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# Human-directed sociability in the domestic dog: A Tinbergian approach

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ABSTRACT

The motivation to interact with humans is central to dogs' domestication process. This review aims to provide a curated overview of the current knowledge about dogs' human-directed sociability using Tinbergen's four questions as a guiding framework. Firstly, we explore its *evolutionary history*, discussing wolf-dog differences in the socialization period, fear response, sociability, and attachment to elucidate the effect of domestication. Secondly, we address its *ontogeny*, highlighting the importance of early life experiences, examining findings on different dog populations to discern the effect of adult life experiences, and reporting changes across the lifespan. Thirdly, we analyse the *adaptive value* of the dog-human relationship, considering the effects of human association on different dog populations. Fourthly, we elaborate on the *mechanisms* involved in the dog-human relationship, discussing underlying cognitive and genetic processes and findings on the neurophysiological effects of interacting with humans. Finally, we identify issues and remaining questions that deserve more scrutiny and suggest innovative approaches that could be explored to improve our understanding of dogs' human-directed sociability.

## 1. Introduction

The motivation to interact and affiliate with humans (i.e., human-directed sociability or social motivation) plays a central role in the domestication process of dogs. Dogs stand out among domesticated species not only for the strength and quality of the bonds they establish with their human caretakers but also for the easiness with which they form these bonds and their adaptability. They have been described as social "generalists" (Udell and Brubaker, 2016) and even claimed to possess a hypertrophied social motivation (*hypersociability hypothesis,* vonHoldt et al., 2017). A large body of research corroborates that the dog-human relationship is characterized by an attachment bond similar to that seen in human infant-parent relationships (reviewed in Payne, Bennett, and McGreevy, 2015; Rehn and Keeling, 2016). However, there are still conceptual and methodological challenges leading to disagreement among scholars and requiring a closer look. Hence, with this review, we summarize and discuss what is known about dogs' social motivation, identify issues and raise as of yet unaddressed questions that deserve more scrutiny using Tinbergen's four questions as a guiding framework (Fig. 1). By adopting a Tinbergian perspective, we provide an integrated, multi-disciplinary overview of past and current research addressing different aspects of dogs' sociability and thereby offering the reader a cohesive update of the progress in the field.

1) How did dogs' social motivation towards humans **evolve** throughout the **domestication process** (i.e., evolutionary history)?
2) How does social motivation **change over the lifespan** and what are the effects of **life experiences** on dogs' tendency to interact with humans (i.e., developmental history/ontogeny)?
3) What is the **adaptive value** of the dog-human relationship for different populations of dogs (i.e., biological function)?
4) What are the underlying **cognitive, neurophysiological and genetic processes** involved (i.e., mechanisms/immediate control or causation)?

Before tackling Tinbergen's four questions, we will briefly discuss terminology relevant to this review. The main topic of this review is dogs' human-directed sociability or social motivation, understood as their motivation to affiliate with humans, i.e., to engage in positive social interactions with them. Numerous positive human-directed behaviours (or affiliative behaviours) have been studied in dogs, but the terminology used in this context has not been consistent. Through this

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review we will generally adopt the terminology used in each respective study but, to clarify what lies behind each label, we will also mention the specific behavioural measures employed. This article covers human-directed behaviours commonly assessed in dogs, which can be a manifestation of their social motivation or sociability, such as proximity and contact-seeking behaviours and gazing. It has been suggested that, compared to wolves, dogs show a heightened motivation to seek social contact or exaggerated social responses, referred to as hypersociability (Bentosela et al., 2016; vonHoldt et al., 2017). The exchange of affiliative behaviours across repeated interactions over time leads to the formation of social bonds. One type of social bond that has gathered substantial attention in research on the dog-human relationship, and hence will also be treated in this review, is the attachment bond, which will be defined in the corresponding section.

