

2.3 Why Wolves Became Dogs: Interdisciplinary Questions on Domestication

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Abstract

During domestication, dogs have evolved human-like skills for functioning effectively in human societies. Findings of comparative psychology have shed light on the question of what skills dogs were selected for during domestication - namely skills that made them better able to communicate and cooperate with humans. However, if we want to understand the whole process of dog domestication, there are many compelling questions. Here we propose three lines of inquiry that should be considered- the starting point, process, and outcomes of domestication. To answer these questions, we need an interdisciplinary approach in which scientists from the fields of archaeology, genetics, anatomy, psychology, sociology, and anthropology work together.

Keywords: domestication, dogs, cognition, behaviour, interdisciplinary.

1 What we know: dogs in comparative psychology

Over the past 20 years, ‘man’s best friend’ - the domestic dog (*Canis familiaris*) - has increasingly become a subject of scientific study for comparative psychologists who study animal cognition. It has been revealed that, compared to other social animals, dogs show special skills. In particular they show remarkable skills in three social domains:

- First, they seem to possess special communicative skills. They are able to produce communicative signals such as barking (Feddersen-Petersen 2000; Pongracz *et al.* 2005) and gaze alternation (Miklósi *et al.* 2000; Kaminski *et al.* 2011; Heberlein *et al.* 2017). Additionally, they are also able to comprehend more typically human forms of communication such as words (Kaminski *et al.* 2004; see also Merola *et al.* 2012), iconic signs (Kaminski *et al.* 2009b), and gestures. One often-used setup is the so-called object choice design, in which a food reward is hidden in one of two cups, out of the dog’s view. When a human provides a communicative cue, such as pointing or gazing at the correct cup, it was found that dogs are better than any other animal species tested at using these cues (see Hare and Tomasello 2005; Bräuer *et al.* 2006; Miklósi and Soproni 2006; Kaminski and Marshall-Pescini 2014 for reviews, see Figure 1). A dog’s ability to use these human gestures probably evolved during domestication (Hare and Tomasello 2005; Bräuer *et al.* 2006; see also Price 1984). Indeed, free ranging dogs and shelter dogs with limited human contact are also able to use

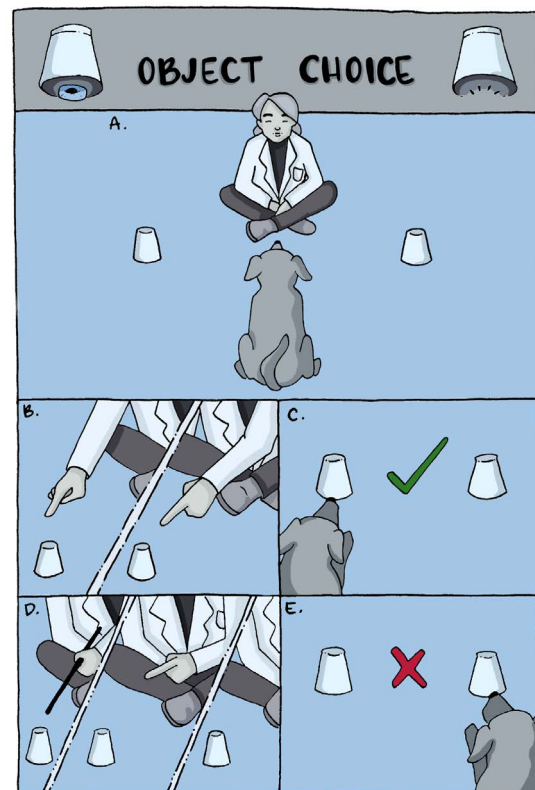


Figure 1. Object choice paradigm. (A) A food reward is hidden in or under one of two cups, so that the dog does not see in which one. (B) Human provides a communicative cue, such as pointing at the correct cup. (C) Dogs approach the correct cup using communicative cues. (D) Human provides no cue or a non-communicative cue (without looking at the dog). (E) Dogs are at chance level in the absence of obvious communicative cues. (Image Credits: Blanca Vidal Orga).

these gestures to locate hidden food (Hare *et al.* 2010; but see Bhattacharjee *et al.* 2017 and Udell *et al.* 2008), whereas apes, our closest living relatives, perform much worse at this task (Bräuer *et al.* 2006). More importantly, dogs are much better at this task than hand-reared wolves; and even six-week-old puppies are already able to use human pointing gestures to locate hidden food (Hare *et al.* 2002; Riedel *et al.* 2008; Gácsi *et al.* 2009a; Gácsi *et al.* 2009b; but see also Lampe *et al.* 2017).

- A second social-cognitive ability that has been intensely investigated in dogs is perspective taking - the ability to assess what others can perceive. In particular, researchers have investigated whether dogs know what humans can see. Dogs are especially sensitive to human attention, i.e., they are able to distinguish between situations in which a human is attentive to them or not (Call *et al.* 2003; Bräuer *et al.* 2004; Gácsi *et al.* 2004; Virányi *et al.* 2004; Kaminski *et al.* 2017). They are also sensitive to the human perspective (Kaminski *et al.* 2009a; Kaminski *et al.* 2013). Finally, dogs are also capable of auditory perspective taking - the ability to assess what humans can hear (Bräuer *et al.* 2013a; see Kunderly *et al.* 2010).
- The third social-cognitive domain in which dogs seem to show special skills is cooperation, defined as a behaviour that is beneficial to another individual or to both individuals involved in a task (Melis and Semmann 2010; Amici 2015). One kind of cooperation is prosocial behaviour, defined as a cooperative behaviour on the part of one individual (the actor) that benefits another individual (the recipient) and occurs voluntarily (see Bräuer 2015; Melis and Warneken 2016 for reviews). Dogs cooperate with humans towards various objectives including protection, hunting, herding, rescuing, searching, servicing, and guiding (Miklósi 2007; Serpell 2016). In all these scenarios, dogs behave beneficially towards humans. However, in most of these cases it is unclear whether dogs actually understand human intentions and are motivated to cooperate with them, or whether they have simply been trained to follow specific commands or react to particular situations in certain ways (Bräuer *et al.* 2013b; Bräuer 2015; Marshall-Pescini *et al.* 2016b). Recent studies have produced mixed evidence (see Bräuer 2015 and Marshall-Pescini *et al.* 2016b for reviews). In the prosocial choice task, subjects are given a choice between two reward combinations, one of which delivers a food item to the subject *and* the recipient (prosocial choice) and the other, which rewards only the subject (selfish choice). Quervel-Chaumette *et al.* (2015) found that dogs showed prosocial preferences towards conspecifics whereas in another version of the prosocial choice task, Dale *et al.* (2016) did not find evidence for prosocial preferences.

