and analyzed by number of dogs used in different hunts. The differences in acquisition time between hunting bouts using one dog and those using multiple dogs are not statistically different. The success rate for hunters using one dog is relatively high, but the use of multiple dogs has an even higher success rate, although the latter is likely inflated by small sample size.

To explore how dogs in this context influence prey encounter rates and search efforts Fig. 2 shows the number of prey encountered and acquired relative to the number of dogs used in a hunt. If dogs increase encounter rates with prey, more animals should be encountered and killed on individual hunts when dogs are present than in hunts that did not include dogs. In this sample, the maximum number of dogs involved in any hunt is four. For the 54 hunts considered in this analysis, there is no statistical relationship between number of prey encountered and/or killed and number of dogs deployed. The mean values of prey encountered and killed in hunts involving different numbers of dogs do not significantly differ. The only significant difference is between the mean number of animals encountered and killed when no dogs were present and those cases where one or more dog was used. Note that the mean number of prey encountered or killed when no dogs were present is actually higher than the value when one or more dogs assisted in the hunt.

These and previously published data show that in the forested contexts of Central Africa dogs decrease the handling costs of certain prey types and improve the success rates of hunters in some, but not all, hunts. Dogs do not appear to influence the search costs or increase the encounter rates with prey, and were not deployed in hunts that targeted the largest-sized and presumably the most highly valued prey. Because dogs influence the costs of prey acquisition for some, but not all, prey and do not increase encounters,

**Table 4**  
Central African dogs and hunting productivity.

Hunting context	N	Proportion success	Mean handling time (min)
<u>Hand capture: giant pouched rat<sup>a</sup></u>			
With dog	46	0.43	29.0
Without dog	82	0.34	49.5
<u>Spear hunts: porcupine<sup>a</sup></u>			
With dog	35	0.45	44.0
Without dog	13	0.46	101.3
<u>Spear hunts: all prey<sup>a,b</sup></u>			
With dog	16	0.69	86.7
Without dog	69	0.88	127.3
<u>Communal net hunts<sup>a</sup></u>			
With dog	38	100	277.0
Without dog	8	100	282.0
<u>Bow and poisoned arrow<sup>c</sup></u>			
With dog	11	0.82	140.1
Without dog	16	0.19	126.6
<u>Communal bow and poisoned arrow<sup>d</sup></u>			
One dog	12	0.58	238.8
>1 dog	4	0.75	110.3

N = number observations.

<sup>a</sup> Data derived from Bofi and Aka forest foragers in the Central African Republic (Lupo, 2011; Lupo and Schmitt, 2005).

<sup>b</sup> Differences in handling time between events with and without dogs is not statistically significant ( $t = 1.285$ ,  $p = 0.10$ ).

<sup>c</sup> Data derived from a study of Mbuti forest foragers (Harako, 1976). Difference in handling time between events with and without dogs is not statistically significant ( $t = 0.621$ ,  $p = 0.270$ ).

<sup>d</sup> Data derived from Boyela agriculturalists (Sato, 1983). Difference in handling time between use of one dog or more than one dog is not statistically significant ( $t = 0.780$ ,  $p = 0.446$ ).

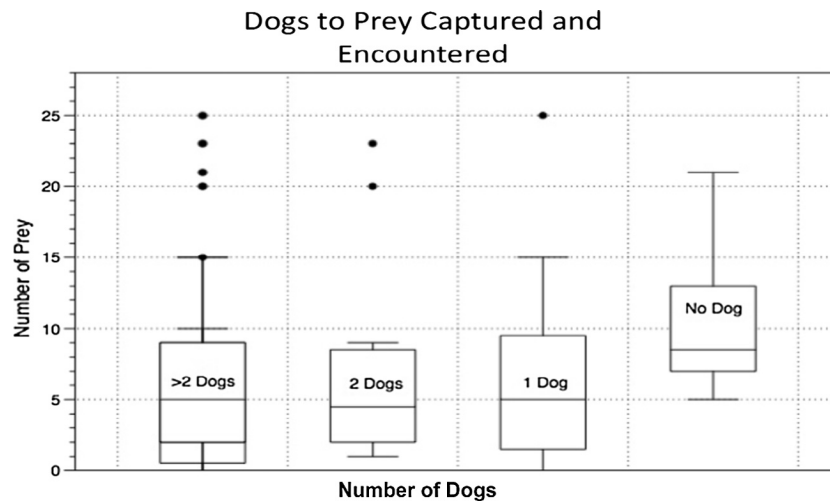


Fig. 2. Box-plot illustrating the mean number of prey taken with different numbers of dogs. Data derived from Lupo (unpublished) and Sato (1983).

their impact on hunting productivity is modest and this may explain, in part, why dogs are not highly valued in this part of Africa.

