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PERSPECTIVE

An assessment of current wolf *Canis lupus* domestication hypotheses based on wolf ecology and behaviour

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ABSTRACT

The dog was the first domesticated animal. Its derivation from grey wolves *Canis lupus* is important to the study of mammalian domestication, and wolf domestication is an active area of investigation. Recent popular books have promoted a hypothesis that wolves domesticated themselves as opposed to the earliest hypothesis that featured pup collection, adoption, and artificial selection. Continuing research has produced a greater understanding of wolf ecology and behaviour, including new insights into the wolf's interaction with humans. Several characteristics make the wolf conducive to domestication: its sociality, catholic diet, excellent individual and cultural memory, inbreeding tolerance, varied personalities, and adaptable lifestyle. The wolf's fear of humans is the main impediment and that alone is a factor strongly disfavouring the self-selection hypothesis. However, collecting young pups from dens and raising them would foster their socialising with humans as pack members. Neither hypothesis explains how wolves undergoing domestication were separated reproductively from their wild relatives, an important condition for domestication. We combine information from the literature with information from our own research on wild wolves, archaeology, and canid morphology. We explain how pup collection and deliberate or incidental selection and encouragement to breed with similarly raised wolves could keep incipient dogs separated reproductively from wild relatives. The key is humans regularly feeding the wolves and keeping only those able to live harmoniously with humans. Well-fed, human-dependent wolves would remain near their food supply and in the company of humans, thus increasing their bonds to humans and *vice versa*. Outbreeding with wild wolves would thus be avoided. Generation after generation of these human-fed, raised, and selected wolves would become increasingly dependent on humans and shaped by them. The pup-adoption hypothesis presented here is more in keeping with basic wolf ecology and behaviour than the self-domestication hypothesis.

INTRODUCTION

Domestication of grey wolves *Canis lupus* is an active area of biological and anthropological research. Several scientific fields are contributing, including molecular genetics (VonHoldt et al. 2017, Bergström et al. 2020), morphology (Janssens et al. 2016, 2019), and wolf ecology and behaviour (Carbyn et al. 1995, Mech & Boitani 2003, Range et al. 2019).

Some wolf-domestication studies relied on incorrect information. One example is Ersmark et al. (2016) citing a single wolf (Mech & Seal 1987) to support a wolf generation time of three years, a critical figure for calculating time since domestication. Data from hundreds of wolves in two studies supported 4.2–4.7 years as generation time (Stahler et al. 2013, Mech et al. 2016), although generation time could be shorter in the company of humans. Another example is Sykes (2019) who cited Mowat's (1963)

fiction about living with wolves as true, despite reviews documenting otherwise (Banfield 1964, Pimlott 1966, Mech 1970, Goddard 1996). In addition, much information as yet unpublished would be useful to wolf-domestication studies. Therefore, collaboration among researchers who are studying wolf domestication and those studying wolves could facilitate wolf-domestication investigations. Various workers have used multidisciplinary approaches to good advantage to facilitate such studies (Baumann et al. 2021), but rarely have these collaborations included wolf biologists.

We use our own studies to discuss wolf biology, ecology, and behaviour relevant to wolf domestication and expand on a hypothesis about how wolf domestication might have proceeded. Our studies include raising wolves at home (Mech 1970) and in colonies (Seal et al. 1979); observing them from aircraft (Mech 1970); live-trapping and radio-tracking them in several areas (Mech & Boitani 2003); living with and observing wild wolves that have become tame to humans (Mech 1988a, 2017); and examining wolf and dog morphology to determine accurately when domestication began (Janssens et al. 2016a, b, 2018, 2019). We are cautious about publications that are not peer-reviewed such as Crisler (1958), Coppinger and Coppinger (2001, 2016), and Sykes (2019), while recognising their value if they are used judiciously. We also caution that popular books that discuss wolf x dog hybrids and castrated wolves (Pierotti & Fogg 2017) have presented misleading views of wolf behaviour (Mech 2019).