Given that dogs prefer humans to other dogs as social partners (Miklósi *et al.* 2003; Gácsi *et al.* 2005; Topál *et al.* 2005) and that the dog-human bond is comparable to the attachment between human infants and their mothers (Prato Previde and Valsecchi 2014), it is likely that dogs might cooperate better in such a task with a human partner than with another dog. However, Kaminski *et al.* (2011) did not find evidence that dogs *helpfully* inform a human about a hidden object (Kaminski *et al.* 2011). Dogs also do not seek help when their owner is simulating a heart attack (Macpherson and Roberts 2006) when they do not have special training. It is possible, however, that in these cases the dogs simply did not understand *how* to support the human partner (Bräuer 2015), thus Bräuer *et al.* (2013b) tried to make the human problem as obvious as possible for the dog. In their study, dogs opened a door when a human expressed that she wanted to enter a target room. Interestingly, the dogs continued to open the door for the human over multiple trials without receiving any reward, indicating a high motivation to support her (Bräuer *et al.* 2013b).

In sum, dogs outperform other social species in their ability to pay attention, to communicate and to cooperate with humans. It is therefore generally accepted that during the process of their domestication, dogs have evolved human-like skills that help them to function effectively in human societies (Hare and Tomasello 2005; Kaminski and Marshall-Pescini 2014). Thus, humans might have selected them to be particularly good cooperative and communicative partners (see Bräuer 2015 for a review).

2 What we do not know

In the previous section, we summarised how the findings of comparative psychology in the last 20 years have shed light on the question of what skills dogs were selected for during domestication - namely, skills that made them able to better communicate and cooperate with humans. However, if we want to understand the whole process of dog domestication, there are many open questions that, in order to be answered, require an interdisciplinary approach.

One general question is *when and where* the process started. Although some authors claim that dogs were domesticated more than 30–40,000 years ago (Vilá *et al.* 1997; Thalmann *et al.* 2013; Wang *et al.* 2013), others doubt that. The common understanding is that dog domestication started *at least* 14,000 years ago, as there is clear social and cultural evidence of domesticated dogs from this time (as illustrated by the Bonn-Oberkassel dog mandible found in a late Paleolithic grave in Germany; Janssens *et al.* 2018). Thus, a more precise date and place of the first domestication event remain unclear. Findings from genetics and archaeology

can elucidate when and where precisely dogs were first domesticated (Wayne and Vilà 2001; Larson and Bradley 2014; Serpell 2016;), and how they spread all over the world (Kaminski and Marshall-Pescini 2014; see also Mitchell 2017; Ní Leathlobhair *et al.* 2018).

Another sub-question might be more difficult to answer: *why* were wolves domesticated in the first place? Clutton-Brock (1977: 1342) has explained domestication as the ‘exploitation of one group of social animals by another more dominant group, which maintains complete mastery over its breeding, organization of territory, and food supply’. Selective breeding over the course of many generations enhances various behavioural and physical characteristics conducive to domestic harmony and utility (Price 1984; Serpell 2016). Other authors, such as Zeder (2012) see domestication from a more mutualistic approach, where both human and domesticate benefit from the relationship (Price 1984; Zeder 2012). If domestication leads to a symbiotic relationship, then we would expect there to be advantages for both species - humans and wolves/dogs.

There is no doubt what the advantage was for the wolves that not only gained a new food resource in human camps but were also protected from predators. However, what was the initial advantage for the human to domesticate the wolf? Hale (1969) has suggested behavioural characteristics that facilitate the domestication process, such as, for example, a hierarchical group structure, a critical period in development of species-bond, being omnivorous, and a short flight distance - meaning they do not run far from humans when they encounter them (Hale 1969; see also Diamond 1997). However, a number of these characteristics do not apply to wolves, such as being precocial and having limited agility. Moreover, wolves and early humans were competitors in hunting the same kinds of prey. So why did we domesticate a species that was a food competitor before we even settled down? A tentative answer to this question might rely on various hypotheses about how wolves/dogs were initially used at the beginning of the domestication process. Humans might have taken advantage of their attentiveness and their hunting abilities. Wolves/dogs probably cleared camps of garbage and vermin, and they also might have been used as a source of meat, of heat, and as a means of transportation (Zimen 1992; Paxton 2000; Miklósi 2007; Serpell 2016). Therefore, wolves might have had specific traits that allowed humans to make advantageous use of them, but whether this is the case or whether they were coincidentally in the right place at the right time for being domesticated remains an open question (Kaminski and Marshall-Pescini 2014).

There are also multiple theories on *how* domestication started. Perhaps it was initiated by humans, as hunters brought wolf pups into the camp, or perhaps wolves approached human camps to feed on discarded food scraps. The first scenario paints a picture where humans actively selected particularly friendly and approachable wolf puppies for companionship (Zimen 1992; Kaminski and Marshall-Pescini 2014). In the second scenario, in line with the so-called self-domestication hypothesis, wolves that were less aggressive or less fearful towards humans would have had the selection advantage to approach and live in close proximity to humans, and so had the opportunity to exploit new and reliable food sources (Hare *et al.* 2012; Kaminski and Marshall-Pescini 2014). Today, many researchers suggest that it was a combination of these two scenarios - that wolves lived in close proximity to humans, and that some of them were tamed by humans and later humans selected for animals showing less aggression and fear (Coppinger and Coppinger 2001; Miklósi 2007; Galibert *et al.* 2011; Kaminski and Marshall-Pescini 2014). Some authors have speculated that social structure and hunting behaviour were similar for early humans and dogs’ ancestors, as wolves also hunt and breed cooperatively (Clutton-Brock 1977; Coppinger and Coppinger 2001; Mech and Boitani 2003). Cooperation skills probably already existed in dogs’ ancestors, as recent studies with hand-reared wolves socialised with humans have confirmed that these wolves not only show high social attentiveness and tolerance but are also highly cooperative. Such characteristics may have provided a good basis for the evolution of dog-human cooperation (see Range and Virányi 2015 for a review).

