Human Ecology (2021) 49:677–689
https://doi.org/10.1007/s10745-021-00234-z

Mothering the Orphaned Pup: The Beginning of a Domestication Process in the Upper Palaeolithic

Mietje Germonpré[1] · Martine Van den Broeck[2] · Martina Lázničková-Galetová[3] · Mikhail V. Sablin[4] · Hervé Bocherens[5]

Accepted: 26 April 2021 / Published online: 20 May 2021

Abstract

Several hypotheses have been proposed to explain the initial steps in the domestication process of the wolf. We discuss the human-initiated model in which wolf pups were brought to camp sites by male hunters and cared for by nursing women. A good relation between the more sociable and playful pups and the women and their children likely formed affiliative bonds and led to the survival of such pups into maturity. Some of these animals could have reproduced and delivered at least one litter. A selection on the behaviour of subsequent generations could ultimately have led to Palaeolithic dogs.

Keywords Upper Palaeolithic · Domestication · Wolf pup · Gender · Age · Animism · Small-scale societies · Northern Eurasia · The Americas

Introduction

According to Ducos (1978, 1989) and Clutton-Brock (1989), domestication is a process that can only start when tamed animals become part of a human socioeconomic structure.

✉ Mietje Germonpré
mgermonpre@naturalsciences.be

Martine Van den Broeck
martine.vandenbroeck@ugent.be

Martina Lázničková-Galetová
laznicko@yahoo.fr

Mikhail V. Sablin
msablin@yandex.ru

Hervé Bocherens
herve.bocherens@uni-tuebingen.de

[1] Operational Direction Earth and History of Life, Royal Belgian Institute of Natural Sciences, Vautierstraat 29, 1000 Brussel, Belgium

[2] Department of Morphology, Faculty of Veterinary Medicine, Ghent University, 9820 Merelbeke, Belgium

[3] Moravian Museum, Zelný trh 6, 65937 Brno, Czech Republic

[4] Zoological Institute RAS, Universitetskaya nab. 1, 199034 Saint-Petersburg, Russia

[5] Department of Geosciences and Senckenberg Centre for Human Evolution and Palaeoenvironment (HEP), Universität Tübingen, Hölderlinstrasse 12, 72074 Tübingen, Germany

Recent studies of human-animal relations in the past emphasize not only strategies of control and domination but also notions of trust, mutualism, interdependency, caretaking, and co-existence (Anderson 2014; Lien 2015; Pasarić and Warren 2019). Galton (1865) was probably the first to propose that domestication developed out of the tendency of prehistoric peoples to keep young wild animals (Loovers *et al.* 2018). His premise of selecting the most docile individuals to be raised and to breed was later adopted by several researchers (e.g., Clutton-Brock 1995; Germonpré *et al.* 2018; Loovers *et al.* 2018; Müller 2005; Sauer 1952). Recently however, the assumption of a self-domestication model of the wolf that proposes less wary wolves were attracted to prehistoric human camp sites to scavenge stored food or refuse dumps, eventually becoming habituated to humans and colonizing the human dominated environment, is gaining favour. According to this premise, the descendants of the habituated wolves would become domesticated through more intensive human selection (e.g., Coppinger and Coppinger 2001; Hare 2017; Larson and Fuller 2014; Stahl 2016; Zeder 2012). Some critiques of this model concerning the accessibility of stored food and garbage and the behaviour of habituated wolves are formulated by Koler-Matznick (2002), Germonpré *et al.* (2018), and Lupo (2019). Further, in the ethnographic context of the circumpolar North, wild animals that come to a camp site uninvited at night or enter a camp to steal food generally induce negative human reactions (Hallowell 1960; Laugrand 2017; Simonova

2018). However, at kill sites meat or spoils are often set aside for wolves and other predators (Brandišauskas 2017; Pierotti and Fogg 2017; Sharp and Sharp 2015). The human-initiated model suggests that wolf pups were taken from their dens by Upper Palaeolithic hunters and brought to the camps to be raised for different motives; the most sociable pups could have survived until adulthood and reproduced; a selection on docile behaviour in subsequent generations could have led in the long run to Palaeolithic dogs (e.g., Germonpré *et al.* 2018, 2020; Müller 2005). We argue that such a domestication process could have started in several hunter-gatherer societies over northern Eurasia during the Upper Palaeolithic. As the scope of this paper is to examine in detail the first steps in the human-initiated domestication path based on arguments derived from developmental biology, archaeology, and ethnography, we do not develop here a more profound analysis of the self-domestication hypothesis. The first incipient dogs, which we describe as Palaeolithic dogs, are all from sites located above 44°N. These canids represent a unique morphotype that is characterised by an absolutely and relatively shorter skull, snout, and jaw and a relatively wide palate and braincase compared to sympatric Pleistocene wolves (Galeta *et al.* 2021; Germonpré *et al.* 2009, 2017a). Although such shape characteristics match well a pattern that has been observed in ancient dog skulls (Morey 1992; Sablin and Khlopachev 2002), Palaeolithic dogs nevertheless differ morphometrically from extant dogs (Galeta *et al.* 2021; Germonpré *et al.* 2017a, b). Yet, the attribution of canid skeletal elements dating from before the Last Glacial Maximum (LGM), an extremely cold and dry period dating from 23,000 years to 19,000 years ago (Mix *et al.* 2001) to incipient dogs is not unequivocally accepted (e.g., Janssens *et al.* 2019; Morey and Jeger 2015), but see a rebuttal in Galeta *et al.* (2021). In this contribution, we review some ideas of how, during the Upper Palaeolithic but at an ontogenetic time scale, wild wolf pups could have been raised at the camp sites and how, after several generations of selection on behaviour, a population of tamed canids living with humans could have evolved into Palaeolithic dogs.

Evidence and Methods

We use ethnographic data on forager societies, especially concerning the relations between humans and wild and tame animals, in conjunction with archaeological and zooarchaeological data gathered from Upper Palaeolithic sites, and zoological data concerning the development and growth of extant wolf and dog pups and their interactions with humans. We searched the ethnographic literature on circumpolar and Amerindian small-scale societies for practices concerning how young, wild animals are integrated in the daily life of the peoples from these societies. Our search was by no means exhaustive nor quantitative. We focused on studies of so-called animist societies (Willerslev 2011) in the circumpolar North and the Americas since it has been proposed that Upper Palaeolithic societies could also have been animistic (Hussain and Floss 2015; Porr and de Maria 2015; Wallis 2014; Willerslev 2011). A word of caution must be added, since this ethnographic documentation deals with peoples who have, in contrast to Palaeolithic populations, knowledge about and/or experience with dogs. In addition, we agree with French (2019) that the diversity of past societies and traditions must have been much richer than can be deduced from ethnographic information concerning contemporary small-scale societies and that there could be an absence of a recent counterpart in the Palaeolithic record. Although the communities that left their traces at these sites have disappeared, we believe that, as proposed by among others Porr (2001) and Hussain (2019), the use of anthropological analogies can facilitate our interpretations of the fossil data, whilst we should not drive the analogies too far. Nevertheless, human behaviour, based on biological and cultural directives, was adaptive in the Late Pleistocene and is today (Kelly 2013). We assume the principle of uniformitarianism as advocated by Kelly (2013: 273): "living foragers are not identical to those of the past but living foragers do operate under the same principles as did prehistoric hunter-gatherers." We use the feeding patterns and requirements of extant canid pups as a basis to detail the first steps in the human-initiated model of the domestication of the wolf. We then discuss some of the advantages of keeping tame wild animals at camp sites. Finally, we synthesize all these outcomes in a tentative narrative on the beginnings of the wolf domestication and point out the possible role of gender and age in this process. We argue that the integration of wild wolf pups in the life of Upper Palaeolithic foragers initiated the domestication of the dog (Germonpré *et al.* 2015, 2018).

Results

Mothering the Orphaned Pup

Numerous descriptions of the bringing home of young wild animals, such as wolf and fox pups, bear cubs, and infant monkeys, by hunters[1] in small-scale societies to be raised there can be found in the ethnographic literature (e.g., Costa 2017; Drucker 1951; Franklin 1824; Hamayon 1990; Murdoch 1892; Walker 2005). In these societies and

[1] Although the ethnographic record indicates that women in several small-scale societies do hunt, hunting is primarily undertaken by men (Kelly 2013).

those of the Upper Palaeolithic, the raising of wild young animals could have fulfilled several roles connected to social organization, prestige display, access to corporal products, symbolic and ritual activities, or could be related to an animistic worldview in which non-human persons are invited to share the space (Germonpré *et al.* 2018, 2020 and references therein). The best way to socialize a wolf is to remove the pups from their mother and hand-rear them before they open their eyes when they are 12 days old. At this tender age they can become attached to their human caretakers (Gaćsi *et al.* 2005; Hall *et al.* 2015; Lord 2013; Ujfalussy *et al.* 2017). One main question is how these young animals could have been fed and taken care of at Palaeolithic camp sites.