## 2. Evolution

### 2.1. Domestication

Dogs were the first domesticated animal species, with estimations placing the starting point of the process between 15,000 and 33,000 years ago (e.g., Ovodov et al., 2011; Savolainen, 2002; Thalmann et al., 2013; Wang et al., 2016). Two main scenarios have been proposed to explain how the domestication process started. The 'commensal scavenger' or 'garbage dump hypothesis' suggests that it began as a process of self-domestication, rather than intentional selection by humans (e.g., Coppinger and Coppinger, 2001; Hare et al., 2012). In this scenario, the least aggressive or fearful individuals would have had a selection advantage over the shyer ones, since their temperament allowed them to approach humans and gain access to new food sources (Zeuner, 1967 as cited in Marshall-Pescini and Kaminski, 2014). Thus, according to this 'self-domestication' perspective, natural selection against aggression and fear would have been the basis for the first stage of wolf domestication (Hare et al., 2012). However, the plausibility of this hypothesis has been increasingly questioned based on current knowledge of ancient hunter-gatherer societies and wolf ecology and behaviour (Mech and Janssens, 2022; Serpell, 2021), and an alternative scenario has recently gained support. The 'pup/cross-species adoption' or 'pet keeping hypothesis' argues that humans may have taken a more active role already in the early stages of the domestication process, namely by adopting


**Fig. 1.** Graphical visualization of the Tinbergian approach. The key points addressed in each section of this review are presented. Photography credits (top to bottom and left to right): DanielaJakob (Pixabay), christels (Pixabay), vlaaitje (Pixabay), Hong Son (Pexels), Sarah Chai (Pexels), Dayvison de Oliveira Silva (Pexels).

young wolf pups and raising them within human families (Mech and Janssens, 2022; Serpell, 2021). In this case, humans would favour and keep the tamest and most cooperative animals, which would have been more likely to reproduce (Mech and Janssens, 2022; Serpell, 2021). What is more relevant to this review is that both scenarios would ultimately result in selection for friendlier, more sociable animals. While selection for social tolerance might have been the first step in early domestication, as the process progressed, we expect a shift towards selection for social motivation, since it was necessary for the establishment of a successful dog-human partnership. Similarly, we presume that natural selection was the main evolutionary force initially and gradually became replaced by artificial selection, which was uncontrolled and blind at first and later became systematic and deliberate (Trut et al., 2021). Therefore, no matter how the domestication process initially started, both frameworks provide evolutionary explanations for dogs' motivation to approach and interact with humans.

### 2.2. Wolf-dog differences

To study changes brought about by the domestication process researchers compare dogs to their closest wild-living relatives, grey wolves (*Canis lupus*). It should be noted that dogs are thought to derive from a population of wolves that is now extinct (Bergström et al., 2020; Frantz et al., 2016; Gojobori et al., 2024), and modern wolves might not be an accurate representation of dogs' ancestors genetically and behaviourally (Range and Marshall-Pescini, 2022). Wolf-dog comparative studies should be interpreted with this caveat in mind. Additionally, conclusions regarding the role of domestication in wolf-dog differences are not valid unless dogs and wolves are exposed to similar developmental contexts and learning opportunities (e.g. Miklósi, 2007; Range and Virányi, 2015; Udell et al., 2012). The debate regarding the relative importance of domestication and life experiences on the development of dogs' social behaviour towards humans permeates the literature (e.g., Hare et al., 2010 vs Udell et al., 2008; Hare and Tomasello, 2005 vs Miklósi and Topál, 2005; Riedel et al., 2008 vs Wynne et al., 2008). Even though wolf-dog differences certainly have an important developmental component, comparative studies on wolves and dogs demonstrate that domestication did modify dogs' social behaviour. Indeed, comparisons regarding human-directed sociability reveal differences between wolves and dogs, even when controlling for life experiences (e.g., Gácsi et al., 2005, 2009; Lazzaroni, Range, et al., 2020; Wirobski, Lazzaroni, et al., 2023). How genetic relatedness to wolves might influence dogs' human-directed social behaviour across breeds has also been investigated. It has been hypothesized that more "ancient" breeds, which are more genetically similar to wolves (Larson et al., 2012; Parker et al., 2004) and have experienced lower selective pressure, might show remnants of wolves' behavioural characteristics and be less skilled at communicating with humans (Konno et al., 2016; Tonoike et al., 2015). This hypothesis has received some support from studies finding that these breeds displayed less human-directed gazing behaviour than other breed groups (Konno et al., 2016; Tonoike et al., 2022; but see Passalacqua et al., 2011; Van Poucke et al., 2021), and in a couple of studies they had a lower score in the "attachment and attention-seeking" factor of the Canine Behavioural Assessment and Research Questionnaire (C-BARQ), which reflects the tendency to maintain proximity to the caregiver or other family members, solicit affection or attention and become agitated when the caregiver gives attention to third parties (Smith et al., 2017; Tonoike et al., 2015).