Two main hypotheses about how wolf domestication began prevail: 1) humans collected young pups from dens, raised them, found them useful, and bred them selectively (perhaps implicitly at first) for certain traits ('pup adoption'; Darwin 1868, Klinghammer & Goodmann 1987, Pierotti & Fogg 2017), and 2) wolves domesticated themselves. The latter self-domestication hypothesis claims that wolves that were less anxious and aggressive increasingly frequented human camp disposal areas and obtained food there, but neither harmed humans nor were harassed by them. Hypothetically, these wolves then became domesticated (O'Connor 1997, Coppinger & Coppinger 2001, 2016, Larson & Fuller 2014, Pierotti & Fogg 2017).

To our knowledge, there have been only three critical evaluations of these theories (Germonpré et al. 2018, 2021, Serpell 2021), each based mainly on archaeological and anthropological information. We undertake a fourth here based primarily on wolf ecology and behaviour.

WOLF BIOLOGY RELEVANT TO WOLF DOMESTICATION

A recurring question regarding Upper Pleistocene wolves that gave rise to dogs about 25000 to 15000 years ago (Bergström et al. 2020) is whether their behaviour may have been fundamentally different from that of modern wolves. We presume, however, that Pleistocene wolf behaviour was not fundamentally different, because a 15000-year separation between American and Eurasian wolves (Loog et al. 2020) has not led to differences in behaviour, feeding strategies, hunting methods, or interaction with humans. Wolf behaviour thus would seem to have been stable over a long period.

WOLF INTERACTIONS WITH HUMANS

Throughout most of their history, wolves and humans have been both competitors for the same prey and adversaries to each other (Fritts et al. 2003, Camarós et al. 2016) and thus must have long feared each other, just as they do currently. Wolves existed about 300000 years ago (Nowak 2003). Even though wolves were capable of killing humans (Linnell et al. 2002, McNay 2002, Linnell et al. 2021), their fear of humans must have resulted from selection acting on wolves' negative interactions with humans, who had weapons that could kill wolves (Thieme 1997) but feared them nonetheless.

In response, wolves have long been persecuted by humans (Fritts et al. 2003, Wam et al. 2012). Even on Isle Royale National Park in Lake Superior, Michigan, USA, where wolves have been protected from humans for 70 years, they continue to fear people (Thurber et al. 1994, RO Peterson, personal communication). This fear on the part of wolves probably explains why wolves do not generally consider humans as prey to eat, contrary to the wolves' approach to every other animal (Newsome et al. 2016).

The only known region where wolves did not fear humans is an area where for centuries wolf–human encounters did not occur. Thus, wolves' natural fear of humans was not reinforced there for this long period, so that fear was lost. This region is the northern Queen Elizabeth Islands, a 400000 km^2 archipelago in the High Arctic of North America, north of 75° North Latitude. Because wolves' lack of fear of humans is so unusual, and because that is relevant to a critique of the two theories of wolf domestication, this situation bears special discussion. The area is farther north than Siberia, and except for scattered 'thermal oases' where wildlife can live, is continually covered with ice and snow. The general region was unfit for humans, except along shores, but the wolves lived inland away from human settlements (Mech 1988a). Thus, inland wolves there have been subjected to little hunting or human harassment for centuries, and very few have even encountered people except in recent times when military bases and weather stations established along shores (Parmelee 1964, Grace 1976, Miller 1978, 1995).

Those wolves that did recently meet humans were generally left undisturbed, sometimes fed (Miller 1995), or very rarely shot (Grace 1976), and those that were fed have become tame (Mech 1988a). Parmelee (1964) captured a three-month-old pup on Ellesmere Island (the northernmost Queen Elizabeth Island), and while he carried it to his tent, the mother followed at his heels, howling, and slept near his tent, with the pup inside. Elsewhere in the archipelago, a wolf licked a human's face (Miller 1978). During 24 summers from 1986 to 2010, the first author lived peacefully with, and studied, such tame-but-wild wolves close-up (Mech 1988a, 2017) near Eureka (80° N) on Ellesmere Island (Figs 1 and 2). The fact that wolves do not regard humans as prey, even in this unusual population, whereas they prey on every other animal, is evidence that selection favoured individuals that feared humans, because humans were too dangerous to prey upon.