##### 5. Discussion: do dogs always improve hunting productivity?

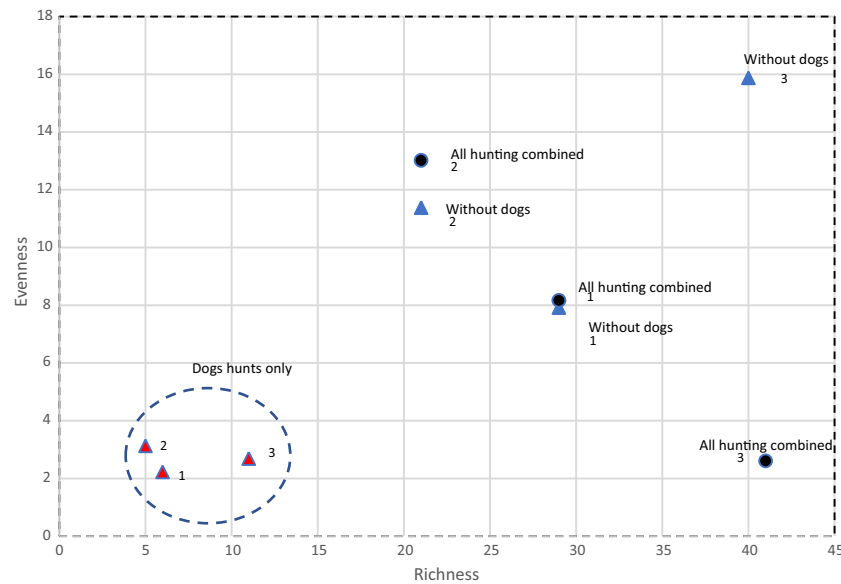
Cumulatively, the admittedly sparse available quantitative data show that there are circumstances when dogs enhance hunting productivity by lowering handling and sometimes search costs. Some of the variation in hunting productivity in these cases is linked to the complex circumstances surrounding the recent spread of domestic dogs. For example, some of the seemingly most profound economic outcomes are noted in insular contexts where dogs were introduced as novel predators, deployed as packs, and were an adjunctive to new dispatch technology (notably firearms). Anecdotal historical descriptions imply a wholesale change in hunting with a narrowing of the diet as the costs of acquiring high value prey decreased and this essentially matches theoretical expectations associated with an increase in hunting productivity linked to reduced search and handling costs. But the historic changes reportedly resulting from the introduction of dogs in these contexts are not corroborated by any zooarchaeological or archeological evidence, and a host of other sociopolitical processes resulting from colonization and hostile occupation such as habitat restriction and destruction and prey depletion as well as demographic, cultural and economic change had dynamic impacts on the hunting decisions of these populations.

In contrast to the dramatic shifts purportedly associated with the introduction of dogs as novel predators, most of the cases discussed here involve dogs reducing the search and/or handling costs associated with specific prey or prey types. Although several of the studies cited here lack details, some show that dogs are not universally deployed for all animals or in all hunts. Among the Agta, Onge, and Penan, dogs were most important in hunting wild pigs. Similarly, Africa basenji's increase hunting success in some, but not all, circumstances. Wilmsen and Durham (1988), for example, report that Xo hunters in Botswana pursued 29 different species, and dogs were only used to target 6 of these animals, especially warthogs (*Phacochoerus africanus*) (also see Lee, 1979). In fact, 73% of all warthogs taken by the Xo were dog acquired. Similar conclusions were reached by Koster and Noss (2014; also see Koster, 2009) who found that Neotropical dogs increased the encounter rates with rodents, felids, semi-terrestrial primates, small marsupials, armadillos and turtles and sometimes tapirs.

While not reviewed in detail here, there are also contexts and dispatch techniques in which dogs are not deployed or do not increase hunting success (Lu, 1999; Saffirio and Scaglione, 1982). Among others these include pursuits that rely on stealth (Harako, 1976), hunts for arboreal prey and/or with blow-guns (Koster and Noss, 2014), cooperative net hunts (Lupo, 2011) or hunts that require concealment such as the use of blinds.