#### 2.2.1. Socialization period and fear response

Changes in the timing of early developmental processes (i.e. heterochrony, Goodwin et al., 1997), and more specifically, developmental delays that lead to the retention of juvenile traits at maturity (i.e., neoteny), are believed to be one of the underlying causes of the behavioural differences between adult wolves and dogs (Trut et al., 2004; Udell and Brubaker, 2016). These neotenic processes are thought to result not only in an increased expression of juvenile-type behaviour in adult dogs (which could include exaggerated social responses, such as prolonged gazing and greeting behaviour; Udell and Brubaker, 2016), but also in the extension of the socialization period (e.g., Wilkins et al., 2014). The socialization period is a sensitive window of time during development that is important for proper species identification and affects the choice of future social partners (e.g., Fox, 1969). This period ends when the gradual increase of fear inhibits the exploration of novelty (Scott and Fuller, 1965). The renowned Siberian farm fox experiment demonstrated that selection for tameness can delay the onset of the fear response, prolonging the socialization period (Trut et al., 2009).

While dog pups can form an interspecific bond if they are exposed to humans before 7–8 weeks of age, wolf pups need to be intensively hand-reared from as early as 2–3 weeks of age to create reliable social bonds with humans (reviewed in Miklósi, 2007; Serpell et al., 2017). Though it has been found that adult, inadequately socialized dogs and untamed wolves can be socialized to humans, this process seems to be considerably more demanding in the case of wolves (Woolpy and Ginsburg, 1967; Niebuhr et al., 1980 as cited in Serpell et al., 2017). Consistent with a delayed onset of the fear response, dogs might be socialized until 12–14 weeks of age or even longer, while wolves that haven't been socialized with humans show strong fear or avoidance of strangers by 6 weeks of age (reviewed in Miklósi, 2007; Serpell et al., 2017). However, a recent study examining object neophobia in wolves and dogs from 6 to 26 weeks of age found a loss of sensitivity toward novelty with age in dogs, rather than a shift in the appearance of the fear response (Hansen Wheat et al., 2019). In accordance with a previous study (Marshall-Pescini, Virányi, et al., 2017), no species differences in fear responses towards a novel object were detected during early development, and it was not until 18 weeks of age that these differences arose due to a progressive reduction in dogs' fearfulness (Hansen Wheat et al., 2019). While adult dogs were less neophobic than wolves in a novel object test (Moretti et al., 2015), no species differences in neophobia were found in a study that combined a foraging task with a novel object, suggesting that domestication effects might have been overshadowed by other factors in the latter study or that they are context-dependent (Jean-Joseph, 2023).

Data from the farm-fox experiment also revealed that the attenuation of the fear response was linked with profound changes in the animals' anatomy and physiology. Most prominently, the hypothalamic-pituitary-adrenal (HPA) axis appeared to play a key role. Foxes of the cohort selected for tameness had significantly smaller adrenal glands, decreased basal cortisol levels compared to the unselected controls after just 20 generations, and lower basal ACTH levels in their blood (Trut et al., 2009). Accordingly, it is often postulated that the domestication process resulted in a decrease of fear mediated by lower HPA axis (re) activity (Buttner, 2016; Ericsson et al., 2014; Künzl and Sachser, 1999). However, to our knowledge, there currently is no published study directly comparing the relative size of medulla and cortex, nor the overall macro- and microanatomy of the adrenal glands, in wolves and dogs. The research on wolf and dog HPA axis correlates has thus far focused on comparing systemic levels of cortisol. While some studies did not find differences between wolf and dog cortisol levels (McLeod et al., 1996; Seal and Mech, 1983), more recent work on enclosure-living wolves and dogs found consistently higher basal cortisol concentrations in dogs than wolves (Vasconcellos et al., 2016; Wirobski et al., 2021b) but a dampened cortisol response to potentially stressful stimuli (i.e., being separated from the pack) in dogs (Wirobski, Range, et al., 2023). In contrast to the fox experiment, studying modern wolves and dogs comes with the limitation of comparing two (sub)species with potentially different metabolic and energetic demands which likely affect the HPA axis and its output. It thus remains to be investigated which factors related to cortisol and its metabolic pathways differ between wolves and dogs and whether these differences are related to behaviour (e.g., by comparing receptor distribution in the brains of these canids). Relatedly, a study investigating diurnal activity patterns

in equally socialized and kept dogs and wolves found no species differences in overall activity level (Jean-Joseph et al., 2022). In another study, pack-living dogs were less aroused (i.e., had lower heart rate and higher heart rate variability) than wolves when resting, but not when awake and inactive (Jean-Joseph et al., 2020; but see Kortekaas and Kotrschal, 2019).