In short, both the reason for domestication and the way in which it started remain highly speculative. But they both depend on the place and timing of the initial domestication. For example, it would be crucial to know whether dogs were domesticated long before or during the Neolithic (see also Ben-Dor *et al.* 2011; Larson and Bradley 2014). Thus, unless the place and timing are not agreed upon, it is nearly impossible to draw conclusions about the reasons and process of initial domestication.

Another crucial point to understanding dog domestication is to take into account non-western cultures. Nearly all of the animal cognition studies mentioned above tested dogs owned by people from ‘WEIRD’ societies, i.e. Western, Educated, Industrialised, Rich, and Democratic societies (Henrich *et al.* 2010). However, the majority of dogs in the world - about 75% - are not kept in the same way as they are in western countries (Gray and Young 2011; Kaminski and Marshall-Pescini 2014). Gray and Young (2011) explored typical dog-human dynamics in 60 different societies, using the electronic global ethnographic database eHRAF. They found that, globally, some dogs served

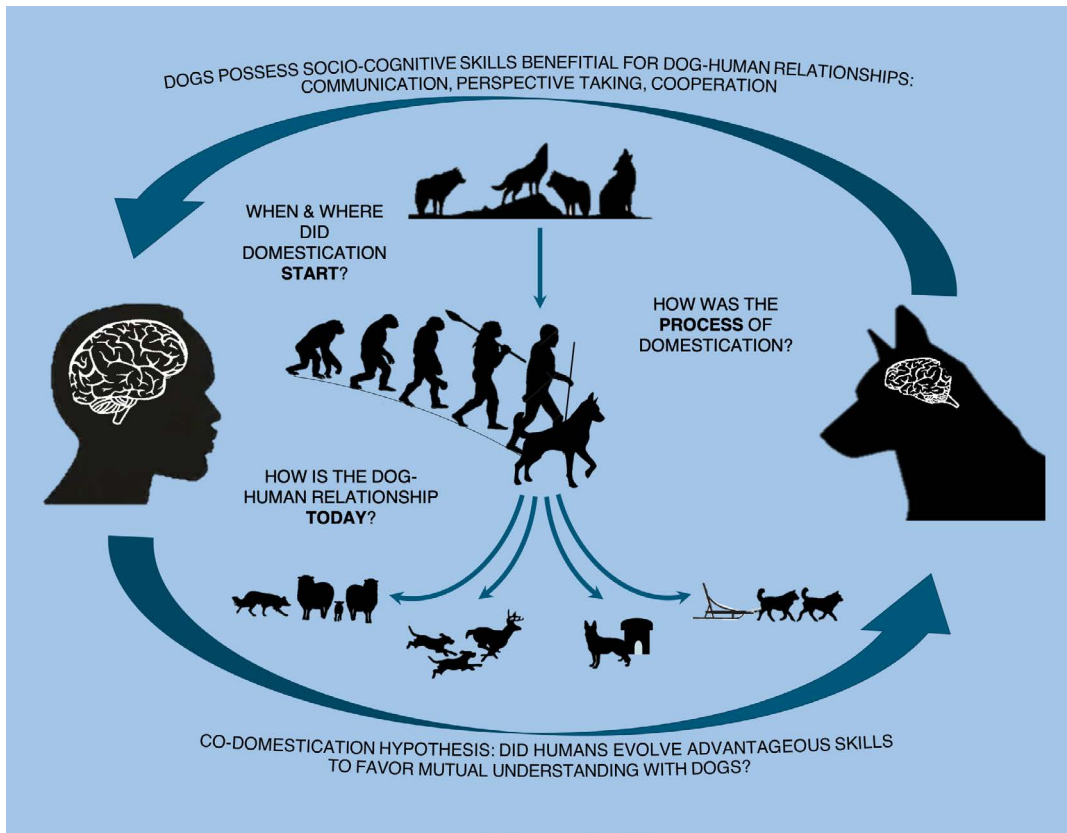


Figure 2. Figure represents the co-evolutionary relationship between dogs and humans. Several questions about dog domestication remain open and can be summarised under three main themes: the starting point, process, and outcomes of domestication. (Parts of this figure were created by Kathryn Kirby and are used with her permission).

practical functions such as aiding in hunting and pest removal, while some were simply kept for pleasure or companionship. Additionally, positive and negative interactions, feeding, and sleeping patterns varied substantially across societies (Gray and Young 2011).

Positive or negative attitudes toward dogs might also influence how dogs are understood. Amici *et al.* (2019) compared how groups of humans with different levels of experience with dogs rated dog emotions from pictures. They found that persons from cultures that are not generally dog-positive (for example, in this study, Muslim cultures in which dogs are often viewed as ‘impure,’ and are rarely integrated as part of the family) perform worse at accurately interpreting a dog’s emotions from a photograph compared to persons who come from cultures that have a generally positive attitude towards dogs (Amici *et al.* 2019). The authors concluded that the ability to recognise dog emotions is mainly acquired through age and experience. However, happy and angry emotions were recognised well independently of participants’ age and experience.

We know, therefore, that there are differences among human cultures in the ways dogs are kept, valued and

communicated with. What we do not know is whether these differences act as different selective pressures on dog cognition and behaviour, and whether any resulting differences are likely to be heritable. Unfortunately, the absence of carefully planned cross-cultural studies means that we do not know whether dogs kept in non-western cultures perform similarly to ‘western’ dogs in cognitive tests.