In the ethnographic cases where dogs are selectively deployed, it is not always clear if canids decreased search and/or handling costs or how they impact overall hunting productivity. To explore how the addition of dogs influences the diet breadth, Fig. 3 plots the taxonomic composition of kills taken by three different ethnographic groups (Mayanga/Miskito, [Koster, 2007]; Xo and Herero, [Wilmsen and Durham, 1988]). Here the diet breadth is measured by taxonomic richness ( $\sum \text{TAXA}$ ) and evenness ( $1/\sum p_i^2$ ). Richness measures the number of species in the diet and evenness measures the representation of different prey within the diet. When these data are segregated by dispatch technique, they show that dogs take a comparatively narrow range of prey in comparison to all other dispatch technologies, and that the addition of dogs does not appreciable change the diet breadth for the Xo or Herero. The addition of dogs to the Mayanga/Miskito dispatch repertoire makes the diet less even with a greater focus on the small prey taken by dogs (agouti, paca and armadillo), even though the number of species in the diet remains broad. Despite the advantages offered by dogs in some hunting contexts, the diet remains broad and is inconsistent with measures for high productivity diets focused on large high value prey. This suggests that the use of dogs is not always associated with dramatic increases in productivity and while canids can sometimes greatly enhance the success of certain hunting activities, they may often have a relatively modest impact on overall diet breadth.

These data invite further questions about why dogs have such modest impacts on productivity in some contexts but are considered absolute necessities in others? Several different complicating factors influence the impact that dogs have on hunting productivity. Recent changes in the availability of prey, territorial circumscription, and access to new dispatch and transport technologies are among the factors that may have diminished or enhanced the value of dogs in the ethnographic record. In recent times the use of motorized vehicles coupled with the scarcity of large macropods in Australia, for example, may have reduced the benefits associated with using hunting dogs (D. Bird, personal communication 2017). Improvements in hunting productivity reported in the Neotropics,



**Fig. 3.** Taxonomic composition of hunts with and without dogs: (1) data derived from Wilmsen and Durham (1988) for the Xo; (2) data derived from Wilmsen and Durham (1988) for the Herero; (3) data derived from Koster (2007) for the Miskito/Mayangna.

New Guinea, and Borneo (Caldecott, 1988) involve dogs and hunters with firearms. But the use firearms alone greatly increases hunting productivity (Yost and Kelly, 1983), and the addition of dogs enhances these returns. Moreover, many of the cases reviewed here involve sedentary hunter-gatherer horticulturalists who are tethered to villages and already have reduced foraging ranges. Sedentary hunter-gatherer horticulturalists often target a wide range of prey and dogs can enhance the productivity of pursuing certain small-sized and locally abundant species within close proximity of their residential camps or in garden hunting (Romanoff, 1984).

While very little research has been conducted on breed introgression and performance abilities, another potential factor is the range of breed specialization in founding populations where dogs were introduced and/or mixed with indigenous canids. In Australia, a variety of specialized, introduced dogs quickly introgressed with one another and with indigenous dingoes creating a pool of mixed heritage canids with diverse characteristics (e.g., Meehan et al., 1999). Introgression among different canid populations can often have profound and sometimes detrimental consequences (Leonard et al., 2012), but among domesticated dogs genetically determined breed characteristics will be unevenly expressed among the offspring (Leonard et al., 2012; Elledge et al., 2006). This creates a pool of animals with high degrees of heterogeneity in skills and unpredictability in performance abilities (Koster and Tankersley, 2012).

However, demographic factors influencing dog populations and longevity may be the most important constraints on hunting productivity in some areas. This is because dogs are most effectively deployed as trained packs, especially in pursuit of large, mobile, and high value prey. Training dogs takes effort and maintaining packs can be costly (see Nobayashi, 2006). Further, because canid hunting abilities usually increase over time with age and experience, effective deployment for large-sized and dangerous prey can require a minimum number of adult animals to comprise a pack. Although dogs are famed for their ability to live on garbage, including human excrement, unless supplemented this diet greatly reduces their lifespans making them susceptible to disease and especially starvation (e.g., Forline, 1997; Lupo, 2011). The advent

