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THE EARLIEST DOMESTICATED WOLVES: ON CREATING DOGS

Abstract

The dog is man's best friend, and the wolf maybe his worst enemy in some circumstances. Yet, the former is only a wolf-type descending from the latter, modified non-intentionally and intentionally, both morphologically and in character. Much of the narrative on how dogs originated has been resolved, but certain aspects remain clouded, such as the geographical origin, chronological time or times, and originating wolf populations. Differences between dogs and wolves are visible in the archaeological record, based on morphology. Genetic analyses of ancient bone also can differentiate the two. People often have wondered why humans may have wanted to domesticate wolves, and several utilitarian reasons have been proposed. Nonetheless, it is difficult to explain how people could have known beforehand that wolves could fulfil desired tasks: There was no blueprint! Here, we propose that emotional reasons may have been pivotal, and the Bonn-Oberkassel burial, on which Martin Street published, is an excellent example of this hypothesis.

Keywords

Canis lupus, dog, domestication, wolf

INTRODUCTION

Martin Street and the first author shared several pleasant weeks in MONREPOS, and during talks it became clear that we disagreed on how wolves entered the human niche and became domesticated. Martin had gained the archaeological status of an ancient Greek demi-god by his wonderful "*Bonn-Oberkassel Arbeit*" (among much more). Martin had questioned the puppy collection hypothesis and rejection of 'protodogs', and seemed more a fan of the self-domestication theory, with domestication occurring during the early Aurignacian-Gravettian.

From those conversations and much more, this article will focus on methods of domestication and the 'protodog' hypothesis, as constructively as possible. The "why" of humans wanting to domesticate wolves also will be considered. According to Coppinger and Coppinger (2002, 2016), only an idiot would try to domesticate one.

The Eurasian grey wolf (*Canis lupus lupus*) is the recognized immediate ancestor of domestic dogs (Thalmann et al., 2013; Thalmann and Perri, 2018). Although wolves have existed for > 300 kya, a global turnover occurred about 25 kya, when Beringian wolves spread over the northern hemisphere, replacing all earlier Pleistocene wolves (Loog et al., 2020). It appears that dogs derived from this Beringian population, although scientists have struggled to define the precise temporal and geographic origins. The timing now seems to have between 25 and 15 kya, the date range between the modern wolf type and the first occurrence of the oldest archaeological dogs. Archaeological dog remains that we accept as dogs consist of about 20 Final-Pleistocene and very early Holocene specimens (**Tab. 1**). Our assessments are based on: Osteomorphology and morphometrics; an anthropogenic context that included dog-human burials; and considerably smaller size than isopatric and contemporaneous wolves. Additionally, certain specimens have

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been shown to possess dog DNA (**Tab. 1**). Most of these specimens are about 45 cm high at the shoulders and weigh approximately 15 kg (wolves: > 50-70 cm and > 40-80 kg).

Larger-sized 'protodogs' had been reported from as early as 40 kya (Camarós et al., 2016; Germonpré et al., 2009, 2012, 2015, 2017; Sablin and Khlopatchev, 2002), mainly in Eastern Europe and Asia. The species assignment of these few large specimens (Germonpré et al., 2009, 2012, 2017) was based mainly on shorter skull and snout, and wider palate (Germonpré et al., 2009, 2012, 2017). Another group of 'protodogs' (n > 30) from Predmosti was so assigned, based on shorter mandibular metrics (Germonpré et al., 2015). The assignment of these 'protodogs' as dogs has been questioned by a large number of investigators (Boudadi-Maligne and Escarguel, 2014; Crockford and Kuzmin, 2012; Janssens et al., 2019a; Jung and Pörtl, 2018; Morey 2014; Morey and Jeger, 2015; Napierala and Uerpmann, 2012; Perri, 2016; Pitulko and Kasparov, 2017; Wilczynski et al., 2020). In summary, morphology (Janssens et al., 2019a) and DNA studies (Thalmann et al., 2013, 2018) validate them as wolves. Their relevant morphometrics do not differ from Pleistocene wolves (Janssens et al., 2019a). Shortened mandibular measurements can be seen in a subgroup of specimens from one breed of modern dogs. Thus, even one dog breed can be split into two morphotypes, based on normal morphological variability (the Gaussian curve), similar to Pleistocene wolf specimens. Recently, arguments have focused on differences in 'protodog' isotopes (Bocherens et al., 2015) and dental wear (Prassack et al., 2020). However, the latter arguments have been questioned as well (Janssens et al., 2021).

Based on archaeological observations, dogs likely originated in Eurasia or the Middle East (Altuna et al., 1984; Baales, 1992; Boudadi-Maligne et al., 2018a; Célérier et al., 1999; Chaix, 2000; Day, 1996; Degerbøl, 1961a, 1961b; Gourichon and Helmer, 2008; Grosman, 2013; Leesch, 1997; Leesch and Müller, 2012; Mertens, 1936; Morel et al., 1997; Napierala and Uerpmann, 2012; Nobis, 1979, 1981; Street, 1991, 2002; Tchernov and Horwitz, 1991; Tchernov and Valla, 1997; Turnbull and Reed, 1974; Vigne, 2006; Vigne et al., 2011; Yeomans et al., 2019).