3 New questions and interdisciplinary approaches

To answer the crucial questions about dog domestication, there has to be an interdisciplinary approach including archaeology, genetics, anatomy, psychology, and anthropology. Below we propose three lines of questions to be considered, see Figure 2.

3.1 The starting point of domestication

Geneticists and archaeologists are continuing to investigate *when* and *where* wolf domestication took place (i.e. Ostrander *et al.* 2019). The particular question to be answered is whether it was only one or a very few domestication events in one place (i.e. Thalmann *et al.* 2013) or whether dogs were domesticated more

than once in multiple places (Mech and Boitani 2003; Frantz *et al.* 2016). The latter scenario would better explain the huge variability in modern dogs that could potentially also involve their cognitive skills. This would raise the possibility that humans from particular cultural backgrounds may have selected their dogs for particular aspects of cognition.

A further related question is *why* wolves were domesticated at that time. More precisely: what skills made dogs valuable for humans so that they were domesticated? The question of what skills made dogs valuable for humans should be investigated. One possibility is their sense of smell. As dogs have an excellent sense of smell, which is 10,000 to 100,000 times better than that of humans (Dalziel *et al.* 2003; Walker *et al.* 2006; Green *et al.* 2012; Hall *et al.* 2015; Polgár *et al.* 2016; Bräuer and Belger 2018), it is feasible that early humans found this skill useful. Wolves probably perceived predators earlier with their nose, and humans might have noticed that. When the bond between the two species became closer, the sensitive nose of dogs may have been very helpful in cooperative hunting.

To answer this question about the benefit for early humans, it is crucial to investigate how dogs were initially used. Archaeological and anthropological findings about the earliest functions of dogs in various cultures can help to answer this question. Moreover, it is also important to directly quantify the benefit of dog keeping. For example, it was found that hunting dogs have a big impact on hunting success (Ruusila and Pesonen 2004). Further studies should also investigate whether there are societies with a long history of cooperating with dogs that have been more successful over evolutionary time periods than societies without dogs (i.e., Shipman 2017).

3.2 The domestication process

One of the most crucial questions about the process of domestication is what skills dogs were selected for. The obvious approach to answer this question is a comparison with their closest living relatives, wolves. Regarding behaviour and cognition, there have been various studies in the last 20 years that directly compare the behaviour of dogs and wolves. In most of these studies, dogs and wolves were raised in an identical way to ensure that the study subjects were truly comparable (i.e. Lampe *et al.* 2017). Although dogs outperform wolves in their ability to use the human pointing gesture (see above), there are various tasks on which they underperform in comparison to their undomesticated relatives. Wolves outperform dogs in quantity discrimination (Range *et al.* 2014) and causal reasoning (Lampe *et al.* 2017). They are more persistent

(Marshall-Pescini *et al.* 2017a; Rao *et al.* 2018; see also Miklósi *et al.* 2003) and more risk prone than dogs (Marshall-Pescini *et al.* 2016a). In their packs, wolves reconcile better than dogs (Cafazzo *et al.* 2018) and share monopolisable food more often (Dale *et al.* 2017). Regarding cooperation tasks, the results are mixed. On some tasks, wolves cooperate better with conspecifics than dogs (Marshall-Pescini *et al.* 2017b), while on other tasks they perform equally well (Bräuer *et al.* 2020). These findings illustrate that wolves have maintained skills that enable them to survive in the wild, and that they are adapted to their life in their cohesive social group.

To characterise changes during domestication, an interdisciplinary approach would be illuminating. For example, it was recently found by a group of anatomists and psychologists that dogs possess a muscle responsible for raising the inner eyebrow intensely that is not present in wolves (Kaminski *et al.* 2019). It is likely for two reasons that domestication transformed the facial muscle anatomy of dogs specifically for facial communication with humans. First, dogs only use this muscle to raise the inner eyebrow when a human is looking at them (Kaminski *et al.* 2017). Second, humans have a preference to adopt dogs that show the inner eyebrow raise (Waller *et al.* 2013). Why exactly humans prefer such dogs is still speculative. It might be related to paedomorphism, i.e., that dogs appear more like wolf puppies. These features were thought to have evolved as a byproduct of the domestication process, and arose accidentally when aggression was actively selected against (Hare *et al.* 2012), but it is also possible that dogs were selected for these features as humans prefer paedomorphic characteristics (Kaminski *et al.* 2019). This combination of behavioural and anatomical studies seems to be very promising to shed light on the selection process during domestication.

Another less obvious approach to understand the domestication process is using linguistics. It is possible that linguistic patterns might provide clues regarding the history of dog-human-relationships in particular societies. For example, linguists often use patterns of colexification and cognacy to make inferences about the origins of particular terms and the extent to which they may have been borrowed from a neighbouring language vs. inherited from a linguistic ancestor. It might be interesting, for example, to examine patterns of colexification between lexemes for 'dog' and those for 'wolf' or other wild canids across as many of the world's ~7000 languages as possible. It could then be tested whether observed patterns of colexification reflect what is known from the historical and archaeological record about dog domestication and dog keeping across regions and language families. Similarly, it might be expected that the standard term for 'dog' in a language

would reflect dogs' dominant function in societies that speak that particular language. This hypothesis could be tested by examining patterns of cognacy (shared word origin) among societies in which dogs share vs. differ in their dominant functions (e.g., hunting, herding, defence).

Finally, to fully understand the domestication process, one should not only investigate dog cognition and behaviour but also the human side of the equation and the possibility of co-domestication. According to the co-domestication hypothesis, not only have dogs evolved special skills to assess humans, but humans may have also evolved special advantageous skills that favour mutual understanding between the two species (Kaminski and Marshall-Pescini 2014; Amici *et al.* 2019).