In North America, during pre-contact and early post-contact times, women cared for dog puppies (Delâge 2005; McCormack 2018; Wilson 1924). Ample ethnographic evidence exists that dog puppies were breastfed by several cultural groups around the world (*e.g.,* Denys 1908; Langkavel 1899; Milliet 1994, 2003; Sauer 1952; Simoons and Baldwin 1982; von Wrangel 1839). And in certain small-scale societies, a tradition existed that young captive wild animals were also nursed by and/or given pre-masticated food by women (e.g., Ainu and Tlinget women nursed bear cubs (Batchelor 1901; de Laguna 1972); bear cubs and wolf pups in Siberia (Hamayon 1990); Guajá women fed infant monkeys (Cormier 2003a); Samoed women cared for arctic fox pups (Klokov 2011)). In Amazonia, if a hunter kills an animal with an infant, the young is taken to the camp site and handed over to the women; it is the wife of the hunter who decides if the infant will be eaten or raised (Cormier 2003a; Costa 2017). Women are perceived to understand pets in a way that men do not (Cormier 2003b). At the camp, the young is tied to a post until it is accustomed to the domestic sphere (Costa 2017). Similarly, in Siberia, Tozhu herders tie up their domestic reindeer at the campsite so that the deer can become familiarized to human smells, voices, and touch (Stépanoff 2012). Many of the wild pets die within weeks or months after their arrival in the camp due to stress, neglect, and/or malnutrition, or they return to their habitat (Costa 2017; Drucker 1951; Simonova 2018). Others are given away by their owner and can then be killed (Costa 2017). If the animal survives, feeding by its woman owner can develop a relationship between the two and can be seen as a form of mothering (Cormier 2003b) since the young animal becomes completely dependent on their caretaker for their survival (Costa 2017). It is interesting in this context that in modern dogs, exposure to human handling during the nesting period seems to have a beneficial influence on developing the desired behaviour of a confident, non-aggressive social companion (Fox and Stelzner 1966; Gazzano *et al.* 2008). Young wild animals reared by women can be considered as surrogate children, as is the case in both Amazonia (Cormier 2003a; Costa 2017) and also in Siberia, where childless Ket families raised bear cubs captured when their mother was killed as their sons or daughters (Alexejenko 1963).

If the beginnings of the wolf domestication process were indeed initiated by humans, this would mean that at Upper Palaeolithic camp sites, captive wolf pups must have been provisioned with appropriate nourishment. This would have included milk and additional food sources (Lupo 2017; Müller 2005; Sauer 1952; Simoons and Baldwin 1982).

Mother's Milk and Egg Yolk

In wolf pups, the transition from milk feeding to solid nourishment begins when the pups are about five to six weeks old. When pups are seven weeks old, they frequently feed on regurgitated food provided by their mother and other pack members. At eight weeks the wolf pups become less dependent on milk. By 11 weeks they are weaned and adapt to non-regurgitated food (Packard 2003, 2019; Packard *et al.* 1992). Nutritional weaning in dogs normally starts at four to four and a half weeks (Mapletoft *et al.* 1974; Peterson 2011; Prendergast 2011), but supplementary feeding (in artificially fed pups) can start as early as at three to four weeks (Case *et al.* 2011; Earle 1939; Hoskins 2001; Rootkustritz 2006). The supplementary feeding comprises introducing semi solid food several times per day initially in small quantities (Case *et al.* 2011; Kirk 2001; Peterson 2011), and gradually increased in solidity and size so that by six to eight weeks the pups should be able to eat solid food (Case *et al.* 2011).

Current wolf-socializing experiments have been conducted mainly by women, based on the few publications that mention the gender of the persons working with the wolves (e.g., Topál *et al.* 2005). In these experiments, wolf pups are separated from their mothers when they are less than ten days old and their eyes are still closed. The pups are at first bottle-fed and from the age of about three to four weeks are gradually hand-fed solid food (Gaćsi *et al.* 2005; Ujfalussy *et al.* 2017). The composition of milk differs greatly amongst species (Jenness 1986; Skibiel *et al.* 2013). The milk of carnivores generally has a higher fat, protein, dry matter, and energy concentrations and a lower lactose concentration than milk of herbivorous and omnivorous species (Iverson 2007; Jenness 1986; Skibiel *et al.* 2013). Of the protein fraction of milk, the casein/whey ratio also differs between species (Case *et al.* 2011; Jenness 1986). Furthermore, in most species milk composition changes over the course of lactation (Iverson 2007; Jenness 1986; Oftedal and Iverson 1995). In dogs, protein concentration decreases in the first three weeks, then slightly increases until weaning; the concentration of lipids follows the same pattern, but less pronounced, and the energy content decreases gradually during peak lactation but then increases till it reaches its highest level at weaning age (Adkins *et al.* 2001; Case *et al.* 2011). Characteristically for

dogs, as for cats, horses, pigs, and ruminants, but in contrast to primates, rodents, and rabbits, puppies are born with very low systemic immunity (Case *et al.* 2011; Chastant-Maillard *et al.* 2017). The intake of colostrum during the first hours after birth and preferably the first two days of life is therefore crucial for the survival of new-born puppies (Case *et al.* 2011; Chastant-Maillard *et al.* 2017). After this, however, it is possible, albeit difficult, to raise orphaned puppies on milk from other species, despite the differences in milk composition. Pups must best be fed every six hours (Buffington *et al.* 2004). In the time before commercial milk replacements were available, homemade formulas for nursing orphaned dog puppies consisted of diluted cow or goat milk, enriched with egg yolk (and sometimes teaspoons of vegetable oil and calcium carbonate) (Hoskins 2001; Mapletoft *et al.* 1974; Prendergast 2011; Rootkustritz 2006). Although already too low in protein, fat, and energy content, cow or goat milk must be diluted because of the high lactose content, which would cause severe diarrhoea in the puppy (Case *et al.* 2011; Mapletoft *et al.* 1974; Peterson 2011; Prendergast 2011). The protein and fat deficiency can partially be compensated by adding egg yolk (Case *et al.* 2011; Mapletoft *et al.* 1974; Peterson 2011; Prendergast 2011).

In Palaeolithic camp sites, the feeding of captive wolf pups must have been most difficult when the pups were less than 10/12 days old—their presumed age at arrival in the human society—and 11 weeks old, when they could feed on solid food. The requirement for the pups to receive milk during their first weeks in order to survive put the role of women, who must be lactating at this precise moment, central in the initiation of the wolf domestication process (Milliet 1994, 2003, 2007; Müller 2005; Sauer 1952). In the Upper Palaeolithic, when cow or goat milk was not yet available, young puppies could have been raised on a combination of human breast milk and raw egg yolk while drinking water was given just before or after nursing in order to dilute the human milk. In Inuit communities, egg gathering is focused on ground nesting species (Natcher *et al.* 2012). In several Upper Palaeolithic sites, bones of ground nesting birds such as swans, geese, ducks, ptarmigans, and grouse have been recovered (Goffette *et al.* 2020; Wertz *et al.* 2016). At the Belgian Magdalenian Trou de Chaleux site, human modifications indicative of meat removal, likely for consumption, occur on bones of duck and ptarmigan (Goffette *et al.* 2020). A few Upper Palaeolithic sites yielded even eggshell fragments: from a swan at the Swiss Magdalenian Champréveyres site (Müller *et al.* 2006) and from a capercaillie at the Gravettian Krems-Hundssteig site in Austria (Wertz *et al.* 2016). This evidence shows that Upper Palaeolithic people killed ground nesting birds and harvested their eggs that could then have been used to supplement the diet of canid puppies.

Eggs have high biological value protein (Sanderson 2013). In diets for pups, the protein efficiency of raw egg yolk is superior to that of beef muscle (Mabee and Morgan 1951) and less of its proteins are needed to supply the essential amino acid requirements compared to other protein sources (Sanderson 2013). Nevertheless, there would have been a high risk of succumbing due to malnutrition and diarrhoea because of the extreme high lactose concentration in human milk (Mitoulas *et al.* 2002). Furthermore, a protein deficient diet could cause reduced growth, anaemia, impaired immune function, and oedema in puppies (Nap and Hazewinkel 1994; Platt and Stewart 1968; Sanderson 2013). Platt and Stewart (1968) demonstrated that beagle pups fed a low-protein diet did not attain a normal adult body size: their maxilla and mandible and their long bones remained shorter than those of well-nourished pups. This was even more pronounced in pups in litters from malnourished bitches. Possibly a suboptimal diet could be one of the causes of the decreased snout length and body mass observed in Palaeolithic dogs (e.g., Germonpré *et al.* 2017b; Morey 1992). Once the pups were three to four weeks old, semi-solid food could have been introduced.

Body Warmth and Massage

Dogs are altricial species: puppies are born poorly developed and dependent (Derrickson 1992). Besides being blind, deaf, and relatively immobile they characteristically have poor self-thermoregulation (Derrickson 1992; Rickard 2011; Santos *et al.* 2020). This is the result not only of a relatively high ratio of surface area to body mass and a limited store of subcutaneous fat, but also because puppies have a poorly developed vasoconstriction mechanism and do not have an active shiver reflex until they are about six days old (Kredatusova *et al.* 2011; Peterson 2011). Nevertheless, it seems that some young wolf pups can withstand inclement environments (Mech 1993). In dog litters, puppies seek reflexively the warmth of their mother and siblings by crawling towards them (Mapletoft 1974). It is essential for orphaned puppies to be kept warm by the surrogate mother and be fed warm milk. Puppies vocalize when suffering cold (Mapletoft 1974; Peterson 2011). Furthermore, during the first three weeks of life, micturition and defecation in puppies is reflex-based and requires perineal stimulation. During that time, the surrogate mother can mimic the mother's licking tongue by gently rubbing the pup's anus and genitals with a moist, warm 'cloth' (Hoskins and Sheldon 2001; Peterson 2011).[2] Baby massage is a traditional practice in several regions of the world to increase stool frequency in new-borns (Basiri-Moghadam *et al.* 2015). It can thus be presumed that Palaeolithic mothers knew about this practice.