Genetic determination of "a dog" is based on differences between dogs and wolves that involve mtDNA, Y-DNA, and nDNA (Botigué et al., 2017; Fan et al., 2016; Frantz et al., 2016; Savolainen et al., 2002; Skoglund et al., 2015; Thalmann et al., 2013; Wang et al., 2013). Based on mtDNA, dogs can be described as having four mtDNA (A-D) clades, that diverge from known wolf signatures (Thalmann et al., 2013). Genetic studies point to geographic origins in Europe (Thalmann et al., 2013); Asia (Botigué et al., 2017; Brown et al., 2011; Ding et al., 2012); the Far East (Pang et al., 2009); Central Asia (Shannon et al., 2015); and with an input from Middle Eastern wolves (Sacks et al., 2013; Savolainen et al., 2002; Pollinger et al., 2010). These varying viewpoints on geography result from complicating influences, such as (not an exhaustive list):

(1) a relatively brief period of divergence, thus only minor differences being present; (2) high mobility of wolves disseminating their genes, indicating possible geographic distancing between ancestral wolf populations and the earliest domestic dogs; (3) incomplete lineage sorting (Thalmann and Perri, 2018), thus possible retention of ancestral polymorphism, clouding real time differences; (4) lack of sufficient high quality aDNA genomes to support reliable conclusions (Pickrell and Reich, 2014); (5) lack of knowledge of the origin region(s) (Irving-Pease et al., 2018; Pickrell and Reich, 2014); (6) limited understanding of long-range migrations and population replacements of humans and accompanying dogs, especially during the late Pleistocene (Botigué et al., 2017; Frantz et al., 2016; Pickrell and Reich, 2014); and (7) hybridization (Fan et al., 2016; Godinho et al., 2011; Khosravi et al., 2013a,2013b; Pilot et al., 2014; Tsuda et al., 1997; Pollinger et al., 2010; Vilà et al., 1997). To be of influence for dog domestication, early offspring must have been progeny of female dogs and male wolves, with pups born in the human niche. However, recent genetic research has pointed to almost exclusive male dog-female wolf hybridization (Bergström et al., 2020), thus complicating associated hypotheses.

Specimens	Country	Chronocultural Context	Direct dating on dog remains Lab no.	Radio-carbon Age [^{14}C BP]	Indirect datings from contexts [^{14}C BP]	mtDNA Clade	MNI	References
Eralla	Spain	Lower/Upper Magdalenian			16,270 ± 240 12,310 ± 190		1	Altuna et al., 1984; Vigne, 2006
Montespan	France	Middle Magdalenian			*ca. 15,500/ 13,500* *		1	Pionnier-Capitan et al., 2011
Le Morin	France	Upper Magdalenian	OxA-23627 OxA-23628	12,540 ± 55 12,450 ± 55			1	Boudadi-Maligne et al., 2012
Bonn-Oberkassel	Germany	Late Magdalenian – Early Federmesser	OxA-4793 KIA-41162 KIA-41161 KIA-41163	12,270 ± 100 12,210 ± 60 12,110 ± 45 11,620 ± 60		C	2	Street, 2002; Janssens et al., 2018
Kesslerloch	Switzer-land	Upper Magdalenian	KIA-33350	12,225 ± 45		C	1	Napierala and Uerpmann, 2012
Grotta Paglicci	Italy	Epigravettian	OxA-26316	12,175 ± 55	?		1	Boschin et al., 2020
Grotta Romanelli	Italy	Final Epigravettian			11,858 ± 85 8,048 ± 75	C	1	Boschin et al., 2020; Calcagnile et al., 2019
Le Closeau	France	Azilian			12,480 ± 70 12,050 ± 100		1	Pionnier-Capitan et al., 2011
Troubat	France	Azilian	OxA-36550	10,600 ± 45			2	Boudadi-Maligne et al., 2020
Palegawra	Iraq	Zarzian			*ca. 12,000* *		1	Turnbull and Reed, 1974
Pont d'Ambon	France	Laborian	GifA 99102 Beta 411309	10,730 ± 100 10,130 ± 40		C	2	Célérier et al., 1999; Pionnier-Capitan et al., 2011; Boudadi-Maligne et al., 2018a
Saint-Thibaud-de-Couz	France	Laborian	Ly23/OxA-4405	10,050 ± 100			1	Chaix, 2000
Kartstein	Germany	Ahrensburgian			10,220 ± 75 9,995 ± 65	C	1	Baales, 1992
Bedburg	Germany	Early Mesolithic			9,780 ± 100 9,600 ± 100		1	Street, 1991
Senckenberg-Moor	Germany	Mesolithic			*ca. 10,000* *		1	Mertens, 1936; Degerbøl, 1961b
Ain Mallaha	Israel	Natufian			10,540 ± 90 10,530 ± 100		2	Tchernov and Valla, 1997; Grosman, 2013
Hayonim Terrace	Israel	Natufian			11,790 ± 120 9,640 ± 100		2	Tchernov and Valla, 1997; Grosman, 2013
Shillouro-kambos	Cyprus	Neolithic (Middle PPNB)			9,525 ± 49 9,432 ± 49		1	Vigne, et al., 2011
Shubayqa 6	Jordan	Neolithic (PPNA)			10,072 ± 43 9,440 ± 50		?	Yeomans et al., 2019
Tell Mureybet	Syria	Late Natufian (Khiamian)			9,905 ± 60 9,945 ± 50		1	Gourichon and Helmer, 2008; Grosman, 2013
Uncertain dog remains								
Monruz	Switzer-land	Upper Magdalenian			13,330 ± 110 12,800 ± 85		3 ?	Morel et al., 1997
Hauterive	Switzer-land	Upper Magdalenian			13,050 ± 155 12,510 ± 130		1	Morel et al., 1997