3.3 The result of dog domestication

The third and final important line of inquiry into the question of dog domestication explores its outcome - the contemporary dog-human relationship. One lingering question is the universality of dog-human interactions, i.e., the extent to which the recently recognised typical social-cognitive skills of dogs are universal or whether they are influenced by the society in which the dogs live. For example, what patterns are found in the differences in keeping, treating, and perceiving dogs across cultures? One hypothesis would be that the dog-human relationship is closer in societies where the dominant dog function requires intense cooperation between humans and dogs (see also Bräuer *et al.* 2020). It is also likely that there is a more positive attitude towards dogs when they have predominantly cooperative functions (i.e., shepherd or hunting dogs), resulting in more careful treatment of these dogs, than when they have predominantly non-cooperative functions (i.e., guard dogs). Moreover, in particular in western societies, sociological studies can describe the influence dogs have on societies today (i.e. Sanders 1999).

Another question is whether there are differences in dogs' cognitive skills and dog-human interactions depending on the cultural practices of the society they live in and dogs' function(s) in that society. Have human cultural differences acted as different selective pressures on dog cognition, and have they produced detectable differences in dog-human interaction? To investigate this, dogs from different cultural contexts should be tested in cognitive experiments about dog-human communication and cooperation (see above).

Finally, to better understand the contemporary dog-human relationship, it would also be important to find ways to quantify the benefit of dog keeping today. A first approach could be to attempt to quantify the

benefit of dog ownership, for example, in western societies (i.e. Cutt *et al.* 2007; Knight and Edwards 2008). By developing new techniques for measuring the benefit to humans of dogs in different contexts, as well as calculating their costs, we can assess whether the dog-human relationship is, as commonly believed, mutualistic or, as some argue, parasitic (Archer 1997).

4 Concluding remarks

We have seen how in recent years, research in comparative psychology has revealed that dogs evolved human-like skills in order to live functionally in human societies. Particularly, dogs show remarkable skills in three social-cognitive domains: communication, perspective taking, and cooperation.

We know that humans might have selected dogs to be good cooperative and communicative partners, however, there are several aspects of this process that are still unknown: When, where, and how did the process of domestication start? Why were wolves a good candidate to be domesticated? How do the results of this process look today and how does dog keeping differ across cultures?

In conclusion, although the research about dog domestication has made great leaps forward in the last 20 years, several open questions remain. These questions can be summarised under three main themes - the starting point, process, and outcomes of domestication. To answer these questions, we need an interdisciplinary approach in which scientists from archaeology, genetics, anatomy, psychology, sociology, and anthropology work together.

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References

- Amici, F. 2015. The evolution and development of human cooperation. *Interaction Studies* 16 (3): 383–418.
- Amici, F., J. Waterman, C.M. Kellermann, K. Karimullah, and K.J. Bräuer. 2019. The ability to recognize dog emotions depends on the cultural milieu in which we grow up. *Scientific Reports* 9: 16414.
- Archer, J. 1997. Why do people love their pets? *Evolution and Human Behavior* 18: 237–259.
- Ben-Dor, M., A. Gopher, I. Hershkovitz and R. Barkai. 2011. Man the Fat Hunter: The Demise of Homo erectus and the Emergence of a New Hominin Lineage in the Middle Pleistocene (ca. 400 kyr) Levant. *PLoS ONE* 6(12): e28689.