[2] Other mammals (e.g., deer, squirrels, rabbits) also require such stimulation (Gage and Duerr 2019).

In summary, the caretaking of young, orphaned mammals does not need sophisticated tools, but can be done by women's use of their own body, bare hands, and basic instruments (Milliet 1994). The new-born pups must have been stimulated to urinate and defecate, and fed by nursing, providing liquid egg yolk and pre-masticated food, and maintaining bodily contact to keep their body temperature stable to survive. The fostering of orphaned wolf pups must have made the caring women the true owners of the captive animals (cf. Costa 2017).

Growing Pets

From the ethnographic literature, it is evident that adopted wild animals do not grow very old in captivity. They succumb to unsuitable treatment, escape, are given away to be eaten, or are killed (Alexiades 1999; Cormier 2003a, b; Costa 2017; Drucker 1951; Murdoch 1892; Simonova 2018; Simoons and Baldwin 1982; Wasselkov 2020). Once physically mature, captive animals can be released in the wild like the bears adopted by the Ket (Alexejenko 1963), the Inuit (Laugrand and Oosten 2015), and other North American Indigenous societies (Heizer and Hewes 1940; Wasselkov 2020) or pet monkeys in Amazonia (Cormier 2003a, b). Grown pets can be given away or exchanged (Costa 2017) or can be ceremonially killed, such as in the tapir-feast of the Amazonian Cashibo (Frank 1987), the bear sending-away ritual of the Ainu (Kitagawa 1961; Yamada 2001), or the Huron bear celebration (Tooker 1964; Trigger 1969). In the latter cases, the animals are eaten, although adopted pets are rarely used as a food source (Alexiades 1999; Cormier 2003a, b; Costa 2017; Descola 2013). However, the meat of a pet can also be consumed once it gives birth to offspring. The she-animal is no longer considered a pet the moment she becomes a mother (Fausto, personal communication cited in Costa 2017). Although in general familiarized animals do not reproduce in captivity (Descola 2013) it nevertheless occurs occasionally. According to Cormier (2003a), two brown capuchin monkeys raised by the Guajá in the 1990s produced offspring.

Children and Wild Pets

Literature on children caring for wild pets is limited (Fig. 1). In North America, several Athabascan groups kept various young animals as pets such as bear cubs, fox and wolf pups, and birds from which both children and adults learned about animal behaviour (Savishinsky 1974) (Fig. 1). Lowie (1935) reported that Crow Indians brought home bison calves from the hunt as pets for their children. In the Californian Tiibatulabal society, young coyotes kept as pets could be inherited by sons from their father (Kroeber 1925). In Amazonia, children can take on responsibility for the care

Fig. 1 Boy with captured and tied up wolf pups, Attawapiskat, Ontario (photo by John Macfie, 1963), photo credit The Archives of Ontario (C 330–12)

and the feeding of a pet from their mother (Costa 2017); girls become the primary caretakers of the pets, boys play with them and can develop their hunting skills through close contacts with the pets (Cormier 2003a, b; Erikson 2000). Ainu children played with small bear cubs brought to the village by the hunters; once the cubs were grown they were placed in cages (Batchelor 1892). In Siberia, Evenki people kept tethered wild animals to learn their behaviour patterns and as amusement for the children, which Shirokogoroff (1935) describes as an example of experiments with the domestication of wild animals. According to Simonova (2018), a single wild animal brought into the camp helps Evenki people to conceptualise their knowledge about an entire species. Furthermore, the invited animal is perceived as a representative of a world of wildness that is willing to become closer to people than to others of their kind (Simonova 2018). The desire to acquire knowledge and to pass this knowledge on to other members of their community could have been one of many intertwined motives for Upper Palaeolithic hunters to bring home wild wolf pups (see also Germonpré *et al.* 2018), although as they grew larger the canids had to be confined in small enclosures or tethered to a post (Fig. 1) to protect children from their natural predatory behaviour (Linnell *et al.* 2002). Interestingly, John Murdoch (1892) noted that an Alaskan Iñupiat family had tethered two wolf pups, captured and raised for their fur, outside the village. In Hare society, dogs are tied to stakes behind the houses so that the central area of the village is free for walking and playing (Savishinsky 1974).

Stress, Sociability, and Size

In several domesticated species widespread changes relative to their wild ancestors to glutamate receptor genes, which account partially for the fear response, have been detected (O'Rourke and Boeckx 2020). In domestic dogs, baseline levels of glucocorticoids, which modulate glutamatergic pathways, are lower than in wolves (Kikusui *et al.* 2019). The glutamate receptors have an important role in regulating and attenuating the stress response of the hypothalamic–pituitary–adrenal (HPA) axis, which is derived from neural crest cells (Li *et al.* 2014; O'Rourke and Boeckx 2020; Pendleton *et al.* 2018). Lowered stress hormone levels in gravid (pre-) domestic females, presumably resulting from a dysregulated HPA-axis possibly due to different types and timing of early life stresses compared to their wild conspecifics, could result in neural crest hypofunction and cell differentiation changes in the embryos they are carrying (O'Rourke and Boeckx 2020). Hypofunction of the neural crest cells can influence the tameness of animals and alter craniofacial proportions (Trut *et al.* 2004; Wilkins *et al.* 2014). In addition, dog pups born from malnourished mothers have different craniofacial proportions compared to pups from well-fed mothers (Platt and Stewart 1968). Also, in Novosibirsk Trut and Kharlamova (2020) observed a decrease in the growth rate of the facial skull of tame farm-bred foxes during the first months of postnatal ontogenesis resulting in a shorter skull compared to unselected foxes. Moreover, Kukekova *et al.* (2018) found in the different strains of the farm-bred foxes several haplotypes in the *SorCS1*gene involved in glutamatergic signalling that differ in frequencies between the tame and aggressive fox strains. The fact that *SorCS1* is involved in aggressive and anxious behaviour supports the hypothesis that genes coding for different types of glutamate receptors are associated with the domestication of the dog. Indeed, Wang *et al.* (2016) found that the glutamate receptor genes in indigenous Chinese dogs show signs of positive selection that likely happened at the beginning of the domestication process. Li *et al.* (2014) showed that genes involved in the glutamate metabolism differ in a whole-genome population comparison between dogs and wolves, suggesting that pleiotropic functions of the glutamate neurotransmitter may have contributed to the domestication of the wolf. In addition to the reactive behaviour of canids, coordination, cooperation, and playfulness must be considered in the domestication process of the wolf (Kikusui *et al.* 2019). The hormone oxytocin is associated with intraspecies prosocial behaviour. In the latter type of functional adaptation, oxytocin plays a critical role as increasing levels of oxytocin inhibits the HPA activation (Kikusui *et al.* 2019). Interestingly, Oliva *et al.* (2016) found that markers close to oxytocin receptor genes differ between extant dogs and wolves. Topál *et al.* (2005) hand-reared wolf pups, which, although they became tame and socialized, did not develop the same strong bond to their handler as dogs do. Human-directed prosocial behaviour of dogs is probably facilitated by oxytocin through interaction with the HPA axis (Buttner 2016). Dogs likely evolved this capacity for attachment to humans during the domestication process.

Playfulness in Children and Pups

In western societies, children who have pets and play with them regularly perceive them as special friends and providers of social interactions (Geerdts *et al.* 2015; Lookabaugh Triebenbacher 1998). Through these interactions children can increase their biological knowledge, develop a more human-inclusive representation of animals and come to regard animals as a community of social others (Geerdts *et al.* 2015; Myers and Saunders 2002). Furthermore, young children living with dogs show advanced socio-emotional development (Dueñas *et al.* 2021). Spencer (1959) noted that Alaskan Iñupiaq little girls treated dog puppies as babies. In Hare society, dogs and children socialize each other; young children care for and feed their pups, while at the same time they learn dogs' behaviours (Savishinsky 1974). In Siberia, a kind of dual apprenticeship (Vaté 2013) develops between children and dog puppies. Among the Chukchi reindeer herders, pups that are the playthings of little children have the reputation of becoming very skilled dogs (Vaté 2013). Oka-Soiot children (Oehler 2018) also play and socialize with their dog puppies. For the Evenki, children and dog puppies are partners in a mutual socialisation process (Safonova and Sántha 2012). Capable children can in this way build up good reputations marking as valuable partners once they become adult (Savishinsky 1974).

The presumed prevalent animistic worldview during the Upper Palaeolithic facilitated the adoption of wild animals (Germonpré *et al.* 2018). In addition, Upper Palaeolithic parents would have noted the beneficial impact on the emotional development of their children of living together with an animal (Dueñas et al 2021). A recent study, based on behavioural data of wolf hybrids and several dog breeds, revealed that playful activities toward humans seems to have formed an important part of the early domestication process of the wolf (Hansen Wheat *et al.* 2018; see also Bradshaw *et al.* 2015; Schleidt and Shalter 2018). Furthermore, a recent genetic comparative analysis of more than 100 modern dog breeds shows that common ancestry of a human-directed playfulness trait seems to have been a driving force in the domestication of the wolf that may have arisen due to selection by humans (Garamszegi *et al.* 2020). Human-directed play reinforces the social relations between dogs and humans (Bradshaw *et al.* 2015; Rooney *et al.* 2000). Another central behavioural trait in the context of the dog domestication is the tendency of prosocial behaviour towards humans. Experiments to socialize wolf pups have shown that

wolves differ in their attitudes of affection towards people and that this affinity extends into the early adulthood of some individuals (Ujfalussy *et al.* 2017). Selection may thus have acted on sets of linked genes that permitted a behavioural separation between early dogs and wolves, facilitating co-existence with humans (vonHoldt *et al.* 2017).