#### 2.2.2. Sociability

Conceivably, domestication not only reduced fear of humans, but also increased sociability (Zimen, 1987), particularly in regard to interspecific interactions, which could include the emergence of a preference towards humans over conspecifics (Miklósi and Topál, 2011). Frank and Frank (1982a) observed that wolf pups showed a clear preference for canine social partners over humans, while Malamute pups expressed the opposite orientation. Indeed, Gácsi et al. (2005) found that although wolf pups do show a preference for their caregiver over another individual or object in some circumstances, this bias disappears when the other individual is a canid (conspecific pup or adult dog), while this does not happen in the case of dogs. It has been suggested that wolf pups only become socialized to humans if there are no adult conspecifics present (Zimen, 1987), and that exposure to conspecifics can reverse the effect of heterospecific stimulation (Miklósi, 2007). Conversely, dogs seem to develop a preference towards humans with age, which is first directed towards their caregiver but then becomes generalized (Gácsi et al., 2005).

Wolf pups are less tractable than dog pups, at least in contexts involving access to a resource, showing more aggression (e.g., growling, biting when physically restrained or when a experimenter tries to take a ball away) and in some cases also more struggling (Gácsi et al., 2009; Ujfalussy et al., 2020). Interestingly, they also show a higher latency for eye contact and display less human-directed communicative behaviours (Gácsi et al., 2005, 2009). In a recent study, dog pups were more likely to touch both a familiar and an unfamiliar human with a piece of food nearby than wolf pups, which was interpreted as a higher social attraction towards humans in dogs (Salomons et al., 2021). In the same study, dog pups also established and maintained eye contact with a human during an unsolvable task for longer than wolf pups. Regarding adult individuals, Bentosela et al. (2016) found that dogs presented higher levels of interspecific sociability (evidenced by proximity measures to both familiar and unfamiliar humans) and gazed longer at a human's face than wolves in the presence of out-of-reach food. However, this study compared pet dogs to captive wolves, hence dogs' prolonged social responses could be partly due to different life experiences and exposure to humans (e.g., learned associations between gazing at a human and receiving food). Thus, studies comparing wolves and dogs that are raised and live in similar circumstances are essential. Results from one such study showed that wolves spent less time in contact with a familiar human than dogs and they were also less likely to actively seek out proximity of a familiar human that ignored them (Lazzaroni, Range, et al., 2020). In contrast, in a social interaction test through a fence, there was no species difference in the duration of contact with familiar and bonded human partners (Wirobski et al., 2021a; Figs. 2 and 3). Interestingly, the variance in sociability observed in wolves (Bentosela et al., 2016; Lazzaroni, Range, et al., 2020; Wirobski et al., 2021a; Fig. 3) could be the basis on which selection acted during domestication, whereas the smaller variance observed in some dog populations could imply that they have undergone strong selection for higher sociability (Lazzaroni, Range, et al., 2020; Wirobski et al., 2021a). On the other hand, another study found that wolf hybrids and dogs did not differ in sociability and aggressiveness, but diverged on playfulness and fearfulness, suggesting that selection for human-directed play behaviour might have played a relevant role in the domestication process (Hansen Wheat et al., 2018; see also Hansen Wheat and Temrin, 2020).

Yet, dogs' high tendency to initiate interspecific social interactions might not be limited to humans. Indeed, dogs easily form social bonds with other species as well, as illustrated by livestock guarding dogs and


**Fig. 2.** Dyadic social interaction test in the animal's home enclosure. Interaction test with a human partner with (A) a hand-raised, pack-living wolf, (B) a hand-raised, pack-living dog. (Reprinted from Wirobski et al., 2021a; licensed under CC-BY 4.0).