- Bhattacharjee, D., N., ND., S. Gupta, S. Sau, R. Sarkar, A. Biswas, A. Banerjee, D. Babu, D. Mehta and A. Bhadra. 2017. Free-ranging dogs show age related plasticity in their ability to follow human pointing. *PLoS ONE* 12(7): e0180643.
- Bräuer, J. 2015. I do not understand but I care: the prosocial dog. *Interaction Studies* 16(3): 341–360.
- Bräuer, J. and J. Belger. 2018. A ball is not a Kong: Odor representation and search behavior in domestic dogs (*Canis familiaris*) of different education. *Journal of Comparative Psychology* 132: 189–199.
- Bräuer, J., J. Call and M. Tomasello. 2004. Visual Perspective Taking in Dogs (*Canis familiaris*) in the Presence of Barriers. *Applied Animal Behaviour Science* 88: 299–317.
- Bräuer, J., J. Kaminski, J. Riedel, J. Call and M. Tomasello. 2006. Making inferences about the location of hidden food: Social dog, causal ape. *Journal of Comparative Psychology* 120: 38–47.
- Bräuer, J., M. Keckeisen, A. Pitsch, J. Kaminski, J. Call and M. Tomasello. 2013a. Domestic dogs conceal auditory but not visual information from others. *Animal Cognition* 16: 351–359.
- Bräuer, J., K. Schönefeld and J. Call. 2013b. When do dogs help humans? *Applied Animal Behaviour Science* 148: 138–149.
- Bräuer, J., K. Stenglein, and F. Amici. 2020. Dogs (*Canis familiaris*) and wolves (*Canis lupus*) coordinate with conspecifics in a social dilemma. *Journal of Comparative Psychology*, 134, 211–221.
- Cafazzo, S., S. Marshall-Pescini, M. Lazzaroni, Z. Virányi and F. Range. 2018. The effect of domestication on post-conflict management: wolves reconcile while dogs avoid each other. *Royal Society Open Science* 5: 171553.
- Call, J., J. Bräuer, J. Kaminski and M. Tomasello. 2003. Domestic Dogs (*Canis familiaris*) Are Sensitive to the Attentional State of Humans. *Journal of Comparative Psychology* 117: 257–263.
- Clutton-Brock, J. 1977. Man-made dogs. *Science* 197: 1340–1342.
- Coppinger, R. and L. Coppinger. 2001. *Dogs: A Startling New Understanding of Canine Origin, Behavior, and Evolution*. New York, NY: Scribner.
- Cutt, H., B. Giles-Corti, M. Knuiman and V. Burke, V. 2007. Dog ownership, health and physical activity: A critical review of the literature. *Health and Place* 13: 261–272.
- Dale, R., M. Quervel-Chaumette, L. Huber, F. Range and S. Marshall-Pescini. 2016. Task differences and prosociality: Investigating pet dogs' prosocial preferences in a token choice paradigm. *PLoS ONE* 11: e0167750.
- Dale, R., F. Range, L. Stott, K. Kotrschal and S. Marshall-Pescini. 2017. The influence of social relationship on food tolerance in wolves and dogs. *Behavioral Ecology and Sociobiology* 71: 107.
- Dalziel, D. J., B.M. Uthman, S.P. Mcgorray and R.L. Reep. 2003. Seizure-alert dogs: a review and preliminary study. *Seizure-European Journal of Epilepsy* 12: 115–120.
- Diamond, J. 1997. *Guns, Germs, and Steel: The Fates of Human Societies*. Scranton, PA: W. W. Norton.
- Feddersen-Petersen, D. U. 2000. Vocalization of European wolves (*Canis lupus lupus* L.) and various dog breeds (*Canis lupus f. fam.*). *Archiv Fuer Tierzucht*.43: 387–397.
- Frantz, L.A.F., V.E. Mullin, M. Pionnier-Capitan, O. Lebrasseur, M. Ollivier, A. Perri, A. Linderholm, V. Mattiangeli, M.D. Teasdale, E.A Dimopoulos, A. Tresset, M. Duffraisse, F. McCormick, L. Bartosiewicz, E. Gál, É.A. Nyerges, M.V. Sablin, S. Bréhard, M. Mashkour, A. Bălăşescu, B. Gillet, S. Hughes, O. Chassaing, C. Hitte, J.-D.C., Vigne, K. Dobney, C. Hänni, D.G. Bradley and G. Larson. 2016. Genomic and archaeological evidence suggest a dual origin of domestic dogs. *Science* 352: 1228–1231.
- Gácsi, M., B. Gyoöri, Z. Virányi, E. Kubinyi, F. Range, B. Belényi and Á. Miklósi. 2009a. Explaining Dog Wolf Differences in Utilizing Human Pointing Gestures: Selection for Synergistic Shifts in the Development of Some Social Skills. *PLoS ONE* 4: e6584.
- Gácsi, M., B. Gyori, A. Miklósi, Z. Virányi, E. Kubinyi, J. Topál and V. Csányi. 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.
- Gácsi, M., E. Kara, B. Belényi and Á. Miklósi. 2009b. The effect of development and individual differences in pointing comprehension of dogs. *Animal Cognition* 12: 471–479
- Gácsi, M., A. Miklósi, O., Varga, J. Topál, and V. Csányi. 2004. Are readers of our face readers of our minds? Dogs (*Canis familiaris*) show situation-dependent recognition of human's attention. *Animal Cognition* 7: 144–153.
- Galibert, F., P. Quignon, C. Hitte and C. André. 2011. Toward Understanding Dog Evolutionary and Domestication History. *Comptes Rendus Biologies* 334: 190–196.
- Gray, P. and S.M. Young. 2011. Human-Pet Dynamics in Cross-Cultural Perspective. *Anthrozoos: A Multidisciplinary Journal of The Interactions of People and Animals* 24: 17–30.
- Green, P.A., B. Van Valkenburgh, B. Pang, D. Bird and A. Curtis. 2012. Respiratory and olfactory turbinal size in canid and arctoid carnivorans. *Journal of Anatomy* 221: 609–621
- Hale, E.B. 1969. Domestication and the evolution of behavior, in E. S. E.Hafez (ed.) *The behaviour of domestic animals* 2nd edition: 22–42. London: Bailliere, Tindall and Cassell.
- Hall, N., K. Glenn, D. Smith and C. Wynne. 2015. Performance of Pugs, German Shepherds, and Greyhounds (*Canis lupus familiaris*) on an odor-