Women and Male Dogs

Ethnographic data reveal that Hidatsa women saved the male pups of litters but kept only one female pup (Wilson 1924). Likewise, Saami women gave away male dog puppies to friends and kin, female pups were culled except for one bitch kept for breeding. Male dogs are preferred because bitches in oestrus cause disruption (Anderson 2018). Interestingly, Phung *et al.* (2018) demonstrated, based on the patterns of genetic diversity on the X chromosome and autosomes, that during the early domestication history of the dog, a higher number of male canids than females were reproducing and that a male-biased expansion occurred during that time. In addition, genetic analyses of ancient dogs found at several prehistoric sites dating from the Neolithic to the Bronze Age revealed male overrepresentation (Bergström *et al.* 2020). Thus, it is likely that in the Upper Palaeolithic, while at seasonal gatherings at aggregation sites the women could have given away, exchanged, or traded their pets, permitting an expansion of the gene pool from which ultimately domestic dogs descend. It is quite possible that many of these transferred pups were males.

Discussion

Based on our non-exhaustive review of ethnographic, archaeological, and zoological data we can present a tentative narrative. We should highlight that the caretaking of wolf pups during the Upper Palaeolithic must not be conceived as an intentional plan to domesticate wolves (Germonpré *et al.* 2018; Müller 2005). We have proposed previously (Germonpré *et al.* 2018) that the early beginnings of the domestication of the wolf can be positioned in the possible framework of an animistic worldview of Upper Palaeolithic societies, in which the value of personal interactions between humans and individual animals is valued and detailed knowledge of animal behaviour was of particular importance (cf. Pasarić and Warren 2019; Porr and de Maria 2015). We have shown that sophisticated tools are not necessary to raise pets, although a worldview that includes non-humans probably is. Such conditions were likely present from the early Upper Palaeolithic on (Germonpré and Hämäläinen 2007; Germonpré *et al.* 2018; Hussain and Floss 2015; Porr and de Maria 2015) and it is possible that the first Modern Humans arriving in Eurasia brought infant animals, such as wolf pups or bear cubs captured or obtained by hunters after killing their mother, back to their settlements. In addition, the role of gender should not be underestimated in the human-initiated domestication path. Interestingly, Chambers *et al.* (2020) show that in a cross-cultural context, women are more closely affiliated with dogs than men in the framework of humans' utility for dogs and in the concept of personhood of dogs. A human-initiated model of the domestication process of the wolf envisions that the adoption of wolf pups in certain Upper Palaeolithic societies must have been a widespread cultural tradition. There was ample time in the Upper Palaeolithic to experiment with keeping and raising of young animals. Nevertheless, the human-initiated domestication path is complex, and it seems that only a selection of one or a few closely-related wolf populations were involved in the domestication process of modern dogs (Bergström *et al.* 2020). Although young of other species were probably also held in captivity, only the wolf became domesticated. It is unlikely that foxes were domesticated in the Upper Palaeolithic. Since foxes are a less dangerous predator, they could have been permitted to visit the camp sites to feed and since they could have been more easily captured than wolves, there was no need to raise and breed them (Baumann *et al.* 2020; Germonpré *et al.* 2018).

Captured wolf pups were initially mothered by nursing women, supplementing human milk in combination with water with egg yolk and from about three weeks old premasticated food. At around 11 weeks the pups had probably adapted to solid food. Also, their surrogate mothers must have stimulated the perineal area of the young pups, so that they could urinate and empty their bowls. During the first weeks of their lives the pups experienced an intense and time-consuming handling by the women and children, not only because they had to be fed regularly but also to be kept warm in order to maintain their body temperature. Such prolonged and close body contact likely allowed development of bonds of attachment between those more sociable and playful wolf pups and caring, empathetic women and their children, and could have led to the survival of these individual animals until maturity, while pups with reactive behaviour (aggressive, extremely fearful/anxious, or lethargic) probably were culled, escaped, or died. Once physically mature, some of the gentler animals may have thwarted human control over their reproduction and produced at least one litter (Germonpré *et al.* 2015). We presume that the growth of tamed female wolves in the Palaeolithic camps, due to a lack of competition with conspecifics, could have resulted in a lower baselevel of glucocorticoids and reduced glutamatergic inputs to their hypothalamus (see Sands and Creel 2004). The modified hormonal concentrations in gravid tamed she-wolves, possibly in combination with a low-protein diet, could have influenced the embryonic development of the litter through alterations in the migration or the activity of the neural crest cells and could have resulted in changes in their pups' behaviour and in the size and shape of their pups'

skull (O'Rourke and Boeckx 2020; Pendleton *et al.* 2018; Platt and Stewart 1968). A preference in every subsequent generation for such puppies with affiliative, cooperative, and playful behaviours towards their caretakers could then further have influenced the enrichment of genetic variants affecting behaviour, physical appearance, and skeletal features in the tamed canid population leading after several generations of selection to Palaeolithic dogs that differed in all these traits from the wild type (cf. Germonpré *et al.* 2018; Kukekova *et al.* 2018; Li *et al.* 2014; Wang *et al.* 2016). The human selection of suitable animals likely endorsed the cooperative dynamics present in the sociobiology of the wolves and seems to have redirected the ability to cooperate towards humans (Cordoni and Palagli 2019).

The existence of a pet-keeping tradition among one or several Upper Palaeolithic cultural groups would have permitted development of a foundation stock of a large enough number of captive wolf pups. In this context, it is likely that captive she-wolves were released or killed shortly after giving birth so that their new-born pups could be adopted. The first generations of these tamed wolves were likely confined in order to limit the risks they posed to young children (Fig. 1). At some point, after a multigenerational selection and once the adult canids were docile and cooperative enough, the she-wolves could be kept. Probably, from this time on crossbreeding with wild wolves was limited. Indeed, Bergström *et al.* (2020) show that past gene flow from wolves into dogs was uncommon.

The timing of the origin of the wolf domestication is highly debated. Based on genetic studies, it is estimated that the ancestors of modern American wolves, modern Eurasian wolves and modern dogs diverged before the onset of the LGM, (Boschin *et al.* 2020; Fan *et al.* 2016; Perri *et al.* 2021; Pilot *et al.* 2019; Skoglund *et al.* 2015; Wang *et al.* 2016). This divergence could have happened as long as 36,000 years ago (Silva *et al.* 2020). Dog-like remains have been reported from several Upper Palaeolithic sites in Europe dating from the pre-LGM (Germonpré *et al.* 2009, 2012; Germonpré and Sablin 2017; Reynolds *et al.* 2019). In addition, an early stage of wolf domestication has been proposed for the middle Upper Palaeolithic site of Yana in Siberia (Nikolskiy *et al.* 2018). Probably, some of these pre-LGM lineages became extinct or were replaced through gift giving or barter of male dogs, or through migration by incoming dogs domesticated in other regions (e.g., Frantz *et al.* 2016; Germonpré *et al.* 2017a, 2018). However, the extinction of these lineages does not preclude the roles Palaeolithic dogs could have played in the daily lives of their young and adult human caretakers. By the end of the Pleistocene, several dog lineages, related to extant dogs and all descending from a now extinct Pleistocene wolf population

Fig. 2 A right mandible (97–584-C-117) from a large canid pup found at the Gravettian site of Předmostí (Czech Republic) that, based on the erupting position of the tip of trigonid of the first molar, died when it was between four and five months old

or closely related wolf populations, were already present (Bergström *et al.* 2020; Frantz *et al.* 2016; Perri *et al.* 2021; Smeds *et al.* 2019).

Limitations and Future Research

Unfortunately, exhaustive analyses of juvenile skeletal remains in canid assemblages from Upper Palaeolithic sites are presently lacking (Perri and Sázelová 2016). At the Gravettian Předmostí site (Czech Republic), a canid pup was, based on the position of the tip of the trigonid of the first molar just above the alveolar rim of its lower jaw, probably between four and five months old when it died (cf. Esaka 1982; Shabestari *et al.* 1967) (Fig. 2). Other juvenile material at this Gravettian site consists of unfused postcranial elements (Germonpré *et al.* 2017b), but this material has not yet been studied in detail.

New multidisciplinary collaboration efforts, integrating morphometric, genetic, biogeochemical and dental microwear texture (DMT) analyses of prehistoric and extant canids are currently helping to clarify, step by step, the complex process that led to the domestic dog (e.g., Bergström *et al.* 2020; Bocherens *et al.* 2015; Germonpré *et al.* 2009; Prassack *et al.* 2020, 2021; Thalmann *et al.* 2013; Silva *et al.* 2020; Sinding *et al.* 2020). In particular it can be hoped that future morphometric, biogeochemical, and DMT studies can disentangle the diet of canid pups and differentiate the juvenile animals that were fed by humans from those pups that received their nutrition from their mother and other conspecifics (cf. Lupo 2017), and that future genetic analyses of canid remains will unravel whether male and female canids have divergent populations histories. Such information could add weight to either the self-domestication hypothesis or the human-initiated domestication hypothesis.