Fig. 1. Many Ellesmere Island wolves are unafraid of humans and can be studied close-up, unlike elsewhere in the world. Here, first author Mech notes the behaviour of a pack's breeding male.

Fig. 2. In this screen print from 'White Wolf' video, Mech attempts to see how closely he can observe a female wolf and her pups around a den on Ellesmere Island (https://www.youtube.com/watch?v=1lPqRY8pn3Q).

The fear and animosity between wolves and humans do not undermine the pup-adoption hypothesis, because that idea holds that humans collected wolf pups at an early age from dens and raised them. Adult wolves do not defend their dens from humans, and, in modern times, humans have taken young pups from dens (Murie 1944, Mills et al. 2008).

INDIVIDUAL VARIATION

Wolves vary considerably in size, colour, and personality. At any given time, some seem shy while others are more outgoing (Mech 1970, Mech & Boitani 2003, Packard 2003). This was apparent with the High Arctic wolves. Those deferential with conspecifics were shy with humans. Those bolder with associates were bolder with humans. However, wolf personalities can change towards other wolves and to humans in the presence of pups and become much more defensive and bold (Mech 1970). High-ranking wolves can become subordinate to other pack-mates and behave more defensively and shy then (Packard 2003). The degree to which wolves are anxious or aggressive towards any individual pack-mate or towards non-prey species depends entirely on current circumstances (Packard 2003). Thus, contrary to the self-domestication hypothesis that 'friendly' or 'subordinate' wolves frequented human areas, any such wolves would not necessarily possess traits that would persist for generations.

SOCIALITY

Wolves are very social, as their pack life implies. Pack members generally are related, except the parents to each other, and they hunt together, gather around the den or at an above-ground 'rendezvous site' in summer, and sleep near each other all year round. The adults play with the pups, and all playfully chase and wrestle. Lone wolves usually are maturing pack members dispersing and seeking mates (Mech & Boitani 2003). Wolves' sociality could motivate individual wolves to frequent human camps if it were not for the animosity between wolves and humans. Sociality would, however, help cause pups raised by humans to bond with those humans (Virány & Range 2014), especially those who raised and fed them.

DENNING

For most of the year, wolf packs travel nomadically around their territories seeking prey. However, in spring, the

pregnant female chooses a den, a hole in the ground, rocky nook or cave, or a shallow pit in the ground (Mech 1993). Wolves tend to locate dens optimally in relation to food supplies (Joly et al. 2018).

The pups are born in a den in spring and remain inside for three weeks, and in or around the den for about eight weeks in total. Thus, humans can observe pups around dens and would have little trouble collecting young pups. If humans adopt pups by three weeks of age and feed them, they bond easily to the humans (Klinghammer & Goodman 1987). Humans could breast-feed them at first (Simoons & Baldwin 1982, Mondry 2017). Wolf nipples during nursing (Mech et al. 1993) are similar in size to those of human females. Pups begin eating solid food at about three weeks (Packard 2003), although they nurse for about nine weeks. The earliest age at which wolf pups can survive without nursing is unknown, but they can survive by 30 days of age (Klinghammer & Goodman 1987). Conceivably, wolf pups could survive without nursing when even younger, which would facilitate human care.

Similar to dog pups, newborn wolf pups require anogenital stimulation to urinate and defecate, but after about 10 days of age, captive pups begin urinating and defecating spontaneously (Klinghammer & Goodman 1987). Thus, for wolf-pup collection to have been instrumental in domestication, humans would best have adopted the pups between the ages of 10 days and three weeks. Having observed older pups around dens, humans would have known that to capture younger ones they would have to extract the pups from the dens before the pups began to emerge naturally.