formal studies in which dog pups were reared with individuals of other species (Cairns and Werboff, 1967; Fox, 1969). The hypersociability hypothesis proposes that dogs are predisposed to heightened affiliative responses, since selective breeding favoured individuals with high social tendencies (vonHoldt et al., 2017). Selection requires heritable traits, and heritability estimates found in several studies suggest that variation in dogs' sociability towards humans has an important genetic component (Bray et al., 2021; Morrill et al., 2022; Persson et al., 2015; Sundman et al., 2016; Van Der Waaij et al., 2008; see Mechanisms section). It has been suggested that the potential genetic basis for dogs' hypersociability are structural variants in genes associated with Williams-Beuren syndrome (WBS) in humans, a neurodevelopmental disorder characterized by hypersocial behaviour (vonHoldt et al., 2017). Wolf-dog comparative studies so far seem to support that dogs show hypersocial responses towards humans. However, alternative interpretations suggest that it might not be higher social interest *per se* but rather a more deferential or submissive attitude towards humans that drives dogs to approach and interact with people whereas wolves might just choose to stay away (Lazzaroni, Range, et al., 2020). On the other hand, the effect of domestication on dogs' social responses towards other species is still severely understudied.

#### 2.2.3. Attachment

Attachment is a highly relevant concept in the study of social bonds. An attachment bond can be defined as a long-lasting affectional bond that an individual forms with another specific individual (i.e., the attachment figure; originally, the concept of attachment was applied to the bond between an infant and their mother) (Ainsworth and Bell, 1970). To be considered an attachment bond, certain operational

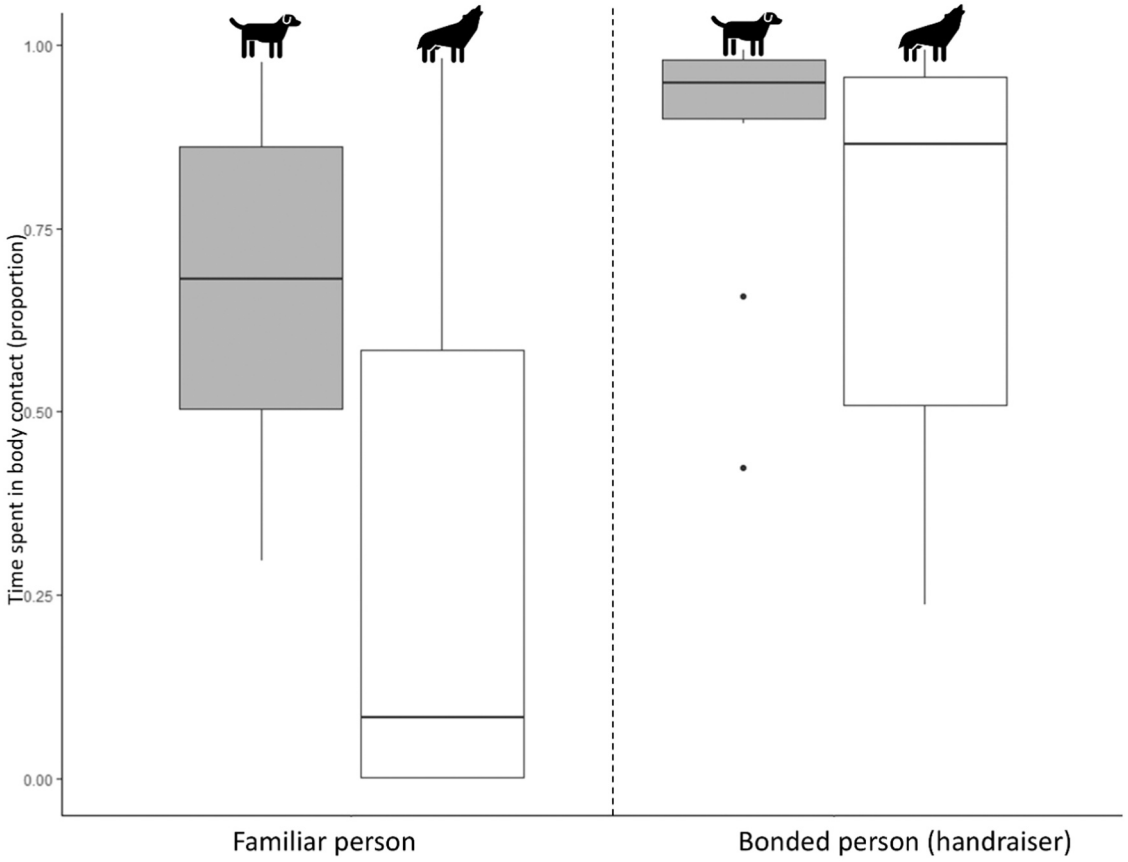


**Fig. 3.** Time spent in body contact (proportion of the total test time) as a measure of sociability during a dyadic social interaction test with a familiar (left panel) and a bonded (right panel) person. Grey boxes refer to dogs' behavioural responses, white boxes to wolves'. (Redrawn from data published in Wirobski et al., 2021a).