Conclusion

Based on evidence derived from archaeology, ethnography, and developmental biology, we conclude that a cultural practice of nurturing and raising wolf pups in the Upper Palaeolithic could have led to the beginning of the domestication process of the wolf. Furthermore, we propose that gender and age of the human caretakers conceivably played an important role at the start of this process. The human-initiated domestication hypothesis poses that wild wolf pups were likely captured and brought to the Upper Palaeolithic camp sites by male hunters. There, across generations, women and children nurtured and interacted with the pups, leading eventually to domestication (see also Manwell and Ann Baker 1984; Milliet 1994, 2003; Müller 2005; Sauer 1952). Finally, we must add that the domestication process of the wolf is a particular case and should be distinguished from domestication processes of other animals (Germonpré *et al.* 2018; Russell 2012; Uerpmann and Uerpmann 2017).

Acknowledgements We thank Luis Pacheco-Cobos for inviting us to contribute to this special issue of Human Ecology on the ethnography and ethnoarchaeology of domesticated canines. We are grateful to the reviewers for their valuable comments that helped to improve our manuscript. We thank Ludomir R. Lozny for his help with the editing. We thank Tamara Janků for her help with Fig. 2.

Funding Martina Lázničková-Galetová was supported by the Ministry of Culture of the Czech Republic by institutional financing of long-term conceptual development of the research institution (the Moravian Museum, MK000094862). Mikhail Sablin was supported by the ZIN RAS (state assignment N° AAAA-A19-119032590102–7).

Declarations

Conflict of Interest The authors declare they have no conflicts of interest.

References

Adkins Y, Lepine A, Lönnerdal B (2001) Changes in protein and nutrient composition of milk throughout lactation in dogs. American Journal of Veterinary Research 62: 1266-1272

Alexejenko JA (1963) Der Bärenkult der Keten (Jenissei-Ostjaken). In: Dioszegi V (ed) Glaubenswelt und Folklore der sibirischen Völker. Akademiai Kiado, Budapest, pp 191-208.

Alexiades MN (1999) Ethnobotany of the Ese Eja: Plants, health, and change in an Amazonian society. PhD dissertation (Department of Anthropology), City University of New York, New York.

Anderson DG (2014) Cultures of Reciprocity and Cultures of Control in the Circumpolar North. Journal of Northern studies 8: 11-27.

Anderson M (2018) Dogs in Saapli: from competition to collaboration to cooperation to now. In: Losey RJ, Wishart RP, Loovers JPL (eds) Dogs in the North, stories of cooperation and co-domestication. Routledge, London, pp 267-277.

Basiri-Moghadam M, Basiri-Moghadam K, Kianmehr M, Jani S (2015) The effect of massage on neonatal jaundice in stable preterm newborn infants: a randomized controlled trial. Journal of Pakistan Medical Association 65: 602-606.

Batchelor J (1892) The Ainu of Japan. The Religious Tract Society, London.

Batchelor J (1901) The Ainu and their Folklore. The Religious Tract Society, London.

Baumann C, Wong GL, Starkovich BM et al. (2020) The role of foxes in the Palaeolithic economies of the Swabian Jura (Germany). Archaeological and Anthropological Sciences 12: 208.

Bergström A, Frantz L, Ryan Schmidt R et al. (2020) Origins and Genetic Legacy of Prehistoric Dogs. Science 370: 557-564.

Bocherens H, Drucker DG, Germonpré M, et al. (2015) Reconstruction of the Gravettian food-web at Předmostí I using multi-isotopic tracking (^{13}C, ^{15}N, ^{34}S) of bone collagen. Quaternary International 359-360: 211-228.

Boschin F, Bernardini F, Pilli E et al. (2020) The first evidence for Late Pleistocene dogs in Italy. Scientific Reports 10: 13313.

Bradshaw JWS, Pullen AJ, Rooney NJ (2015) Why do adult dogs 'play'? Behavioural Processes 110: 82-87.

Brandišauskas D (2017) Leaving footprints in the Taiga: luck, spirits and ambivalence among the Siberian Orochen reindeer herders and hunters. Berghahn Books, New York.

Buffington CAT, Holloway C, Abood SK (2004) Chapter 2 - Normal Dogs. In: Fathman L (ed) Manual of Veterinary Dietetics. Saunders Elsevier, Philadelphia, pp 9-26.

Buttner AP (2016) Neurobiological underpinnings of dogs' human-like social competence: How interactions between stress response systems and oxytocin mediate dogs' social skills. Neuroscience & Biobehavioral Reviews 71: 198-214.

Case LP, Daristotle L, Hayek MG, Foess Raasch M (2011) Chapter 21, Nutritional Care of Neonatal Puppies and Kittens. In Graham-Jones O (ed) Canine and Feline Nutrition. Third edition. Mosby, Elsevier, pp 209-219.

Chambers J, Quinlan MB, Evans A, Quinlan RJ (2020) Dog-Human Coevolution: Cross-Cultural Analysis of Multiple Hypotheses. Journal of Ethnobiology 40: 414–433.

Chastant-Maillard S, Aggouni C, Albaret A, Fournier A, Mila H (2017) Canine and feline colostrum, Reproduction in Domestic Animals 52: 148-152.

Clutton-Brock J (1989) Introduction to domestication, In: Clutton-Brock J (ed) The walking larder: patterns of domestication, pastoralism, and predation. London, Unwin Hyman, pp 7-9.

Clutton-Brock J (1995) Origins of the dog: Domestication and early history. In Serpell J (ed) The Domestic Dog: Its Evolution, Behaviour and Interactions with People. Cambridge University Press, Cambridge, pp 7-20.

Coppinger R, Coppinger L (2001) Dogs: A Startling New Understanding of Canine Origin, Behavior, and Evolution. Scribner, New York.

Cordoni G, Palagi E (2019) Back to the Future: A Glance Over Wolf Social Behavior to Understand Dog–Human Relationship. Animals 9: 991.

Cormier LA (2003a) Kinship with monkeys: The Guajá foragers of eastern Amazonia. Columbia University Press, New York.

Cormier LA (2003b) Animism, Cannibalism, and Pet-keeping among the Guajá of Eastern Amazonia. Tipití: Journal of the Society for the Anthropology of Lowland South America 1: 81–98.

Costa L (2017) The owners of kinship. Asymmetrical relations in indigenous Amazonia. Hau Books, Chicago.

Delâge D (2005) "Vos chiens ont plus d'esprit que les nôtres" : histoire des chiens dans la rencontre des Français et des Amérindiens. Les Cahiers des dix 59: 179-215.

de Laguna F (1972) Under Mount Saint Elias: The History and Culture of the Yakutat Tlingit. Smithsonian Contributions to Anthropology 7.