- discrimination task. *Journal of Comparative Psychology* 129: 237–246.
- Hare, B., M. Brown, C. Williamson and M. Tomasello. 2002. The domestication of social cognition in dogs. *Science* 298: 1634–1636.
- Hare, B., A. Rosati, J. Kaminski, J. Bräuer, J. Call and M. Tomasello. 2010. The Domestication Hypothesis for Dogs' Skills with Human Communication: A Response to Udell *et al.* (2008) and Wynne *et al.* (2008). *Animal Behaviour* 79: e1–e6.
- Hare, B. and M. Tomasello. 2005. Human-like social skills in dogs? *Trends in Cognitive Sciences* 9: 439–444.
- Hare, B., V. Wobber and R.W. Wrangham. 2012. The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. *Animal Behavior* 83: 573–585.
- Heberlein, M.T., D.C. Turner, and M. Manser. 2017. Dogs' (*Canis familiaris*) attention to human perception: Influence of breed groups and life experiences. *Journal of Comparative Psychology* 131: 19–29.
- Henrich, J., S.J. Haine and A. Norezavan. 2010. The weirdest people in the world? *Behavioural Brain Science* 33: 61–83.
- Janssens, L., L. Giemsch, R. Schmitz, M. Street, S. Van Dongen and P. Crombé. 2018. A new look at an old dog: Bonn-Oberkassel reconsidered. *Journal of Archaeological Science* 92: 126–138.
- Kaminski, J., J. Bräuer, J. Call and M. Tomasello. 2009a. Domestic dogs are sensitive to a human's perspective. *Behaviour* 146: 979–998.
- Kaminski, J., J. Call, and J. Fischer. 2004. Word learning in a domestic dog: Evidence for 'Fast Mapping'. *Science* 304: 1682–1683.
- Kaminski, J., J., Hynds, P. Morris, and B.M. Waller. 2017. Human attention affects facial expressions in domestic dogs. *Scientific Reports* 7: 12914.
- Kaminski, J. and S. Marshall-Pescini. 2014. *The social dog: Behaviour and cognition*. San Diego, CA: Academic Press/Elsevier.
- Kaminski, J., M., Neumann, J. Bräuer, J. Call, and M. Tomasello, 2011. Domestic Dogs Communicate to Request and Not to Inform. *Animal Behaviour* 82: 651–658.
- Kaminski, J., A. Pitsch and M. Tomasello. 2013. Dogs steal in the dark. *Animal Cognition* 16: 385–394.
- Kaminski, J., S., Tempelmann, J. Call and M. Tomasello. 2009b. Domestic dogs comprehend human communication with iconic signs. *Developmental Science* 12: 831–837.
- Kaminski, J., B.M. Waller, R. Diogo, A. Hartstone-Rose and A.M. Burrows. 2019. Evolution of facial muscle anatomy in dogs. *Proceedings of the National Academy of Sciences* 116(29): 14677–14681.
- Knight, S. and V. Edwards. 2008. In the Company of Wolves: The Physical, Social, and Psychological Benefits of Dog Ownership. *Journal of Aging and Health* 20: 437–455.
- Kundey, S.M.A., A. De Los Reyes, C. Taglang, R. Allen, S. Molina, E. Royer and R. German. 2010. Domesticated Dogs (*Canis familiaris*) React to What Others Can and Cannot Hear. *Applied Animal Behaviour Science* 126: 45–50.
- Lampe, M., J. Bräuer, J. Kaminski and Z. Virányi. 2017. The effects of domestication and ontogeny on cognition in dogs and wolves. *Scientific Reports* 7: 11690.
- Larson, G. and G. Bradley. 2014. How Much Is That in Dog Years? The Advent of Canine Population Genomics. *PLOS Genetics* 10: 1004093.
- Macpherson, K. and W. Roberts. A. 2006. Do Dogs (*Canis familiaris*) Seek Help in an Emergency? *Journal of Comparative Psychology* 120: 113–119.
- Marshall-Pescini, S., I. Besserlich, C. Kratz and F. Range, F. 2016a. Exploring Differences in Dogs' and Wolves' Preference for Risk in a Foraging Task. *Frontiers in Psychology*, 7: 1241.
- Marshall-Pescini, S., R. Dale, M. Quervel-Chaumette and F. Range. 2016b. Critical issues in experimental studies of prosociality in non-human species. *Animal Cognition* 19: 679–705.
- Marshall-Pescini, S., A. Rao, Z. Virányi and F. Range. 2017a. The role of domestication and experience in 'looking back' towards humans in an unsolvable task. *Scientific Reports* 7: 46636.
- Marshall-Pescini, S., J.F.L. Schwarz, I. Kostelnik, Z. Virányi and F. Range. 2017b. Importance of a species' socioecology: Wolves outperform dogs in a conspecific cooperation task. *Proceedings of the National Academy of Sciences* 114: 11793–11798.
- Mech, L.D. and L. Boitani, L. 2003. *Wolves: Behavior, Ecology, and Conservation*. Chicago, IL: University of Chicago Press.
- Melis, A.P. and D. Semmann. 2010. How is Human Cooperation Different? *Philosophical Transactions of the Royal Society of London B Biological Sciences* 365: 2663–2674.
- Melis, A.P. and F. Warneken. 2016. The psychology of cooperation: insights from chimpanzees and children. *Evolutionary Anthropology* 25: 297–305.
- Merola, I., E. Prato-Previde, and S. Marshall-Pescini. 2012. Dogs' Social Referencing towards Owners and Strangers. *PLoS ONE* 7(10): e47653.
- Miklósi, A. 2007. *Dog Behaviour, Evolution, and Cognition*. Oxford: Oxford University Press.
- Miklósi, A., E. Kubinyi, M. Gácsi, Z. Virányi, and V. Csányi. 2003. A simple reason for a big difference: wolves do not look back at humans but dogs do. *Current Biology* 13: 763–766.
- Miklósi, A., Polgárdi, J. Topál and Csányi, V. 2000. Intentional behavior in dog-human communication: An experimental analysis of 'showing' behaviour in the dog. *Animal Cognition* 3: 159–166.
- Miklósi, A. K. and Soproni. 2006. A comparative analysis of the animals' understanding of the human pointing gesture. *Animal Cognition* 9: 81–93.