of domesticated foods and increased reliance on starches is identified as pivotal in the global spread of canids, but small sedentary communities in the ethnographic record often fail to produce enough refuse to support large numbers of dogs, and those that manage to survive are usually in very poor physical condition (e.g., Forline, 1997; Ikeya, 1994; Lee, 1979; Lupo, 2011; Stillitoe, 2003). Ikeya (1994), for example, reports that in the Central Kalahari canids were used by the San for hunting after dog numbers increased as a result of dietary improvement. The San food supplies were subsidized by government cornmeal which the people fed to dogs. Among the Central African Bofi and Aka, dogs are minimally cared for and rarely fed. Dogs largely subsist on refuse but successful hunting dogs are sometimes fed internal organs (intestines) and allowed to lick up blood of prey at kill sites. Even so most of these animals only live two to three years (Lupo, 2011). Mortality is attributable to many different causes, including disease, but hunting accidents and injuries are common (also see Lee, 1979). Although dog populations are sustainable under these circumstances, there is no real growth in numbers and a sudden reduction in the number of dogs through disease, starvation or other stochastic factors is a very real possibility (see Forline, 1997). Even in rural settings where high densities of people produce large amounts of garbage that support population growth among feral and free-ranging domestic dogs, high mortality limits hunting ability. For example, Butler et al. (2004) found that high mortality in rural Zimbabwe resulted in a dog population where 75% of the individuals were juveniles (<1 year old) that represented highly ineffectual hunters due to their lack of strength and experience.

High mortality rates and the resulting demographic structure among dogs can influence how much investment people are willing to make in training the animals to hunt, especially if the hunting abilities increase with age and experience (Koster and Tankersley, 2012). The short lifespans of dogs, in concert with high pup mortality, can seriously restrict adult canid population densities and longevity and limit the deployment and productivity of dogs in hunting (Ikeya, 1994; Koster and Tankersley, 2012; Stillitoe, 2003; also see Butler et al., 2004; Fiorello et al., 2006). Under these circumstances, people may be unwilling to invest substantial effort training, feeding and caring for dogs. With minimal

effort, dogs that survive for only a few years can modestly influence hunting productivity and this may represent a low investment hunting adjunctive associated for some small-scale societies.

## 6. Archaeological implications for early protodogs and domesticated dogs

Key questions going forward include how might we apply these data to the prehistoric record of early dogs and the circumstances that supported effective canid deployment in hunting? Despite the inherent differences between ethnographic observations and prehistoric remains, these data can provide guidelines and expectations for the archaeological record. Specifically what do we expect if dogs significantly improved hunting efficiency, and if dogs collaborated with people to target megafauna? These data also point to important future questions concerning the circumstances that would support the spread of dogs as effective hunters.

If proto and early dogs significantly changed hunting efficiency than it should be reflected by changes in the taxonomic composition of the zooarchaeological record. There are two scenarios under which the use of early proto and domesticated dogs could significantly increase hunting productivity either by reducing the search costs of high value prey or the search and handling costs of high value but expensive prey, such as mammoth. Lupo and Schmitt (2016) suggest that Pleistocene proboscids were associated with excessive handling costs primarily because of high hunt failure rates. Byers and Ugan (2005) argue that mammoth hunting was constrained by high search costs. If the primary target was mammoths, then early protodogs would have had to realize a significant reduction in both the handling and search costs to make proboscids an efficient prey. Assuming that protodogs could significantly lower both the search and handling costs of mammoths, the zooarchaeological record should show a marked increase in the abundances of mammoths and possibly, other high value, but costly prey.

The existence of so-called Gravettian and Epigravettian mammoth megasites that contain large quantities of mammoth skeletal remains might appear to confirm the idea of increased hunting productivity associated with a new hunting technology. But the origins and formational history of these sites are complex and controversial with some reflecting the collection of bone and ivory from natural death sites (see Perri et al., 2015; Pitulko et al., 2014). While there is substantial evidence that mammoth bones and ivory were exploited as building materials, tools and decorations and that mammoth meat was consumed by some populations, direct indications of hunting are limited (Basilian et al., 2011; Bocherens et al., 2015; Nikolskiy and Pitulko, 2013; Pitulko et al., 2016; Svoboda et al., 2005).