Denys N (1908) The Description and Natural History of the Coasts of North America (Acadia). The Champlain Society, Toronto.
Descola P (2013) Beyond nature and culture. University of Chicago Press, Chicago.
Derrickson EM (1992) Comparative reproductive strategies of altricial and precocial eutherian mammals. Functional Ecology 6: 57-65.
Drucker P (1951) The Northern and Central Nootkan tribes. Bulletin Smithsonian Institute, Bureau American Ethnology 144.
Ducos P (1978) "Domestication" defined and methodological approaches to its recognition in faunal assemblages. In: Meadow H, Zeder MA (eds) Approaches to faunal analysis in the Middle East. Peabody Museum Bulletin 2: R53–56.
Ducos P (1989) Defining domestication: a clarification. In: Clutton-Brock J (ed) The walking larder: patterns of domestication, pastoralism, and predation. Unwin Hyman, London, pp 28-30.
Dueñas J-M, Gonzàlez L, Forcada R et al. (2021) The Relationship Between Living with Dogs and Social and Emotional Development in Childhood. Anthrozoös, https://doi.org/10.1080/08927936.2021.1878680
Earle IP (1939) The nutrition of very young animals. Yearbook of Agriculture: 501–518.
Erikson P (2000) The social significance of pet-keeping among Amazonian Indians. In: Podberscek AL, Paul ES, Serpell JA (eds) Companion animals and us: exploring the relationships between people and pets. Cambridge University Press, Cambridge, pp 7-26.
Esaka S (1982) Development of rotation of mandibular premolar tooth germs in the dog. Acta Anatomica Sinica 114: 211-227.
Fan Z, Silva P, Gronau, I et al. (2016) Worldwide patterns of genomic variation and admixture in gray wolves. Genome Research 26: 163-173.
Fox MW, Stelzner D (1966) Behavioural effects of differential early experience in the dog. Animal Behaviour 14: 273-281.
Frank E (1987) Das Tapirfest der Uni Eine funktionale Analyse. Anthropos 82: 151-181.
Franklin J (1824) Narrative of a Journey to the Shores of the Polar Sea, in the Years 1819, 20, 21, and 22. John Murray, London.
Frantz LAF, Mullin VE, Pionnier-Capitan M, et al. (2016) Genomic and archaeological evidence suggest a dual origin of domestic dogs. Science 352: 1228-1231.
French JC (2019) The use of ethnographic data in Neanderthal archaeological research, recent trends and their interpretative implications. Hunter Gatherer Research 4: 25-49.
Gácsi M, Győri B, Miklósi Á, et al. (2005) Species-specific differences and similarities in the behavior of hand-raised dog and wolf pups in social situations with humans. Developmental Psychobiology 47: 111-122.
Gage LJ, Duerr RS (2019) Principles of Initial Orphan Care In: Hernandez SM, Barron HW, Miller EA et al (eds) Medical Management of Wildlife Species: A Guide for Practitioners. Hoboken, Wiley, pp. 145-157.
Galeta P, Lázničková-Galetová M, Sablin M, Germonpré M (2021) Morphological Evidence for Early Dog Domestication in the European Pleistocene: The Randomization Approach. The Anatomical Record 304: 42-62.
Galton F (1865) The First Steps towards the Domestication of Animals. Transactions of the Ethnological Society of London 3: 122-138.
Garamszegi LZ, Temrin H, Kubinyi E, Miklósi A, Kolm N (2020) The role of common ancestry and gene flow in the evolution of human-directed play behaviour in dogs. Journal of Evolutionary Biology 33: 318-328.
Gazzano A, Mariti C, Notari L, Sighieri C, McBride EA (2008) Effects of early gentling and early environment on emotional development of puppies. Applied Animal Behaviour Science 110: 294-304.
Geerdts MS, Van de Walle GA, LoBue V (2015) Daily animal exposure and children's biological concepts. Journal of Experimental Child Psychology 130: 132-146.
Germonpré M, Fedorov S, Danilov M, et al. (2017a) Palaeolithic and prehistoric dogs and Pleistocene wolves from Yakutia: Identification of isolated skulls. Journal of Archaeological Science 78: 1-19.
Germonpré M, Hämäläinen R (2007) Fossil bear bones in the Belgian Upper Palaeolithic: The possibility of a proto-bear ceremonialism. Arctic Anthropology 44: 1-30.
Germonpré, M., Lázničková-Galetová, M., Jimenez, E.-L. et al. (2017b). Consumption of canid meat at the Gravettian Předmostí site, the Czech Republic. Fossil Imprint, 73(3-4): 360–382.
Germonpré M, Lázničková-Galetová M, Sablin M (2012) Palaeolithic dog skulls at the Gravettian Předmostí site, the Czech Republic. Journal of Archaeological Science 39: 184-202.
Germonpré M, Lázničková-Galetová M, Sablin MV, Bocherens, H (2018) Self-domestication or human control? The Upper Palaeolithic domestication of the dog. In: Stépanoff C, Vigne JD (eds) Hybrid Communities, Biosocial Approaches to Domestication and Other Trans-species Relationships. London, Routledge, pp 39-64.
Germonpré M, Lázničková-Galetová M, Sablin MV, Bocherens H (2020) Could incipient dogs have enhanced differential access to resources among Upper Palaeolithic hunter-gatherers in Europe? In: Moreau L (dir.) Social inequality before farming? Multidisciplinary approaches to the study of social organization in prehistoric and ethnographic hunter-gatherer-fisher societies. Cambridge, McDonald Institute Conversations [Book Chapter eBook].
Germonpré M, Sablin MV (2017) Chapter 2. Humans and mammals in the Upper Palaeolithic of Russia. In: Albarella U, Rizzetto M, Russ H, Vickers K, Viner-Daniels S (eds) Oxford Handbook of Zooarchaeology. Oxford, Oxford University press, pp 25-38. https://www.oxfordhandbooks.com/view/10.1093/oxfordhb/9780199686476.001.0001/oxfordhb-9780199686476
Germonpré M, Sablin MV, Lázničková-Galetová M et al. (2015) Palaeolithic dogs and Pleistocene wolves revisited: A reply to Morey (2014). Journal of Archaeological Science 54: 210-216.
Germonpré M, Sablin MV, Stevens RE et al. (2009) Fossil dogs and wolves from Palaeolithic sites in Belgium, the Ukraine and Russia: Osteometry, ancient DNA and stable isotopes. Journal of Archaeological Science 36: 473-490.
Goffette Q, Germonpré M, Lefèvre C et al. (2020) Bird bones from Trou de Chaleux and the human exploitation of birds during the late Magdalenian in Belgium. Journal of Archaeological Science: Reports 29: 102096.
Hall NJ, Lord K, Arnold A-MK et al. (2015) Assessment of attachment behaviour to human caregivers in wolf pups (*Canis lupus lupus*). Behavourial Processes 110: 15-21.
Hallowell AI (1960) Ojibwa ontology, behavior, and world view, In: Diamond S (ed) Culture in history: essays in honor of Paul Radin. New York, Columbia University Press, pp. 19-52.
Hamayon RN (1990) La chasse à l'âme. Esquisse d'une théorie du chamanisme sibérien. Société d'Ethnologie, Nanterre.
Hansen Wheat C, Fitzpatrick J, Tapper I, Temrin H (2018) Wolf (*Canis lupus*) hybrids highlight the importance of human-directed play behaviour during domestication of dogs (*Canis familiaris*). Journal of Comparative Psychology 132: 373-381.
Hare B (2017) Survival of the Friendliest: Homo Sapiens Survived through Selection for Prosociality. Annual Review of Psychology 68: 155–186.
Heizer RF, Hewes GW (1940) Animal ceremonialism in Central California in light of archaeology. American Anthropologist 42: 587-603.

Hoskins JD (2001) Chapter 21 - Nutrition and Nutritional Problems. In: Hoskins JD (ed) Veterinary Pediatrics. Dogs and Cats from Birth to Six Months. (Third Edition). Saunders, pp 476–489.

Hoskins JD, Shelton OD (2001) Chapter 19 - The Nervous and Neuromuscular Systems. In: Hoskins JD (ed) Veterinary Pediatrics. Dogs and Cats from Birth to Six Months. (Third Edition). Saunders, pp 425–462.

Hussain ST (2019) Gazing at Owls? Human-strigiform Interfaces and their Role in the Construction of Gravettian Lifeworlds in East-Central Europe. Environmental Archaeology: The Journal of Human Palaeoecology 24: 359-376.

Hussain ST, Floss H (2015) Sharing the world with mammoths, cave lions and other beings: Linking animal-human interactions and the Aurignacian 'belief world'. Quartär 62: 85-120.

Iverson SJ (2007) Milk composition and lactation strategies across mammalian taxa: implications for hand-rearing neonates. In: Ward A, Hunt A, Maslanka M (eds) Proceedings of the Seventh Conference on Zoo and Wildlife Nutrition, AZA Nutrition Advisory Group, Knoxville.

Janssens L, Perri A, Crombé, P, et al. (2019) An evaluation of classical morphologic and morphometric parameters reported to distinguish wolves and dogs. Journal of Archaeological Sciences: Reports 23: 501–533.

Jenness R (1986) Lactational performance of various mammalian species. Journal of Dairy Science 69: 869-885.

Kelly RL (2013) The lifeways of hunter-gatherers. The foraging spectrum. Cambridge University Press, Cambridge.

Kikusui T, Nagasawa M, Nomoto K, et al. (2019) Endocrine Regulations in Human–Dog Coexistence through Domestication. Trends in Endocrinology & Metabolism 30: 793-806.

Kirk CA (2001) Clinical theriogenology. New concepts in pediatric nutrition. Veterinary Clinics of North America: Small Animal Practice 31: 369-392.

Kitagawa JM (1961) Ainu bear festival (iyomante). History of Religions 1: 95-151.

Klokov K (2011) The Sustaining Landscape and the Arctic Fox Trade in the European North of Russia 1926-1927. In: Anderson DG (ed) The 1926/27 Soviet Polar Census Expeditions. Berghahn, New York, pp 155-179.

Koler-Matznick J (2002) The origin of the dog revisited. Anthrozoös 15: 98-118.

Kredatusova G, Hajurka J, Zakallova I, Valencakova A, Vojtek B (2011) Physiological events during parturition and possibilities for improving puppy survival: a review. Veterinarni Medicina 56: 589-594.

Kroeber AL (1925) Handbook of the Indians of California. Bureau of American Ethnology Bulletin 78.

Kukekova AV, Johnson JL, Xiang X et al. (2018) Red fox genome assembly identifies genomic regions associated with tame and aggressive behaviours. Nature Ecology and Evolution 2: 1479-1491.

Langkavel B (1899) Dogs and Savages. Annual report of the Smithsonian Institution for the year ending June 30, 1898, pp 651–675.

Larson G, Fuller DQ (2014) The Evolution of Animal Domestication. Annual Review of Ecology, Evolution, and Systematics 45: 115-136.

Laugrand F (2017) How Inuit in the Canadian North Perceive the Wolverine: From Past to Present. Inuit studies 41: 243-263.

Laugrand F, Oosten J (2015) Hunters, Predators and Prey: Inuit Perceptions of Animals. Berghahn, New York.

Li Y, Wang G-D, Wang M-S, Irwin DM, Wu D-D, Zhang Y-P (2014) Domestication of the dog from the wolf was promoted by enhanced excitatory synaptic plasticity: a hypothesis. Genome Biology and Evolution 6: 3115-3121.

Lien M (2015) Becoming Salmon: Aquaculture and the Domestication of a Fish. University of California Press, Oakland.

Linnell JDC, Andersen R, Andersone Z et al. (2002) The fear of wolves: A review of wolf attacks on humans. Oppdragsmelding, Trondheim: Norwegian Institute of Nature Research 731: 1–65.

Lookabaugh Triebenbacher S (1998) Pets as Transitional Objects: Their Role in Children's Emotional Development. Psychological Reports 82: 191-200.