Tab. 1 The earliest small stature dogs. Note: all radiocarbon dates (^{14}C) are uncalibrated.
* Age estimates based on stratigraphic data.

Genetic dating of divergence timing is based on wolf generation time and mutation rate (Botigué et al., 2017; Frantz et al., 2016; Fan et al., 2016; Koch et al., 2019; Larson et al., 2012; Larson and Bradley, 2014; Mech et al., 2016; Pang et al., 2009; Savolainen et al., 2002; Skoglund et al., 2015; Thalmann et al., 2013; Vilà et al., 1997; Wang et al., 2013). Investigators historically have suggested a timing of divergence between 6 and 135 kya (Savolianen et al., 2002; Vilà et al., 1997). The most recent dating is unrealistic, since the oldest archaeological dog finds date from 15 kya. The oldest genetic dating also is questionable, since the geographic spread from the most probable immediate dog ancestor, the modern wolf type from Beringia, began around 25 kya (Loog et al., 2020). The most used wolf and dog generation time is 3 years (Ersmark et al., 2016). However, Mech and colleagues have indicated a longer wolf generation time (4.2-4.7 years) (Mech et al., 2016), while we suggest a shorter generation time for dogs, beginning at year one, and once yearly with some variability (Spotte, 2012). The use of such different generation times would result in mean divergence timing estimates 25 % more recent.

Mutation rate uses estimates ranging from 1×10^{-8} to 6.6×10^{-9} per autosomal site, per generation (Botigué et al., 2017; Fan et al., 2016: Fig. 6; Frantz et al., 2016; Freedman et al., 2014, 2017; Koch et al., 2019; Skoglund et al., 2015; Wang et al., 2013), and depends on the accepted divergence times between wolf and coyote (varying from 750 kya to 1,000 kya) and of canids and felids. This huge variability helps to explain the large spread in estimated divergence timing dates between wolves and dogs, having occurred, in any event, just a few thousand years ago.

Hypotheses about the number of times that wolves were domesticated include: A single event (Freedman et al., 2014; Savolainen et al., 2002; Bergström et al., 2020); dual origins (Frantz et al., 2016); or multiple origins (Skoglund et al., 2015; Vilà et al., 1997). It is beyond the scope of this article to elaborate on these differences.

Here, we focus on smaller size as the most important morphological difference between wolves and dogs. We discuss probable primary causes for this difference in physiological and genetic terms and consider related historical explanations. Further, we evaluate domestication pathways that have been proposed, in light of the best circumstantially-likely hypotheses, to explain smaller size as a stress-related growth response.

MORPHOLOGY CHANGES IN DOGS VERSUS WOLVES

Osteological distinguishing of ancient dogs and wolves (Olsen and Olsen, 1977) involves morphology, morphometrics (Harcourt, 1974; Stockhaus, 1965), and geometric morphometrics (GM) (Adams et al., 2004; Ameen et al., 2017; Drake, 2011; Drake and Klingenberg, 2010; Drake et al., 2015; Fondon and Garner, 2007; Ledoux and Boudadi-Maligne, 2015; Rizk, 2012). Historically, distinguishing traits for dogs have included: more tooth crowding; greater oral pathology; smaller sagittal crest; caudal curving of the coronoid process of the vertical mandibular ramus; smaller tympanic bulla; paedomorphism; difference in mandible mass; convex ventral horizontal mandibular ramus; more caudal position of the hard palate caudal border; different micro anatomy of the maxillary p4 protocone; shorter snout-length ratio; and higher snout ratio. All of these now have been rejected (for detailed review and references, see Janssens et al., 2019a).