Wolf pups usually remain in the den for about three weeks and then increase their time outside the den over the next five weeks. If raised in a human settlement during this period, pups would have considerable time to bond to humans (Klinghammer & Goodman 1987, Germonpré et al. 2018). In the wild, the breeding pair of wolves and their offspring of the previous one to three years travel from the den to hunt throughout the territory, bringing food to the female and pups intermittently, carrying it, or regurgitating it (Mech et al. 1999). Wild pups might go days without solid food, but if being raised by humans, probably would have been fed well and more regularly, thus furthering their bonding with the humans.

When about eight weeks old, wild pups are moved from the den to other protected sites above ground, called rendezvous sites. They often headquarter near food sources, for example, carcasses, while they grow for another three to four months. Although the adults might move the pups to several such rendezvous sites during this period, once established at such a site, the pups remain there while the adults travel far and wide hunting. Thus, pups raised by humans would be mentally adapted to remaining in human camps or moving with the humans. When almost fully grown and with adult dentition replacing milk teeth at about six months, the pups begin travelling with the pack nomadically within the territory, and no longer use dens or rendezvous sites (Mech & Boitani 2003).

LIVING SPACE

Most wolf-pack territories range over 50–1000 km^2 depending on pack size and prey density. Wolves advertise and defend that territory via howling, scent-marking, and direct killing of trespassers (Mech & Boitani 2003).

However, where food is abundant, i.e. where prey densities are high, or when humans are feeding them, wolves will live in a smaller area. For example, in north-eastern Minnesota, one pack of six occupied a territory of only 33 km^2 (Mech & Tracy 2004). Currently, the first author is studying female wolf 7268 that has at least four pups surviving to 10 months of age and whose locations are centred near a small settlement where these wolves were being fed by humans. From 1 February 2018 to 25 February 2019, 76% of her 42 daytime locations were within 2.5 km of the settlement (SM Barber-Meyer and LD Mech, unpublished data). The wolf's nocturnal locations are unknown. If they were being fed entirely by humans, wolves would have little reason to stray far from their food source.

BEHAVIOUR OF WOLVES FED BY HUMANS

Free-ranging wolves that humans feed directly from the hand, but not those that feed indirectly from human refuse, can become tame and behave much like domestic dogs. They condition quickly and habituate readily to the person feeding them or to humans in general (Fritts et al. 2003). Common behaviours shown by such wolves include frequenting the areas where fed, approaching and following humans on foot or in vehicles, and inspecting human belongings such as tents and camping gear. Wolves seem to generalise being fed, so, having been fed, they often will approach anyone possibly offering food. Humans have fed free-ranging wolves in modern times in several situations: 1) when pups stray from their den or rendezvous site and appear near workers such as loggers or pipeline employees, or local residents or tourists; 2) near frequently used campsites; 3) around isolated outposts such as military bases, weather stations, and research camps; 4) in national parks such as Yellowstone National Park and Denali National Park and Preserve in the United States and Algonquin Provincial Park and Banff National Park in Canada; and 5) for research (Mech 1988a, 2017).

During the first author's interactions with wolves near Eureka, Ellesmere Island, they allowed him and co-researchers to routinely observe, study (Fig. 1), and follow them on all-terrain vehicles for many kilometres (Mech 1988a, 2017). Individuals would, at times, lie around the researchers' tents. The breeding female brought her pups to the researchers and watched while they threw food to the pups. Even when researchers were on foot, most of the wolves were tolerant, although a few were shyer. In 1987, the first author lay near the den taking notes while the breeding female and pups ventured to within a few metres of him (Fig. 2). On 31 July 1987 at about 17:00 h, the breeding male (formerly 'alpha male'; Mech 1999), feeding on a musk-ox *Moschatus ovibos* calf that his pack of seven had killed hours before, even allowed Mech to crawl to within about 15 m of him feeding on the calf.

Although the above information might seem to evince that wolves could self-domesticate, it is important to understand that in these cases humans were actively feeding the wolves, whereas the self-domestication hypothesis proposes that wolves were scavenging food with no direct interaction with humans.