In fact, several different archaeological evidentiary lines seem to suggest that early Upper Palaeolithic diets were geographically variable and broader and more flexible than the Middle Paleolithic. As summarized by Bocherens et al. (2015), isotopic signatures from Gravettian-age human remains in different parts of Europe reflect a high degree of geographic variation in diets depending on location. A range of existing data suggest that the diet of Upper Paleolithic populations in Europe <40,000 years BP was broader than that of Neanderthals (Stiner, 2010; Richards, 2009; Richards and Trinkaus, 2009; Richards et al., 2001; but also see Bocherens et al., 2014). In Eastern Europe, the sites of Kostenki reveal a broadening diet (<30,000 yrs ago) that included large mammals, fish, hares, and birds (Hoffecker, 2009). Isotopic signatures comparing early modern humans to Neanderthals also show a broadening of the diet with a wider range of isotopic values showing the inclusion of aquatic resources in some areas (Dobrovolskaya et al., 2012; Richards and Trinkaus, 2009; Richards et al., 2001). A range of specialized tools and technologies are associated with

exploitation of these resources including projectiles (Hoffecker, 2009; Shea, 2009). The fact the modern humans possessed these technologies suggests the adoption of a flexible dietary pattern rather than a specialized one. Proto or early domesticated dogs may or may not have played a role in the prey acquisition techniques used by these populations but there is no indication of a significant increase in productivity as reflected by a narrow diet associated with the acquisition of high value prey.

What archaeological evidence do we expect if early or protodogs collaborated with human hunters to target mammoths? The ethnographic record reviewed here is particularly revealing because none of these examples cite hunters pursuing megafauna with dogs. Central African forest foragers historically hunted elephants, the only extant proboscid and largest terrestrial animal, but as discussed above, they did not deploy dogs in these hunts (e.g., Lupo, 2011; Lupo and Schmitt, 2016). However, the ethnographic record from many parts of the world shows that indigenous hunters often used dogs deployed in packs to hunt certain large-sized prey such as buffalo, reindeer and bears. Further historical records of 19th and 20th century sport big-game hunters in Africa and elsewhere show that they relied almost entirely on trained dog packs to target megafauna such as elephants and giraffes (*Giraffa camelopardalis*) and other high value prey including buffalo and rhinoceros (*Rhinocerotidae*) (e.g., Gordon-Cumming, 1857; Foa, 1899; Richardson, 1851; Sanderson, 1878). Most of the dogs used in these contexts were imported European breeds or hybrids (indigenous and imported breeds). In Africa, sport hunters often reported being constrained by high rates of dog attrition and lamented at the inability of indigenous dogs to pursue these prey (see Andersson and Andersson, 1873; Chapman, 1868; Foa, 1899). Historical hunters often possessed large packs of between four and 50 dogs trained to respond to the report of a gun and to bay and chase big-game. Mortality rates for these canids was especially high, indeed striking, due to injuries sustained in the hunt (Andersson and Andersson, 1873; Gordon-Cumming, 1857; Sanderson, 1878). Furthermore, these dogs were only deployed under controlled conditions (i.e., usually led on slip leashes to the prey location) because unrestrained canids chased the prey away before the hunters could approach (Selous, 1881).

If protodogs and early dogs were involved in the acquisition of megafauna, then the expectation is that there will be evidence of highly trained canid packs. Specifically we might expect evidence of feeding efforts aimed at increasing the number of available adult dogs and promote longevity of those animals already experienced in hunting. Ethnographic evidence presented here implies that people may be less willing to make training investments in canids until longevity and survivorship increases.

Although archeological research identifying the diets of prehistoric dogs and canids through isotopic analysis is well-developed (see Guiry, 2012, 2013), establishing intentional provisioning of canid populations by humans is a different question that requires several different lines of supporting evidence aimed at reconstructing the life history of canids. Traditional approaches identify deviations between the isotopic signatures of prehistoric dogs and humans or among wild and putative domesticated canids that may reflect instances of human provisioning (Bocherens et al., 2014), but these could also result from canid self-hunting or a variety of the different circumstances (Guiry, 2013). If the identity of the canid is in question, dietary differences could be the result of intraspecific variation in prey targets rather than intentional feeding by humans (see Leonard et al., 2002). Other lines of circumstantial evidence might include isotopic signals that putative domesticated canids were being consistently fed a diet that not only contained meat but consistently also included less costly resources such as wild plant foods. Wild plants were exploited by some semi-sedentary Middle Paleolithic and early Upper

Paleolithic hunter-gatherer populations (Henry et al., 2011; Lev et al., 2005), but the proportional contribution of low protein and supplementary plant foods in the diet of early canids may be masked by standard isotopic analyses. Aquatic resources, especially fish, could also represent a low cost canid food sources and ethnographic and archeological evidence show that dogs often subsisted on aquatic resources (Losey et al., 2013).