Loovers JPL, Losey RL, Wishart RP (2018) Dogs in the North. In: Losey RJ, Wishart RP, Loovers JPL (eds) Dogs in the North, stories of cooperation and co-domestication. Routledge, London, pp 278-292.

Lord K (2013) A comparison of the sensory development of wolves (*Canis lupus lupus*) and dogs (*Canis lupus familiaris*). Ethology 119: 110-120.

Lowie RH (1935) The Crow Indians. Farrar and Rinehart, New York.

Lupo KD (2017) When and where do dogs improve hunting productivity? The empirical record and some implications for early Upper Paleolithic prey acquisition. Journal of Anthropological Archaeology 47: 139–151.

Lupo KD (2019) Hounds follow those who feed them: What can the ethnographic record of hunter-gatherers reveal about early human-canid partnerships? Journal of Anthropological Archaeology 55: 101081.

Mabee DM, Morgan AF (1951) Evaluation by dog growth of egg yolk protein and six other partially purified proteins, some after heat treatment. The Journal of Nutrition 43: 261–279.

Manwell C, Ann Baker CM (1984) Domestication of the dog: Hunter, food, bed-warmer, or emotional object? Journal of Animal Breeding and Genetics 101: 241-256.

Mapletoft RJ, Schutte KJ., Coubrough AP, Kohne RJ (1974) The perinatal period of dogs. Nutrition and management in the hand-rearing of puppies. Journal of the South African Veterinary Association 45: 183-189.

McCormack PA (2018) An ethnohistory of dogs in the Mackenzie Basin (western Subarctic). In: Losey RJ, Wishart RP, Loovers JPL (eds) Dogs in the North, stories of cooperation and co-domestication. Routledge, London, pp 105-51.

Mech LD (1993) Resistance of Young Wolf Pups to Inclement Weather. Journal of Mammalogy 74: 485–486.

Milliet J (1994) Y a-t-il une domestication féminine ? Les exemples du porc et du chien. Ecologie humaine 12: 65-82.

Milliet J (2003) Entre douceur et violence. Le statut particulier des animaux allaités au sein par des femmes. In: Soule M, Blin D, Thoueille E (eds) L'allaitement maternel: Une dynamique à bien comprendre. Éres, Ramonville, pp 151-176.

Milliet J (2007) L'allaitement des animaux par des femmes, entre mythe et réalité. In : Dounias E, Motte-Florac E, Dunham M (eds) Le symbolisme des animaux : l'animal, clef de voûte de la relation entre l'homme et la nature ? IRD Éditions, Paris, pp 881-899.

Mitoulas LR, Kent JC, Cox DB, Owens RA, Sherriff JL, Hartmann PE (2002) Variation in fat, lactose and protein in human milk over 24h and throughout the first year of lactation. British Journal of Nutrition 88: 29-37.

Mix AC, Bard E, Schneider R (2001) Environmental processes of the ice age: land, oceans, glaciers (EPILOG). Quaternary Science Reviews 20: 627-657.

Morey DF (1992) Shape and development in the evolution of the domestic dog. Journal of Archaeological Science 19: 181-204.

Morey DF, Jeger R (2015) Paleolithic dogs: Why sustained domestication then? Journal of Archaeological Science: Reports 3: 420-428.

Müller W (2005) The domestication of the wolf – the inevitable first? In: Vigne J-D, Peters J., Helmer D (eds) The first steps of animal domestication. Proceeding 9th ICAZ Conference, Durham 2002. Oxbow Books, Oxford, pp 34–40.

Müller W, Leesch D, Bullinger J, et al. (2006) Chasse, habitats et rythme des déplacements: Réflexions à partir des campements magdaléniens de Champréveyres et Monruz (Neuchâtel, Suisse). Bulletin de la Société Préhistorique Française 103: 741-752.

Murdoch J (1892) Ethnological results of the Point Barrow expedition. In: Power JW (ed) Ninth Annual Report of the Bureau of Ethnology to the Secretary of the Smithsonian Institution 1887–'88. Government Printing Office, Washington, pp 19-441.

Myers Jr. O E, Saunders C (2002) Animals as links to developing caring relationships with the natural world. In: Kahn Jr PH, Kellert SR (eds) Children and nature: Theoretical and scientific foundations. MIT Press, Cambridge, pp 153-178.

Natcher D, Felt L, Chaulk K, Procter A (2012) The Harvest and Management of Migratory Bird Eggs by Inuit in Nunatsiavut, Labrador. Environmental Management 50: 1047–1056.

Nap RC, Hazewinkel HA (1994) Growth and skeletal development in the dog in relation to nutrition; a review. Veterinary Quarterly 16: 50-59.

Nikolskiy PA, Sotnikova MV, Nikol'skii AA, Pitulko VV (2018) Predomestication and Wolf-Human Relationships in the Arctic Siberia of 30,000 Years Ago: Evidence from the Yana Palaeolithic Site. Stratum Plus 2018/1: 231-262.

Oehler AC (2018) Hunters in their own right. Perspectival sharing in Soiot hunters and their dogs. In: Losey RJ, Wishart RP, Loovers JPL (eds) Dogs in the North, stories of cooperation and co-domestication. Routledge, London, pp 28-44.

Oftedal OT, Iverson SJ (1995) Comparative analysis of nonhuman milks. A. Phylogenetic variation in the gross composition of milks. In: Jensen RG (ed) The Handbook of Milk Composition. Academic Press, Orlando, pp 749-789.

Oliva JL, Wong YT, Rault J L, Appleton B, Lill A (2016) The oxytocin receptor gene, an integral piece of the evolution of Canis familaris from Canis lupus. Pet Behaviour Science 2: 1-15.

O'Rourke T, Boeckx C (2020) Glutamate receptors in domestication and modern human evolution. Neuroscience and Biobehavioral Reviews 108: 341-357.

Packard JM (2003) Wolf behavior: Reproductive, social and intelligent. In: Mech LD, Boitani L (eds) Wolves: Behavior, Ecology and Conservation. The University of Chicago Press, Chicago, pp 35-65.

Packard JM (2019) Wolves. 14. Landmarks Studies. Encyclopedia of Animal Behavior, Second Edition, Volume 3. Academic Press, Amsterdam, pp 262–278.

Packard JM, Mech LD, Ream RR (1992) Weaning in an arctic wolf pack: behavioral mechanisms. Canadian Journal of Zoology 70: 1269-1275.

Pasarić M, Warren G (2019) Interactions of Care and Control: Human–animal Relationships in Hunter-gatherer Communities in Near-contemporary Eastern Siberia and the Mesolithic of Northwest Europe. Cambridge Archaeological Journal 29: 465-478.

Pendleton AL, Shen F, Taravella AM et al. (2018) Comparison of village dog and wolf genomes highlights the role of the neural crest in dog domestication. BMC Biology 16: 64.

Perri AR, Feuerborn TR, Frantz LAF, et al. (2021) Dog domestication and the dual dispersal of people and dogs into the Americas. Proceedings of the National Academy of Sciences 118: e2010083118.

Perri A, Sázelová S (2016) The role of large canids: preliminary variabilities forming the population structure in Moravia. In: Svoboda J (ed) Dolní Věstonice II: Chronostratigraphy, Paleoethnology, Paleoanthropology. Brno, Academy of Sciences of the Czech Republic, Institute of Archeology, The Dolní Věstonice Studies 21: 138–146.

Peterson ME (2011) Chapter 9 - Care of the Orphaned Puppy and Kitten. In: Peterson ME, Kutzler MA (eds) Small Animal Pediatrics. The First 12 Months of Life. Saunders/Elsevier, St Louis, pp 67–72.

Phung TN, Wayne RK, Wilson Sayres MA, Lohmueller KE (2018) Complex patterns of sex-biased demography in canines. Proceedings of the Royal Society B 286: 20181976.

Pierotti R, Fogg BR (2017) The First Domestication: how wolves and humans coevolved. Yale University Press, New Haven.

Pilot M, Moura AE, Okhlopkov IM et al. (2019) Global Phylogeographic and Admixture Patterns in Grey Wolves and Genetic Legacy of An Ancient Siberian Lineage. Scientific Reports 9: 17328.

Platt BS, Stewart RJC (1968) Effects of Protein-Calorie Deficiency on Dogs 1. Reproduction, Growth and Behaviour. Developmental Medicine & Child Neurology 10: 3-24.

Porr M (2001) Between Nyae Nyae and Anaktuvuk – Some Remarks on the Use of Anthropology in Palaeolithic Archaeology. Ethnographisch-archäologische Zeitschrift 42: 159–173.

Porr M, de Maria K (2015) Perceiving animals, perceiving humans. Animism and the Aurignacian mobiliary art of Southwest Germany. In: Sázelová S, Novák M, Mizerová A (eds) Forgotten Times and Spaces: New Perspectives in Paleoanthropological, Paleoetnological and Archeological Studies. 1st Edition. Institute of Archeology of the Czech Academy of Sciences, Masaryk University, Brno, pp 293-302.

Prassack K, DuBois J, Lázničková-Galetová M, Germonpré M, Ungar PS (2020) Dental microwear as a behavioral proxy for distinguishing between canids at the Upper Paleolithic (Gravettian) site of Předmostí, Czech Republic. Journal of Archaeological Science 115: 105092.

Prassack K, DuBois J, Lázničková-Galetová M, Germonpré M, Ungar PS (2021) Of dogs, wolves, and debate: A reply to Janssens et al. (2020). Journal of Archaeological Science 126, 105228.