Smaller size is the most robust trait for distinguishing wolves from dogs (Benecke, 1987, 1994; Bökönyi, 1975; Boudadi-Maligne et al., 2012; Clutton-Brock, 1962, 1963, 2012; Davis and Valla, 1978; Dayan, 1994a, 1994b; Degerbøl, 1961b; Kurtén, 1965; Mertens, 1936; Napierala and Uerpmann, 2012; Rütimeyer, 1861, 1875; Studer, 1901; Wolfgram, 1894). The oldest archaeological dogs are about ⅔ of the size of contemporaneous isopatric wolves (Janssens et al., 2019a; Kurtén, 1965). The Hayonim (Tchernov and Horwitz,

1991; Tchernov and Valla, 1997) and Bonn-Oberkassel (Street and Jöris, 2015) human-dog burial specimens are about 45 cm high at shoulders, compared to > 60 cm for most wolves. Early Holocene and Neolithic dogs, such as in Jericho, are even smaller, at 30-40 cm (Horard-Herbin et al., 2014; Zeuner, 1963). This trend also is observed in dogs at Neolithic Alpine lake Pfahlbauten settlements (Rütimeyer, 1875).
Additional morphological wolf-dog differences that can be accepted for species assignment include, for dogs:

Differences related to smaller size:

- Isometric size reduction (cranial and post-cranial) such as shorter skull length (Lawrence and Bossert, 1967; Gaudry and Boule, 1892);
- Shorter mandibular m1 mesio-distal diameter < 21.8 mm (Janssens et al., 2019a);
- Shorter maxillar p4 mesio-distal diameter < 22.5 mm (Janssens et al., 2019a).

Differences related to change in facial morphology:

- Wider snout-width index (Morey, 1992, 2010; Wayne, 1986);
- Higher skull-height index (Pitulko and Kasparov, 2017);
- Higher orbital angle > 60° (Janssens et al., 2016);
- Higher stop (Drake et al., 2015).

Differences related to the brain:
- Smaller brain-size ratio in dogs (Arbuckle, 2006; Zeder, 2006, 2012),
- Inner ear morphology (Janssens et al., 2019b).

It is important to understand that these distinguishing facial morphology traits are not independent. They are related, based on changes such as different closure times for the maxillary, temporal, and zygomatic skull suture lines (compared to wild wolves), probably driven by differences in the Runx-2 and Twist-1 alleles (Fondon and Garner, 2007). The outcome is dorsolateral orbital expansion that creates a larger orbital angle, higher nasal stop (height difference between nasal and frontal bones), wider snout and higher skull ratio, compared to skull length (Drake and Klingenberg, 2010; Drake, 2011; Drake et al., 2015; Janssens et al., 2019a; Rizk, 2012). The smaller size and skull morphology thus should be considered as a morphological unit.
Development of smaller size (Aaris-Sørensen, 1977, 2005) appears to have occurred at the end of the Pleistocene in several species, and likely was related to Holocene temperature rise (Bergmann's law) (Tchernov and Horwitz, 1991). But in early domesticates, the proportional size reduction is substantially larger, and is localized to the specific domestication geography. Therefore, nearby wild isopatric conspecifics may not be revealing in every instance (Davis, 1977, 1981; Tchernov and Horwitz, 1991).

DIFFERENCES BETWEEN DOGS AND WOLVES THAT ARE NOT OSTEOLOGICAL

Genetics of integumental traits

Although non-osteological traits are invisible in the archaeological record, they can be explored genetically to document changes in dogs that do not occur in wolves. Some examples follow:

Coat texture

Wolves have a double coat, with a dense short undercoat, longer guard hairs, and hair-shedding during summer (Pocock, 1935). Most modern dogs also possess a double coat, although some breeds have only short hair or even baldness (mutation of FOXI3 gene on chromosome 17) (Drögemüller et al., 2008). Dogs on Egyptian bas-reliefs (Pfluger, 1947) already possess coats seen in modern breeds (long, fluffy, curly). Genetic analyses proved the involvement of three genes for these new coat forms in dogs: FGF5, KRT71, and RSPO2 (Cadieu et al., 2009). These changes in allelic composition can be searched for in archaeological specimens.

Coat colour

Wolves carry a variant of the wild colour gene (agouti) (Schmutz and Berryere, 2007) and demonstrate colour variations between dark grey and white, with coloured undercoat, although *C. l. arabs* has a light-brown coat (Pocock, 1935, 1939). Black and red colour variants in wolves are results of hybridizing: black is caused by backcrossing with dogs, red by crossing with coyotes (*Canis latrans*) (Wayne and Jenks, 1991). Dogs have a wide variety of coat colours: Red, white, grey, blue, brindle, gold, and a wide variety of different colour patterns, of which most are heritable (Ollivier et al., 2013; Schmutz et al., 2007, 2009). Coat colours are expressed by complex interactions among 1) pigment synthesis, mainly eu- and pheo-melanin produced from tyrosine through tyrosinase, and 2) receptor access (Sponenberg and Rothschild, 2001). Mutations in > 150 different colour genes have been discovered in the genome of modern dogs (Kerns et al., 2007; Kim et al., 2005). Coat colours as seen in modern dogs were present by 10 kya (Kim et al., 2005; Ollivier et al., 2013).

Ear carriage

Wolves and many dogs have prick (standing) ears, but some modern breeds possess proportionately large floppy ears. Darwin wrote that there were no wild animals with floppy ears, apart from elephants (Darwin, 1868). The genetic architecture of floppy ears in dogs is localized in regions CFA10 and MSRB3 (Boyko et al., 2010), allowing for genetic search of archaeological specimens. Clutton-Brock (1995, 1999) suggested that floppy ears are degenerate and reduce biological fitness, based on reduced hearing and a smaller social communication palette. However, no documenting scientific evidence exists to support this hypothesis.