But future studies aimed at demonstrating human intentionality in raising early dogs should attempt comparative studies among wild and putative early canids focusing on dietary trends throughout the life history of the animal. Specifically, if humans were intentionally and consistently provisioning canids than there might be evidence of supplemental feeding during the critical weanling period. Several different ethnographic and historical sources document human investment in sustaining juvenile canids that include instances of women breast-feeding puppies and administering premasticated food (Simoons and Baldwin, 1982). Dentine collagen analysis would be particularly valuable here for examining dietary trends over the animals lifetime and may provide important evidence of intentional provisioning of canid juveniles by humans (e.g., Balasse et al., 2001; Balasse and Tresset, 2002). Additional supporting evidence from prehistoric canid age profiles could also demonstrate intentional investment in sustaining early and protodog populations. Very few studies report the age-profiles of archeological canids largely because of preservational biases against the survivorship of neonate and juvenile skeletal remains and the difficulties associated with aging adult specimens. However, Germonpré et al. (2016) recently used the prevalence of spondylosis deformans (SD), a disease that progresses with age, in concert with tooth wear patterns as a proxy for aging Gravettian canid specimens from Předmostí. Their analysis did not support increased longevity among putative protodogs in comparison to wolves, but represents an important step in establishing prehistoric age profiles.

Clearly, evidence of intentional provisioning alone does not indicate that early dogs were used to hunt large prey. The hunting of megafauna and/or large dangerous prey will be associated with high rates canid mortality and should be reflected by skeletal pathology and high rates of healed injuries resulting from hunts. Common hunting injuries sustained by wild canids occur on the ribs, legs and occasionally the jaw (Spotte, 2012) and similar injury distributions might be expected among prehistoric hunting dogs (see Perri, 2016b). Only a few studies have reported lesions displayed on archaeological canid skeletal remains and most recent analyses are focused on skeletal damage that might be associated with haulage (Germonpré et al., 2016; Lawler et al., 2016; Snyder, 1995; Warren, 2000; but also see Losey et al., 2014).

Irrespective of how or when they emerged, early dogs appear to become widespread in archaeological sites outside of areas where wolves are naturally distributed after the advent of domesticated foods, especially starches (Larson et al., 2012; Sablin and Khlopachev, 2002). An increased reliance on domesticated starches, reduced population mobility and the attendant build-up of garbage middens are viewed by many as critical prerequisite cultural processes in the domestication process(es) and spread of dogs globally (e.g., Boitani et al., 2007; Coppinger and Coppinger, 2001; Crockford, 2006; Morey, 2010). As canid populations became tethered to anthropogenic resource patches, they extended their geographic range, and changed the nature of human-canid interrelationships (Axelsson et al., 2013). But if the hunting productivity of prehistoric and early dogs was constrained by the same demographic factors discussed above, then archaeologists need to reconsider the minimum size and density of early settlements (and refuse) required to successfully support a sufficient number dogs and deploy them in hunting large prey. When do anthropogenic patches become large enough to support a sustainable adult dog

populations and especially hunting packs? And when do these anthropogenic patches reach a crucial level to support a growing dog populations?

## 7. Conclusions

Contemporary dogs are the product of long-term, episodic processes that not only resulted in morphological change but also underwrote behavioral and cognitive changes that allowed dogs to recognize, respond to, and even solicit human communication cues (e.g., Hare et al., 2002). If, as many now believe, dogs possess a high degree of versatility in their ability to influence hunting outcomes, then more information on how this is manifested in different hunting populations is needed. As demonstrated here, in an exhaustive review of the existing data, most of the very sparse information demonstrates that while dogs can impact hunting productivity their overall effect may be quite modest, with the exception of a few narrow cases where they are introduced as novel predators and/or used with new dispatch technologies. In considering the evolution and spread of dogs, archeologists can no longer assume that early and protodogs necessarily conferred an economic advantage of prehistoric populations. Some of the specific expectations for the zooarchaeological record outlined here might shed light on the role that early dogs played in hunting but this is a first step. Clearly, researchers still have quite a bit of work to do before we can begin to make conclusions about how early dogs may or may not have enhanced prehistoric subsistence and human societies. There is a very important role that ethnoarchaeology can play in these studies especially among small-scale societies that continue to hunt and use dogs. Future research should be focused on understanding how demographic variables influence productivity in dogs in different contexts and how these measures influence human investment in the training and care of dogs. Investigations should be aimed at increasing our understanding of why dogs are highly valued as hunting assets in some contexts but not others, and this may shed light on why domesticated dogs spread slowly after initial domestication and the variation in their impact across time and space.

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