Prendergast H (2011) Chapter 8 - Nutritional Requirements and Feeding of Growing Puppies and Kittens. In: Peterson ME, Kutzler MA (eds) Small Animal Pediatrics. The First 12 Months of Life. Saunders/Elsevier, St Louis, pp 58–66.

Reynolds N, Germonpré M, Bessudnov AA, Sablin MV (2019) The Late Gravettian Site of Kostënki 21 Layer III, Russia: a Chronocultural Reassessment Based on a New Interpretation of the Significance of Intra-site Spatial Patterning. Journal of Paleolithic Archaeology 2: 160-210.

Rickard V. (2011) Chapter 2. Birth and the first 24 hours. In: Peterson ME, Kutzler MA (eds) Small Animal Pediatrics. The First 12 Months of Life. Saunders/Elsevier, St Louis, pp 11–19.

Rooney NJ, Bradshaw JWS., Robinson IH (2000) A comparison of dog-dog and dog-human play behaviour. Applied Animal Behaviour Science 66: 235-248.

Rootkustritz MV (2006) 1. Nutrition. In: Fatham L (ed) The Dog Breeder's Guide to Successful Breeding and Health Management. Saunders/Elsevier, Missouri, pp 2-20.

Russell N (2012) Social Zooarchaeology: Humans and Animals in Prehistory. Cambridge University Press, Cambridge.

Sablin MV, Khlopachev GA (2002) The earliest Ice Age dogs: Evidence from Eliseevichi. Current Anthropology 43: 795-799.

Safonova I, Sántha I (2012) Stories about Evenki people and their dogs: communication through sharing context. In: Brightman M, Grotti VE, Ulturgasheva O (eds), Animism in Rainforest and Tundra: Personhood, Animals, Plants and Things in Contemporary Amazonia and Siberia. Berghahn, New York, pp 82-95.

Sanderson SL (2013) Nutritional Requirements and Related Diseases of Small Animals. MSD Veterinary Manual https://www.msdvetmanual.com/management-and-nutrition/nutrition-small-animals/nutritional-requirements-and-related-diseases-of-small-animals

Sands J, Creel S (2004) Social dominance, aggression and faecal glucocorticoid levels in a wild population of wolves, *Canis lupus*. Animal Behaviour 67: 387-396.

Santos NR, Beck A, Fontbonne A (2020) A review of maternal behaviour in dogs and potential areas for further research. Journal Small Animal Practice 61: 85-92.
Sauer CO (1952) Agricultural origins and dispersals. The American Geographical Society, New York.
Savishinsky JS (1974) The trail of the Hare, life and stress in an arctic community. Gordon and Breach Science Publishers, New York.
Schleidt WM, Shalter MD (2018) Dogs and Mankind: Coevolution on the Move - an Update. Human Ethology Bulletin 33: 15-38.
Shabestari L, Taylor GN, Angus WV (1967) Dental Eruption Pattern of the Beagle. Journal of Dental Research 46: 276-278.
Sharp HS, Sharp K (2015) Hunting Caribou: Subsistence Hunting Along the Northern Edge of the Boreal Forest. University of Nebraska Press, Lincoln.
Shirokogoroff, SM (1935) The Psychomental Complex of the Tungus. Kegan Paul, Trench, Trubner and Co., London.
Silva P, Galaverni M, Ortega-Del Vecchyo, D et al. (2020) Genomic evidence for the Old divergence of Southern European wolf populations Proceedings of the Royal Society B: Biological Sciences 287: 1931.
Simonova VV (2018) The wild at home and the magic of contact. Stories about wild animals and spirits from Amudisy Evenki hunters and reindeer herders. Etudes mongoles et sibériennes, centrasiatiques et tibétaines 49.
Simoons F, Baldwin JA (1982) Breast-feeding of animals by women: its socio-cultural context and geographic occurrence. Anthropos 77: 421-448.
Sinding M-HS, Gopalakrishnan S, Ramos-Madrigal J et al. (2020) Arctic-adapted dogs emerged at the Pleistocene–Holocene transition. Science 368: 1495-1499.
Skibiel AL, Downing LM, Orr TJ, Hood WR (2013) The evolution of the nutrient composition of mammalian milks. Journal of Animal Ecology 82: 1254–1264.
Skoglund P, Ersmark E, Palkopoulou E, Dalén L (2015) Ancient wolf genome reveals an early divergence of domestic dog ancestors and admixture into high-latitude breeds. Current Bioliology 25: 1515-1519.
Smeds L, Kojola I, Ellegren H (2019) The evolutionary history of grey wolf Y chromosomes. Molecular Ecology 28: 2173-2191.
Spencer RF (1959) The North Alaskan Eskimo. A study in ecology and society. Smithsonian Institution Bureau of American Ethnology Bulletin 171.
Stahl PW (2016) Old dogs and new tricks: Recent developments in our understanding of the human–dog relationship. Reviews in Anthropology 45: 51-68.
Stépanoff C (2012) Human-animal "joint commitment" in a reindeer herding system. HAU: Journal of Ethnographic Theory 2: 287–312.
Thalmann O, Shapiro B, Cui P et al. (2013) Complete mitochondrial genomes of ancient canids suggest a European origin of domestic dogs. Science 342: 871-874.
Tooker E (1964) An Ethnography of the Huron Indians 1615-1649. Bureau of American Ethnology Bulletin 190: 1-183.
Topál J, Gácsi M, Miklósi A et al. (2005) Attachment to humans: a comparative study on hand-reared wolves and differently socialized dog puppies. Animal Behaviour 70: 1367-1375.
Trigger BG (1969) The Huron: Farmers of the North. New York: Holt, Rinehart, and Winston.
Trut LN, Kharlamova AV (2020) 19 - Domestication as a process generating phenotypic diversity. In: Levine H, Jolly MK, Kulkarni P, Nanjundiah V (eds) Phenotypic Switching. Academic Press/ Elsevier, Massachusetts, pp. 511-526.
Trut LN, Plyusnina IZ, Oskina IN (2004) An experiment on fox domestication and debatable issues of evolution of the dog. Russian Journal Genetics 40: 644-655.
Uerpmann H-P, Uerpmann M (2017) Chapter 7: The 'commodification' of animals. In: Tsuneki A, Yamada S, K.-I. Hisada K-I (eds) Ancient West Asian Civilization. Springer Science+Business, Singapore, pp 99–113.
Ujfalussy DJ, Kurys A, Kubinyi E, Gácsi M, Virányi Z (2017) Differences in greeting behaviour towards humans with varying levels of familiarity in hand-reared wolves (*Canis lupus*). Royal Society Open Science 4: 160956.
Vaté V (2013) Le chien chez les éleveurs de rennes chouktches. In: Stépanoff C, Ferret C, Lacaze G, Thorez J (eds) Nomadisme d'Asie centrale et septentrionale. Armand Colin, Paris, pp 206-207.
vonHoldt BM, Shuldiner E, Koch IJ et al. (2017) Structural variants in genes associated with human Williams-Beuren syndrome underlie stereotypical hypersociability in domestic dogs. Science Advances 3: e1700398.
Von Wrangel FP (1839) Reise des kaiserlich-russischen Flotten-Lieutenants Ferdinand von Wrangel längs der Nordküste von Sibirien und auf dem Eismeere, in den Jahren 1820 bis 1824. Nach den handschriftichen Journalen und Notizen bearbeitet von G. Engelhardt. Herausgegeben nebst einem Vorwort von C. Ritter. Voss'schen Buchhandlung, Berlin.
Walker, B. L. 2005. The Lost Wolves of Japan. University of Washington Press, Seattle.
Wallis RJ (2014) Exorcizing "spirits": approaching "shamans" and rock art animically. In: Harvey G (ed.) The handbook of contemporary Animism. Routledge, Abingdon, pp 307-324.
Wang G-D, Zhai W, Yang H-C et al. (2016) Out of southern East Asia: the natural history of domestic dogs across the world. Cell Research 26: 21-33.
Wasselkov A (2020) Ethnohistorical and Ethnographic Sources on Bear-Human Relationships in Native Eastern North America. In: Lapham H, Wasselkov G. (eds) Bears: Archaeological and Ethnohistorical Perspectives in Native Eastern North America. University Press of Florida, Gainesville, pp 16-47.
Wertz K, Wilczyński J, Tomek T, Roblickova M, Oliva M (2016) Bird remains from Dolni Vestonice I and Predmosti I (Pavlovian, the Czech Republic), Quaternary International 421: 190-200.
Wilkins AS, Wrangham RW, Tecumseh Fitch W (2014) The 'domestication syndrome' in mammals: A unified explanation based on neural crest cell behavior and genetics. Genetics 197: 795-808.
Willerslev R (2011) Frazer strikes back from the armchair: a new search for the animist soul. Journal of the Royal Anthropological Institute (N.S.) 17: 504–526.
Wilson GL (1924) The horse and the dog in Hidatsa culture. Anthropological Papers of the American Museum of Natural History 15: 125-311.
Yamada T (2001) The World View of the Ainu: Nature and Cosmos Reading from Language. Routledge, Oxford.
Zeder MA (2012) Pathways to animal domestication. In: Gepts P, Famula TR, Bettinger RL, Brush SB, Damania AB, McGuire PE, Qualset CO (eds) Biodiversity in Agriculture: Domestication, Evolution, and Sustainability. Cambridge University Press, Cambridge, pp 227-259.