Reproductive differences

Wolves breed annually (monestrous; Mech, 1970) and stay in family groups (Mech and Boitani, 2003). Most female wolves reach puberty between ages 2 and 5 years (Mech et al., 2016). Mating usually is restricted to the dominant (parental) pair that generally are monogamous (Stahler et al., 2013). The pack includes parents and the most recent immature offspring from the previous 1-3 years (Mech and Boitani, 2003). All pack members assist in care and feeding of pups, by carrying and regurgitating food (Mech, 1988). Mating occurs in late winter, with pup birth in spring (about 2 months after mating) depending on latitude (later at more northern latitudes).

Free-roaming dogs have no pack structure (Spotte, 2012), have mono-parenting, and lack monogamy. Bitches experience the first estrus at any time of year, starting between age 6-12 months, usually cycling twice per year, although some breeds express only one cycle per year (Basenji, Dingo, and Afghan hound). Estrus disengagement from seasons allows dog pups to be born all-year long, but pup survival can be assured only in a domestic environment. This argument is supported by the 100 % puppy death rate in feral dogs that do not whelp in spring or summer (Spotte, 2012). Hybrids between wolves and dogs are reported to have one estrous cycle per year (Buffon, 1799).

More frequent and earlier estrous cycles lead to more offspring through the breeding lifetime (Spotte, 2012). The reason for earlier sexual maturity in dogs lies in progenesis. The latter has been observed in all basic domesticates (pigs, cattle, sheep, goats) and has been related to a less stressful anthropogenic niche and to relative smaller brain-size (Healy and Rowe, 2006; Hemmer, 2005; Morey, 1992, 2010; Nehring, 1888; Nobis, 1981; Olsen and Olsen, 1977; Stockhaus, 1965; Tchernov and Horwitz, 1991; Zeder, 2012). Relative smaller brain size also is seen in island dwarfism, when stress levels are lower due to lack of competitors and/or predators (Heaney, 1978; Hofman et al., 2015; Lomolino, 1985; Lomolino et al., 2013; Meiri et al., 2004, 2008; Prothero and Sereno, 1982). Smaller brain size is not general, but is restricted to downsizing of specific brain stress centres, such as the reticulo-activated system (Kruska, 1988a, 1988b; O'Regan and Kitchener, 2005).

Based on the foregoing reports, the hypothesis states that reduced production of corticotropin-releasing-hormone results in lower production and release of adrenocorticotropic hormone (ACTH). Less circulating ACTH results in turn in less adrenal stimulation and thus lower glucocorticoid production and release (Arbuckle, 2006; Hemmer, 2005; Trut, 1999; Trut et al., 2009). This chain of events would result in greater production of gonadotropin releasing hormone (GnRH), thus activating follicle stimulating hormone (FSH) (Klütsch and De Caprona, 2010) that induces earlier gonadal estrogen production in mammals (Grumbach, 2000; Matsuo and Fujieda, 2006; Van der Eerden et al., 2003; Verdonck et al., 1998a, 1998b). Additionally, epiphyseal chondrocytes in growth plates are stimulated, leading to increased earlier chondrocyte activity and creating a growth spurt. Chondrocytes die thereafter, and growth plate closure occurs, leading to earlier growth cessation (Kreeger, 2003; Wilkins et al., 2014; Zeder, 2012; Zeder et al., 2006). Modern wolves that grow up in a human environment (Janssens et al., 2019a; Viranyi, Ernstbrunn, Austria, wolf science centre, pers. comm.), or those that grow up in the wild with an abundance of prey when competition is lacking (Gould, 1966; Mech et al., 2016; Medjo and Mech, 1976; Risenhoover and Bailey, 1988), show earlier estrus.

DOMESTICATION PATHWAYS

Pup collection

The proper age for ancient humans to have collected wolf pups from dens would have been prior to age two weeks, as after this time they will become less sociable, behave uncooperatively, and fear humans. Any success certainly would require wolf puppies younger than age 4 weeks (Fentress, 1967), and before eye opening (Darwin, 1868; Dehasse, 1994; Frank et al., 1989; Klinghammer and Goodmann, 1987; Kubinyi et al., 2007). The pups would have been breastfed and raised in the anthropogenic pack (Simoons and Baldwin, 1982), where it is likely that they were pleasant pets until sexual maturity (as demonstrated by modern ethology experiments and many individual reports) (Crisler, 2000; Hell and Paule, 1982; Hellmuth, 1965; Hillis and Mallory, 1996; Jolicoeur, 1959; Stockhaus, 1965; Wolfgram, 1894). During this period, they were fed and protected from competitors and predators, and they did not have to hunt large prey. Interestingly the foregoing are the factors that define island dwarfism (Heaney, 1978; Hofman et al., 2015; Lister, 1989; Lomolino, 1985; Meiri et al., 2004; Meiri et al., 2008; Prothero and Sereno, 1982; Wasserburg et al., 1979; Weston and Lister, 2009) that involves progenesis and smaller size, including smaller relative brain size.