criteria must be met: (1) staying near to and avoiding separation from the attachment figure ("proximity maintenance"), (2) feeling discomfort when separation occurs ("separation distress"), (3) resorting to the attachment figure as a source of comfort in situations of perceived danger or anxiety ("safe haven"), and (4) using this figure as a base of security from which to explore ("secure base") (Hazan and Zeifman, 1999). Modified versions of Ainsworth's Strange Situation Procedure (ASSP), which was initially developed to study attachment relationships in human infants (Ainsworth and Bell, 1970), have been used to investigate the formation of attachment bonds in non-human species, including dogs and wolves. Of interest for this review is the application of these tests, such as the Strange Situation Procedure/Test (SST) and the Secure Base Test (SBT), in research concerning the animal-human caregiver relationship. It should be noted that this methodology has been evolving to address concerns that have been raised as research on this area expanded (for a review and analysis of dog-human attachment methodology see Udell et al., 2021).

Topál et al. (1998) were the first to adapt the ASSP to analyse the bond between pet dogs and their caregivers. Later, when comparing dog and wolf pups extensively socialized with humans, Topál et al. (2005) found that, in contrast to dogs, 16-weeks-old wolves did not show a pattern of attachment towards the caregiver. This led the authors to conclude that domestication had a substantial effect on the emergence of the dog-human bond. However, later studies showed that wolves, even at 6 months of age, display attachment-like behaviours, including preferential proximity seeking, contact and greeting of a human caregiver or raiser over other humans (Hall et al., 2015; Ujfalussy et al., 2017). Since these tests did not cover the dependency aspect of attachment (i.e., secure base and safe haven effects), these results can be interpreted as simply reflecting distinctive affiliation and affinity towards the caregivers that persists during adulthood. Nevertheless, more recent studies have demonstrated that hand-raisers can buffer stress responses in 5–7-week-old wolf pups (Cimarelli et al., 2024), that wolves display attachment behaviours towards human caregivers as late as 23 weeks of age (i.e., between 5 and 6 months of age) (Hansen Wheat et al., 2020), and that adult wolves react similarly to dogs when separated from their handler compared to an unfamiliar human, showing signs of separation distress and contact seeking behaviour, as well as possibly using their handler as a secure base (Lenkei et al., 2020). Taken together, these findings suggest that rather than providing dogs with the ability to form attachments to humans, domestication could have changed the ease with which these bonds are formed and the conditions that elicit attachment behaviours (Hall et al., 2015; see also Cimarelli et al., 2024) or the way these behaviours are expressed. The capacity to form these interspecific bonds might originate from the ability to form social bonds with pack members, which was then redirected to humans through domestication (Lenkei et al., 2020; see also Cimarelli et al., 2021).

### 2.3. Conclusion

All in all, the domestication process resulted in fundamental changes in the basic features of the socialization process: fear and sociability (Zimen, 1987). During the first stages of domestication, dogs probably experienced a selection for reduced fear of humans (Hare et al., 2012), which led to changes in the ontogeny of the fear response, delaying its onset (Trut et al., 2009) and/or initiating a progressive reduction with age (Hansen Wheat et al., 2019). The decreased fear would then allow dogs' social tendencies to develop without constraints. At the same time, these social tendencies were also transformed during domestication, apparently being intensified and resulting in the characteristic hypersociability of dogs (vonHoldt et al., 2017). Alternatively, domestication could have increased dogs' deferential behaviour and submissiveness

towards humans resulting in more agreeable and compliant social partners (Range et al., 2019; Wynne, 2021). In any case, from evidence presented in this first section we can conclude that dogs' motivation to interact with humans has been shaped by the domestication process, as evidenced by the presence of wolf-dog differences in human-directed sociability even when controlling for life experiences (Lazzaroni, Range, et al., 2020).