BREEDING AND DISPERSAL

Some female wolves can breed when 10 months old, but they usually reach first oestrus and ability to breed when about two to four years old (Mech & Seal 1987, Mech et al. 2016). When wolves become sexually mature, many males and females disperse from their natal pack, attempting to find mates and a place with adequate prey unoccupied by other wolves (Mech & Boitani 2003). This process may take them only a few or hundreds of kilometres away. However, if food is plentiful, maturing wolves remain with their natal pack for three or four years and might even produce their own pups with that pack (Stahler et al. 2013).

INBREEDING TOLERANCE

Generally, wolves do not inbreed (Smith et al. 1997). However, they can sustain considerable inbreeding at population levels. This is evidenced by the population on Isle Royale. This population, founded by one female and two males in 1948 (Wayne et al. 1991) and consisting of up to 50 wolves, survived for 70 years. Two or three immigrants did bolster the population (Adams et al. 2011), and some Isle Royale wolves did sustain deleterious inbreeding effects. However, the population functioned well enough to survive for decades (Räikkönen et al. 2009). Similarly, a Mexican wolf reintroduction project with seven founders increased to over 115 in the wild (Harding et al. 2016). This small inbred population and that of Scandinavian wolves also survived and increased, although smaller bodies have been reported (Laikre & Ryman 1991, Fredrickson & Hedrick 2002), along with defects, such as transitional, low-lumbar vertebrae (Räikkönen et al. 2009). Nevertheless, wolves inbred for only a few generations function well (as above), so human-raised wolves could breed with relatives in the same camp. This practice would not only prevent outbreeding with their wild congeners, but also tend to fixate and promote phenotypes favourable to living with humans.

ALARM SIGNALS

Wolves bark when alarmed or to threaten, similar to humans shouting (i.e. sharp, staccato sounds). Thus, human-raised wolves and humans might readily have developed some understanding of each other's alarm behaviour. Anecdotal evidence that wolves can recognise the intent of shouting comes from the first author's experience in the High Arctic with wolves tame to humans. He usually tented near a wolf den and spent most of his time there. When an intruding photographer approached the wolves surreptitiously, the breeding female stood beside the first author, who was shouting at the intruder. She looked intently into the valley, and even barked, the first author recalls.

HUNTING BEHAVIOUR

Although wolves eat almost anything, most often they hunt hoofed mammals to obtain enough energy. These prey possess dangerous hooves, and many wield sharp horns or antlers (Mech et al. 2015). Searching for vulnerable prey requires long-distance travel, usually about 25 km per day. With most attacks on their main prey, wolves risk their lives, including even with smaller prey such as white-tailed deer *Odocoileus virginianus* (Mech et al. 2015). Thus, if an easier or less dangerous way exists to obtain enough food, wolves tend to use it. This tendency explains why wolves long remember locations of their caches. Totally subsidised human-raised wolves would experience none of the stress involved in stalking, chasing, and attacking prey, so would be highly motivated to remain in the company of the humans feeding them.

INDIVIDUAL AND CULTURAL MEMORY

Wolves remember where they can obtain easy food and that information can pass on for several generations. This individual and cultural memory was apparent during the first author's studies of the High Arctic wolves. One example involved a wolf that headed directly to a cache without any indication of smelling it, and unearthed a

black, mud-laden young arctic hare *Lepus arcticus* that must have been buried for at least a year, for this happened before hare leverets had even been born that year (LD Mech, unpublished data).

An example of wolves' cultural memory derives from the first author's experience with these same wolves frequenting a garbage landfill on Ellesmere Island for years and intermittently obtaining garbage, avoiding the risk of attacking prey (Mech et al. 2015). The pack often numbered around 20 (Mech & Cluff 2011), so even when food was available, it would hardly satisfy the whole pack. Still in 2010, long after the dump had closed, wolves continued to visit it briefly, while mostly hunting wild prey (Mech & Cluff 2011). Wild wolves can live up to 13 years (Mech 1988b), so their attraction to a location could be learned by several litters, thus maintaining the pack's memory for long periods.