Behaviourally unsuitable pups likely would have been chased away, starved, or killed, as suggested anecdotally today in some rural settings. When mature, reports suggest unruly behaviour and permanent departure, with the associated risks of being killed by surrounding wolf packs, or starving because they had not learned to hunt. Another possibility is that several collected pups were in one camp, perhaps deriving from different dens and different years. Subsequent to finding mates in the camp, they had no need to escape. If they did escape, they self-isolated from wild wolves in the region, thus creating the necessary genetic isolation for speciation. Did any of this actually happen? We do not know!

Self-domestication

In a self-domestication hypothesis, wolves sought contact with humans based on certain interests (Larson and Fuller, 2014; Zeder, 2012). For this domestication pathway, association with humans must have occurred when the domesticates were adults, as immature wolves would have been kept away from humans, safe in wolf territory. Adult wolves could not show progenesis and concurrent morphological changes in size and skull. A further complication relates to why wolves would seek human contact. The latter does not occur in modern times, and it is unreported in historical and ethnology sources up to 4,200 years ago. Finally, during the time period of wolf domestication, humans were hunter-gatherers, many following migrating herds over long distances. Rationalizing wolf self-domestication under such circumstances is quite difficult, particularly considering the possibility of humans' "companion" wolves being killed by foreign wolf packs (Binford, 1983, 1990; Campbell, 1973; Houtsma et al., 1996; Testart, 1982).

PROPOSED REASONS FOR WOLF DOMESTICATION

Most domestication hypotheses are utilitarian, yet through logic alone, we should question how people could have known what to anticipate from wolves as a part of the human niche, since they had no related prior experience or knowledge.

Hunting

The possibility that early domesticated dogs hunted in collaboration with humans, thereby increasing hunting success, was among the earliest proposed reasons to domesticate wolves (Hare et al., 2012; Hare and Tomasello, 2005). Recently, scientists are much more cautious about accepting this hypothesis, as the result of increased knowledge of past climate and landscapes, new ethnological observations, and more advanced understanding of wolf hunting behaviour in the wild. Wolves are excellent pack hunters, just as humans are skilful group hunters. Both hunted the same large ungulate species, prompting some scientists to suggest that humans, if assisted by early dogs, could reduce their own energy costs, increase prey encounter rates, and improve efficiency of attack and pursuit of prey (Lupo, 2017).

However, if dogs had been accustomed to hunting large prey, major skeletal injuries would be expected in zooarchaeological remains. Such lesions are not found in the archaeological record, whereas they are recorded routinely in wild wolves (Mech and Peterson, 2003; Spotte, 2012). Another aspect to consider is that, if cooperative hunts were done with wolves still functioning as a pack, it is difficult to imagine how the human interactions would have been possible. Contrary to dogs that can be controlled by voice commands, wolves hunt instinctively, and would hunt independently of their human companions. Also, following the wolves around would be energy-inefficient for humans, because of the speed and endurance of the wolves. In the latter circumstance, humans likely would not increase prey contact and would increase their energy expenditure. However, once wolves were domesticated (being then dogs) to the point of control by human voices, they could have been useful. If this happened over a few generations after puppy collection, such aid then may have been a powerful motivation to pursue additional domestication.

Conceivably, dogs might have been used for hunting during the Magdalenian, the period coinciding with the end of the LGM and the onset of a warmer climate and concurrent faunal changes (Aranbarri et al., 2014; Miller, 2012). The European environment shifted from an open landscape (steppe-tundra) during the LGM to a closed landscape (boreal-, later deciduous forest) (Perri, 2016). This was a time of considerable change in animal targets, weapons, and hunting strategies. Use of the spear, atlatl, and dart shifted to the bow and arrow. Group hunting shifted to more individual hunting (Angelbeck and Cameron, 2014), and hunting via sight shifted to hunting strategies that became more focused on auditory and olfactory cues. Additionally, there were new hunting challenges, such as retrieving wounded prey hiding in the bush, or locating prey hidden in dense forest.

This increasingly closed environment may have favoured use of early dogs in hunting, with Magdalenian humans benefitting from the superior auditory and olfactory abilities of dogs (Hepper and Wells, 2006). Wolves and dogs have about 200 million olfactory neurons (humans have about 5 million) and sense odours 100-1,000 times more efficiently than humans (Moulton, 1977). Dogs' auditory frequency ranges up to 80 kHz, while humans detect < 20 kHz. Wolves and dogs also detect low-decibel sounds from kilometres away (Asa and Mech, 1995; Heffner and Heffner, 2007; Lipman and Grassi, 1942). Lastly, but yet not identified in literature, dogs may have helped in guiding hunters back to camp at night (Arsenyev, 2016).