- Mitchell, P. 2017. Disease: A Hitherto Unexplored Constraint on the Spread of Dogs (*Canis lupus familiaris*) in Pre-Columbian South America. *Journal of World Prehistory* 30: 301–349.
- Ní Leathlobhair, M., A.R. Perri, E.K. Irving-Pease, K.E. Witt, A. Linderholm, J. Haile, O. Lebrasseur, C. Ameen, J. Blick, A.R. Boyko, S. Brace, Y.N. Cortes, S.J. Crockford, A. Devault, E.A. Dimopoulos, M. Eldridge, J. Enk, S. Gopalakrishnan, K. Gori, V. Grimes, E. Guiry, A.J. Hansen, A. Hulme-Beaman, J. Johnson, A. Kitchen, A.K. Kasparov, Y.-M. Kwon, P.A. Nikolskiy, C.P. Lope, A. Manin, T. Martin, M. Meyer, K.N. Myers, M. Omura, J.-M. Rouillard, E.Y. Pavlova, P. Sciulli, M.-H.S., Sinding, A. Strakova, V.V. Ivanova, C. Widga, E. Willerslev, V.V. Pitulko, I. Barnes, M.T.P. Gilbert, K.M. Dobney, R.S. Malhi, E.P. Murchison, G. Larson and L.A.F. Frantz. 2018. The evolutionary history of dogs in the Americas. *Science* 361: 81–85.
- Ostrander, E.A., G.-D. Wang, G. Larson, B. M. Vonholdt, B. W. Davis, V. Jagannathan, C. Hitte, R.K. Wayne, Y.-P. Zhang, and D.K. Consortium. 2019. Dog10K: an international sequencing effort to advance studies of canine domestication, phenotypes and health. *National Science Review* 6: 810–824.
- Paxton, D.W. 2000. A Case for a Naturalistic Perspective. *Anthrozoös* 13: 5–8.
- Polgár, Z., M. Kinnunen, D., Újváry, Á. Miklósi, and M. Gácsi. 2016. A Test of Canine Olfactory Capacity: Comparing Various Dog Breeds and Wolves in a Natural Detection Task. *PLoS ONE* 11: e0154087.
- Pongracz, P., C. Molnar, A. Miklósi and V. Csányi. 2005. Human Listeners Are Able to Classify Dog (*Canis familiaris*) Barks Recorded in Different Situations. *Journal of Comparative Psychology* 119: 136–144.
- Prato Previde, E. and P. Valsecchi. 2014. The immaterial cord: the dog-human attachment bond, in J. Kaminski and S. Marshall-Pescini (eds) *The Social Dog*: 165–189. San Diego, CA: Academic Press/Elsevier.
- Price, E.O. 1984. Behavioral Aspects of Animal Domestication. *Quarterly Review of Biology* 59: 1–32.
- Quervel-Chaumette, M., R. Dale, S. Marshall-Pescini and F. Range. 2015. Familiarity affects other-regarding preferences in pet dogs. *Scientific Reports* 5: 18102.
- Range, F., J. Jenikejew, I. Schröder and Z. Virányi. 2014. Difference in quantity discrimination in dogs and wolves. *Frontiers in Psychology* 5: 1299.
- Range, F.Z. and Virányi. 2015. Tracking the evolutionary origins of dog-human cooperation: The ‘Canine Cooperation Hypothesis’. *Frontiers in Psychology* 5: 1582.
- Rao, A., F. Range, K. Kadletz, K. Kotrschal and S. Marshall-Pescini. 2018. Food preferences of similarly raised and kept captive dogs and wolves. *PLoS ONE* 13: e0203165.
- Riedel, J., K. Schumann, J. Kaminski, J. Call and M. Tomasello. 2008. The Early Ontogeny of Human-Dog Communication. *Animal Behaviour* 75: 1003–1014.
- Ruusila, V. and M. Pesonen. 2004. Interspecific Cooperation in Human (*Homo sapiens*) hunting: the benefits of a barking dog (*Canis familiaris*). *Annual Zoological Fennici* 41: 545–549.
- Sanders, C.R. 1999. *Understanding Dogs: living and working with canine companions*. Philadelphia, PA: Temple University Press.
- Serpell, J. 2016. *The domestic dog: Its evolution, behaviour and interactions with people*. Cambridge: Cambridge University Press.
- Shipman, P. 2017. *The Invaders: How Humans and Their Dogs Drove Neanderthals to Extinction*. Cambridge, MA: Harvard University Press.
- Thalmann, O., B. Shapiro, P. Cui, V.J. Schuenemann, S.K. Sawyer, D.L. Greenfield, M.B. Germonpré, M.V. Sablin, S. López-Giráldez, X. Domingo-Roura, H. Napierala, H.-P. Uerpmann, D.M. Loponte, A.A. Acosta, L. Giemsch, R. W. Schmitz, B. Worthington, J.E. Buikstra, A. Druzhkova, A.S. Graphodatsky, N.D. Ovodov, N. Wahlberg, A.H. Freedman, R.M. Schweizer, K.-P. Koepfli, J.A. Leonard, M. Meyer, J. Krause, S. Pääbo, R.E. Green and R.K. Wayne 2013. Complete mitochondrial genomes of ancient canids suggest a european origin of domestic dogs. *Science* 342: 871–874.
- Topál, J., M. Gácsi, A. Miklósi, Z. Virányi, E. Kubinyi, and V. Csányi. 2005. Attachment to humans: A comparative study on hand-reared wolves and differently socialized dog puppies. *Animal Behaviour* 70: 1367–1375.
- Udell, M.A.R., N.R. Dorey and C.D.L. Wynne. 2008. Wolves Outperform Dogs in Following Human Social Cues. *Animal Behaviour* 76: 1767–1773.
- Vilá, C., P. Savolainen, J.E. Maldonado, I.R. Amorim, J. Rice, R.L. Honeycutt, K.A. Crandall, J. Lundeberg and R. K. Wayne. 1997. Multiple and ancient origins of the domestic dog. *Science* 276: 1687–1689.
- Virányi, Z., J., Topál, M. Gácsi, A. Miklósi, and V. Csányi. 2004. Dogs respond appropriately to cues of humans’ attentional focus. *Behavioural Processes* 66: 161–172.
- Walker, D.B., J.C. Walker, P.J. Cavnar, J.L. Taylor, D.H. Pickel, S.B. Hall and J.C. Suarez. 2006. Naturalistic quantification of canine olfactory sensitivity. *Applied Animal Behaviour Science* 97: 241–254.
- Waller, B.M., K. Peirce, C.C. Caeiro, L. Scheider, A.M. Burrows, S. McCune and J. Kaminski. 2013. Paedomorphic Facial Expressions Give Dogs a Selective Advantage. *PLoS ONE* 8: e82686.
- Wang, G.-D., W. Zhai, H.-C. Yang, R.-X. Fan, X. Cao, L. Zhong, L. Wang, F. Liu, H. Wu, L.-G. Cheng, A.D. Poyarkov, N.A. Poyarkov Jr, S.-S. Tang, W.-M. Zhao, Y. Gao, X.-M. Lv, D. M. Irwin, P. Savolainen, C.-I. Wu and Y.-P. Zhang. 2013. The genomics of selection in dogs and the parallel evolution between dogs and humans. *Nature Communications* 4: 1860.
- Wayne, R.K. and C. Vilá, 2001. Phylogeny and origin of the domestic dog, in A. Ruvinsky and J. Sampson

- (eds) *The Genetics of the Dog*: 1–14. Wallingford: CAB International.
- Zeder, M. A. 2012. Pathways to Animal Domestication, in A.B. Damania, C.O. Qualset, P.E. Mcguire, P. Gepts, R.L. Bettinger, S.B. Brush, and T.R. Famula (eds) *Biodiversity in Agriculture: Domestication, Evolution, and Sustainability*: 227–259. Cambridge: Cambridge University Press.
- Zimen, E. 1992. *Der Hund*. Munich: Wilhelm Goldmann Verlag.