During the first author's studies, he fed these wolves by throwing various foods on the ground, and the animals grabbed them (Documentary National Geographic 100 Years Vol 038 White Wolf 2017). Using pieces of arctic hare or seal *Phoca* spp., cheese, or dry dog food, he could assess the wolves' hunger by which they ate and how eagerly they acted (Mech 2017). With meat, the wolves grabbed even the tiniest pieces, indicating how favoured this food was.

The wolf's long-term ability to remember favoured free-food sources is one characteristic that is in keeping with both the self-domestication and pup collection hypotheses. It is crucial to the former but also supports the idea that pups fed directly by humans will remember that.

DOMESTICATING WOLVES

Domesticating wolves began around the last glacial maximum, probably from an Asian wolf clade that remains yet unrecognised because of extinction, hybridisation, or lack of discovery (Bergstrom et al. 2020, Loog et al. 2020). Both hypotheses of wolf domestication require that the population undergoing domestication be isolated reproductively from its surrounding ancestor population (Bridle & Ritchie 2001, Wu 2001, Wayne & Vila 2003, Hey & Pinho 2012). To our knowledge, however, no one has explained satisfactorily how this could be done. Reproductive isolation is a primary problem for the self-domestication hypothesis. Without it, genes of self-domesticating individuals would be diluted by mating with wild congeners. Although sympatric speciation (Fitzpatrick et al. 2008) can occur, some mechanism of genetic separation such as allochrony or niche separation still is required. Coppinger and Coppinger (2001) did propose niche separation for the self-domestication hypothesis, with dog ancestors being wolves whose niche was to feed regularly at human dumps. However, Lupo (2019) challenged that possibility based primarily on the lack of sufficient food in human camps and dumps of the period to support creatures the size of wolves.

When wolf domestication started (>15000 years ago), humans were nomadic (Driscoll et al. 2009) and would not have had regular disposal middens that numbers of wolves could live around and scavenge. However, there could have been enough food stored and cached for people to allocate some to a few wolves that they were raising. The widespread and persistent wolf fear of humans and the human animosity towards wolves also present major challenges (Germonpré et al. 2018) to the self-domestication hypothesis.

Therefore, like Germonpré et al. (2018, 2021) and Serpell (2021), we discount the hypothesis of self-domestication because it fails to accord with the above-described wolf ecology and behaviour. In addition, it clashes with the human lifestyle of the time. This leaves the hypothesis of pup collection and adoption and conscious or unconscious selection, which we accept and expand upon. We also explain, based on wolf behaviour and ecology, how this domestication approach could have maintained reproductive separation between the wolves being domesticated and their surrounding wild populations.

AN EXPANDED HYPOTHESIS OF WOLF DOMESTICATION

Once pups are collected, fed, and nurtured, they tame easily and become reliant on humans for food, tend to remain near their food source, and generally remain friendly towards humans (Hall et al. 2015, Marshall-Pescini et al. 2017, Range et al. 2019). Although human-raised wolves in modern society can be problematic (Mech 1970, Fritts et al. 2003), most problems stem from the structure of modern human living that would not have prevailed long ago. Tamed wolves then would have been free to roam and behave naturally, tied to humans by food dependence.

Several motives for domesticating wolves have been offered of which most are utilitarian. Such motives include 1) to aid in hunting (Driscoll et al. 2009, Derr 2011, Shipman 2015; but see Mech 2019); 2) to help guard human interests (Driscoll et al. 2009, Derr 2011, Horard-Herbin et al. 2014, Shipman 2015); 3) to clean up settlement debris (carrion, leftovers, commensals, human faeces; Derr 2011, Horard-Herbin et al. 2014); and 4) as food (canophagy; Degerbøl 1961). However, we believe the most reasonable motivation is for use as pets and companions (Zeuner 1963, Clutton-Brock 1981, Germonpré et al. 2018, Janssens et al. 2018). Wolves' strong social nature helps them develop a rapport with humans who raise and feed them (Crisler 1958, Zimen