Some archaeological data challenge and complicate the hunting aid hypothesis. Bow hunting existed already in Southern Portugal during the Solutrean (25,000-20,500 cal BP), changing then to spear hunting again during the Magdalenian (Bicho, 2013). This evolution is contrary to what is known about the rest of Europe. Also, it is contrary to the logic behind a shift to bow hunting with use of dogs to retrieve prey. Dogs have been used in hunting in open landscapes, such as for beach seal (*Phoca* spp.), during the early Mesolithic in Denmark (Clark, 1936, 1946), or chasing fish into nets in Patagonian rivers (ethnographic data) (Darwin, 1868). Ethnographic data further complicate the hunting aid debate, because of contradictory reports. Some studies confirm the general beneficial use of dogs for hunting (Bicho, 2013; Kelly, 2013; Perri, 2016; Turney-High, 1941), whereas others confirm this benefit only for specific prey. Still others report opposing thoughts, with dogs chasing prey away (Hamilton, 1972), thus resulting in their exclusion from at least some hunting (Manwell and Baker, 1984).

Lastly, Lupo (2017, 2019) additionally proved that wolves do not hunt prey as large as mammoths. Intra-site archaeology of early sites with mammoth concentrations with tusk huts, such as Mezin and Mezhyrich, revealed hardly any bite marks on mammoth bones, thus excluding wolf or dog presence (Wilczynski et al., 2010).

Guarding

It is well-documented that wolves and both domestic and feral dogs guard their territory against wolves and other dangers (Boitani et al., 1995; Fritts et al., 2003). Based on these observations, some researchers have suggested that wolves were kept as guards against other wolves and carnivores, such as brown bears

(*Ursus* spp.), that repopulated the Magdalenian European landscape from southern refugia (Hescheler and Rüeger, 1942; Pacher and Stuart, 2009; Stewart and Lister, 2001; Tetzlaff et al., 2007). Other hypotheses include using dogs as alerts to signal nearby possibly dangerous prey (Shipman, 2015). Guarding could be done by barking (Harrington and Paquet, 1982; Spotte, 2012) or by alerting humans via restless behaviour. Guarding differs from hunting in that guarding behaviour can be expressed by very young dogs. This might have been the first wolf behaviour that humans appreciated, and thus a possible reason to domesticate wolves on a continuing basis.

Transport

It has been suggested that dogs were kept for transport, as seen ethnographically. There is archaeological support for this hypothesis, as dog harness-gear was excavated at a 9,000-year-old Neolithic settlement at Zhokov (Russia), confirming the existence of dog sledges (Pitulko and Kasparov, 2017). Items to be transported could include meat, various gear, and raw materials, as seen with Indigenous Americans using dogs to pull travois. Inuit (formerly Eskimo) dogs wear harnesses to pull sleds. In other populations, dogs may wear backpacks made of reeds (Aaris-Sørensen, 2005; Germonpré et al., 2017; Lupo, 2017; Pitulko and Kasparov, 2017; Turney-High, 1941).

Some archaeological publications have indicated that spinal morphological observations of archaeological dogs prove human use in transport. Such "pathology" included asymmetric dorsal vertebral spinous processes, flattening of the dorsal aspect of the dorsal spinous process, and spondylosis (Grandal-d'Anglade et al., 2019; Germonpré et al., 2015). However, these same pathological changes are observed among modern wolves and modern dog populations, in non-sporting dog breeds, and in dogs that are not loaded with weights on their backs or pulling travois. This demonstrates that these deformities are not evidence of ancient use of dogs for transport, but rather reflect either fluctuating asymmetry, normal ageing, or taphonomic changes in some instances (Lawler et al., 2016; Janssens et al., 2018). As with the hunting-aid hypothesis, aid-with-transport probably was not a motive to domesticate wolves but could have been a reason that domestication continued as humans imagined such uses for domestic dogs, over time.

Herding

Some authors proposed herding as a reason for domesticating wolves (Coppinger and Coppinger, 2002). However, domesticated animals were not available in pre-Neolithic societies, so this is not a valid hypothesis in the case of the dog.

Canophagy

Canophagy has been hypothesized as a reason to keep dogs (Degerbøl, 1961b; Horard-Herbin et al., 2014). Undoubtedly, wolves and dogs were used as food during periods of starvation (Manwell and Baker, 1984) or even symbolically when brains were eaten, as documented for some Upper-Palaeolithic canids (Germonpré et al., 2012). However, canophagy is improbable as a primary factor for wolf domestication. Dogs were rare during the Palaeolithic (Aaris-Sørensen, 2005; Pionnier-Capitan, 2010; Pionnier-Capitan et al., 2011;

Rütimeyer, 1861) and cannot have been an important food source. Cut-marks on Palaeolithic dog bones, as direct evidence for their consumption, also are rare (Boudadi-Maligne et al., 2012; Boudadi-Maligne and Escarguel, 2014; Boudadi-Maligne et al., 2018b; Harcourt, 1974; Manwell and Baker, 1984; Pionnier-Capitan, 2010), and more probably indicate skinning and opportunistic defleshing (Manwell and Baker, 1984). More recently, canophagy may have been systematic: Small dogs from the Neolithic *Pfahlbauten* villages at the Alpine lakes show many cut-marks, demonstrating defleshing (Becker and Johansson, 1981). Nevertheless, raising wolves for food would lack time and energy efficiency. Further, there would be no reason to domesticate them because humans could just use wolves.