1987, Hall et al. 2015). Early humans had an aesthetic sense (Lyons 1967), and humans find canid pups cute (Lorenz 1942, Chersini et al. 2018) and thus would be attracted to them. Humans who raised wolf pups might have enjoyed the same benefits that modern humans gain from pets (Amiot et al. 2016). Early humans may have possessed a general empathy (Bradshaw & Paul 2010) for young wolves or derived other psychological benefits (Amiot et al. 2016). Wolves sometimes bear pups (average litter size is six; Mech 1970) above ground in shallow pits (Mech 1993) that would allow human observation and collection for food (Degerbø1961, Germonpré et al. 2018) or to admire and raise. Furthermore, any pups that were raised for any reason would have been available to humans for food if necessary.

Below is an expanded version of the pup-adoption and artificial-selection hypothesis, similar to that of Morey (1994) and Germonpré et al. (2018), based on information about wolves.

1. Humans remove pups ≤3 weeks old from dens and feed them, including by breastfeeding (Simoons & Baldwin 1982, Mondry 2017), thus making the animals dependent on humans, friendly with them, and bonded to them (Hall et al. 2015). This is similar to the indigenous Australian practices with dingoes (Smith & Litchfield 2009). As the pups grow and develop, the humans keep the more mellow, tractable, and cooperative individuals (Range & Virányi 2014). This selection probably would be deliberate, but could be inadvertent, as the more rambunctious individuals might stray more or be more difficult to deal with.
2. The humans continue to feed the surviving animals, thus keeping them close until they mature.
3. The mature females mate, either with siblings, with males from other litters being raised similarly, or, less likely, with wild male wolves.
4. Breeding siblings or other camp wolves, the breeding pair scent-marks a territory that includes the camp and howl frequently, thus keeping wild wolves away (Mech & Boitani 2003).
5. The females den nearby, possibly in the camp where food is available (Joly et al. 2018) and where they are protected by their human 'pack'. Female wild wolf 7268, mentioned above, denned within 1 km of humans who were feeding her; wolves raised by humans and totally dependent on them for food would den closer to them. Nomadic humans might collect one or two newborn pups and destroy the others, so the mother would follow them.
6. The humans then feed the new pups, generation after generation, while either deliberately or implicitly selecting for progressive tameness. Eventually, repeated selection on character, aberrant coat colours, tail and ear carriage, etc., as conducted by Beylaev and Trut with silver foxes *Vulpes vulpes* (Trut et al. 2009), would tend to preserve the preferred traits in the population.

The key to this process is humans regularly feeding the wolves and continually keeping only those living peacefully and with the least trouble. Such human-dependent and bonded wolves still might roam from camp and even occasionally breed with wild wolves. However, if fed well enough and regularly enough, as conditions at the time would have allowed (Lahtinen et al. 2021), they would have little reason to kill their own prey, the main reason wild wolves roam so much (Mech et al. 2015). The probability of breeding with littermates or with human-selected, mellow males from other human-raised litters, would be high, thus keeping them reproductively separated from wild wolves. Wolves are only in oestrus for two to four weeks (Kreeger 2003), so with the proximity of other wolves similarly raised, their chances of mating with those wolves, rather than with wild wolves that range much father and normally would avoid humans, is much greater.

This hypothesis of wolf domestication would work best, or possibly only, in a philopatric culture where human-selected wolves could use the same den each year, where pairs could defend the same territory, and where other environmental influences on the human–wolf relationship remained stable. During the wolf-dog whelping season, the hunter–gatherer group would best have to return to the same location, as some did at times (Binford 1983). A regular surplus of meat would be needed, such as reindeer *Rangifer tarandus* hunters had (Binford 1990, Lahtinen et al. 2021).

We offer the above pup-adoption hypothesis as more in keeping with basic wolf ecology and behaviour than other hypotheses, and as the hypothesis that better explains why and how humans could have isolated wolves from their ancestors, bred them selectively, and shaped them into domestic dogs.

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