Bed warmer

Some aboriginals sleep with dogs (huddling together) to keep warm during cold nights. Based on that information, maintaining warmth has been suggested as a reason to domesticate wolves (Manwell and Baker, 1984). Although it is easy to accept that wolf pups could be sleeping closely to humans, it is more difficult to accept the same regarding adult wolves. Still, experiments in Ernstbrunn, Austria, have demonstrated that such behaviour exists with sub-adult wolves (Viranyi, pers. comm.).

Symbolic and spiritual reasons

The Bonn-Oberkassel burial of two humans and two dogs is the oldest reported dog burial (14,300 ya) (Street and Jöris, 2015), together with the Natufian terrace dogs of Hayonim and Ain Mallaha (Grosman, 2013). Dog burials are found more frequently from more recent periods, such as the Stilwell, Stilwell II, and Koster sites, Illinois USA, and those in Mesolithic Scandinavia (10,200-6,500 ya) (Aaris-Sørensen, 1977; Morey, 2010; Perri, 2016). Dog burials became progressively more abundant during the Bronze Age (Perri, 2016). Massive dog burials took place in Ashkelon (Israel) with 1,200 dogs buried about 2,500 ya (Morey, 2010). Dog burials and human-dog burials represent symbolic behaviour in humans (Morey, 2006, 2010), possibly related to a belief in afterlife, wherein the dog would guard against evil or assist humans with hunting (Grünberg, 2013; Losey et al., 2013). A further possibility is a continued emotional bond with the deceased human. For an overview on dog burials, see Morey (2006) and Losey et al. (2013). There are rare indications wolves also were buried symbolically (Germonpré et al., 2012). We suggest that domesticating wolves exclusively for these purposes would indicate considerable human foresight.

Ornamental use

Some authors hypothesize that domestication was based on use of dog pelts, teeth, and bones for clothing and ornamentation (Boudadi-Maligne et al., 2018a). While cut-marks on dog bones and perforated dog teeth and metapodia have been documented in the archaeological record, perforated teeth and bones of wolf, bear, and other wild animals have been recovered from the Gravettian onward (Becker and Johansson, 1981; Boudadi-Maligne et al., 2018b). Thus, it is improbable that this was an important motivation for domestication. There is no indication that dogs would provide any better pelts, teeth, or bones for ornamental use, compared to wolves.

Warfare

Warfare against Neanderthals was proposed to explain their demise and the superiority of *Homo sapiens* (Shipman, 2009, 2010, 2015). Early dogs could have assisted modern humans in hunting mammoths, thus providing modern humans a competitive advantage over Neanderthals. This hypothesis is highly speculative, since there are no dog remains known from the Châtelperronian or the initial Aurignacian, the periods and contexts during which *Homo sapiens* and Neanderthals co-existed. Furthermore, the demise of Neanderthals increasingly has been suggested to be within the context of "make love not war" (Kuhlwilm et al., 2016).

THE NON-UTILITARIAN SCENARIO: AS PETS

It has been hypothesized that the emotional bond between humans and wolves, and later dogs, may have been an important drive for domestication (Aaris-Sørensen, 2005; Horard-Herbin et al., 2014; Serpell, 1995; Street, 2002; Tchernov and Valla, 1997). One of several prominent examples is suggested by the Bonn-Oberkassel human-dog burial (Street, 2002).

Wolves and dogs have several behaviours (Packard, 2003; Scott 1950, 1967) in common with humans. These include (1) a home site (the territory, campsite); (2) a group identity (the pack, eventually including close humans); (3) functioning in a dominance-ordered micro-society; (4) defence of the pack/home site; (5) expressing social altruism (sharing food, helping others, cooperation); and (6) playful behaviours.

Playful behaviours include (Harrington and Asa, 2003): 1) out-of-context or conceptual behaviour (playing with a feather or branch as if it were small prey; 2) exaggerated activity such as galloping rounds when happy; 3) meta-communication (tail wagging when expecting something positive); and 4) changing roles (running behind another pack member, "hunting" it, then turning around and asking to be hunted).

Research on attachment between either dogs or wolves and humans has not revealed important differences (Gásci et al., 2005, 2010; Topál et al., 2005), since both dogs and wolves display a complex social palette, comparable to that of primates and humans (Mech and Boitani, 2003). Therefore, it is natural for wolves and dogs to adapt to humans and their environment, but only if socialisation is initiated early enough; socialization ages are 2-4 weeks for wolves and 7-10 weeks for dogs (Darwin, 1868; Frank et al., 1989; Klinghammer and Goodmann, 1987; Kubinyi et al., 2007). The interest in the relationship is bidirectional with dogs, with humans recognizing puppy behaviour as attractive (Scott, 1950) and considering dogs as full family members (Berryman et al., 1985; Mitchell, 2001). All of the characteristics described in this section help us understand why Palaeolithic humans may have been attracted to wolves and their pups, incorporating them into their micro-social system.

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