## 3. Development

Even if domestication has given dogs a genetic predisposition to form interspecific social bonds (Persson et al., 2018; vonHoldt et al., 2017), the environment in which each individual develops plays a major role in determining which bonds will actually be created and how easily this takes place. In other words, although dogs may have hypersocial tendencies due to the domestication process, life experiences determine whether and how these tendencies are expressed. In this section we will examine how dogs' motivation to interact with humans is shaped by life experiences and how it changes across the lifespan.

### 3.1. Early life experiences

Early life experiences are crucial for the establishment of social relationships with other individuals. The amount of maternal care received has been shown to affect the expression of pups' social behaviour towards humans, with individuals that received more maternal care showing a higher interest in an unfamiliar person than those that received less (Guardini et al., 2017, but see Guardini et al., 2016), and these effects might persist until adulthood (Foyer et al., 2016). Importantly, although we will address this issue in general terms, breed-specific and individual differences exist with respect to characteristics of the socialization process (e.g. Morrow et al., 2015; Scott and Fuller, 1965).

The socialization period, which is generally accepted to extend from the 3rd to the 12th-14th week of life in dogs (Scott and Fuller, 1965), determines the selection and acceptance of future social partners (e.g., Fox, 1969). In consequence, if puppies are separated from their littermates and hand-raised by humans, they will form their strongest bonds with humans, while if contact with humans is delayed until after the socialization period, these bonds will be relatively weak (Scott and Fuller, 1965). In fact, if dog pups grow up isolated from humans, they show a preference towards conspecifics and they can be extremely fearful of human beings (Freedman et al., 1961; Scott and Fuller, 1965). This would be the case of populations of feral dogs (Miklósi, 2007), as we will comment below. High sensitivity during the socialization period facilitates the formation of strong social relationships (Scott and Fuller, 1965). Successful socialization of puppies can be achieved with only two contact periods of 20 minutes per week (Fuller, 1961 as cited by Scott and Fuller, 1965), and even when the human partner remains completely passive during daily contact sessions (Stanley and Elliot, 1962).

### 3.2. Adult life experiences and social environment

Besides the importance of early life experiences, dogs' behaviour towards humans is shaped by their experiences as adults and the role that humans play in their environment. For example, human-oriented gazing behaviour, particularly during problem-solving, is affected by ontogenetic factors (reviewed in Cavalli et al., 2018), including the relationship with the caregiver (Topál et al., 1997), living conditions (D'Aniello and Scandurra, 2016; Scandurra et al., 2015; Wallner Werneck Mendes et al., 2021), prior training (e.g., Carballo, Cavalli, Gácsi, et al., 2020; Marshall-Pescini et al., 2008) and previous experiences with specific humans (Carballo, Cavalli, Martínez, et al., 2020). Research on different populations of dogs can be helpful in determining the effect of life experiences and social environment on their motivation to interact with humans. Although working dogs could be informative in this regard (e.g., Lazarowski et al., 2020; Mariti et al., 2013), selective breeding for particular roles can be a confounding factor, so we focus on studies of shelter and free-ranging dog populations.

#### 3.2.1. Shelter dogs

Dogs living in shelters typically encounter an environment that provides limited opportunities for close social contact. Regardless of this relative social deprivation, shelter dogs retain the ability to form new bonds with humans. Indeed, only 10 minutes of handling on three consecutive days was enough to elicit attachment-like behaviours in adult shelter dogs towards a previously unfamiliar person (Gácsi et al., 2001). However, the attachment style of shelter dogs, which have presumably experienced abandonment and bond disruption, might differ from that of pet dogs. Thielke and Udell (2020) found that attachment bonds of shelter dogs towards their temporary caregivers are more likely to be insecure compared to pet dog-owner bonds. Moreover, although dogs adopted from shelters are able to create strong bonds with their new caregiver, there are some differences in attachment-related behaviours when compared with dogs living in the same household since puppyhood that might imply a less secure bond in former shelter dogs and/or differences in how these dogs react to unfamiliar stimuli, including strangers (Cimarelli, Schindlbauer, et al., 2021; Prato-Previde et al., 2003; Prato-Previde and Valsecchi, 2007, 2014).

The easiness with which shelter dogs formed new bonds led to the proposal that limited social contact might make dogs more responsive towards humans (Gácsi et al., 2001), paralleling symptoms of disinhibited social engagement disorder (DSED) observed in children who experienced social neglect or institutional rearing. DSED (previously considered an attachment disorder, termed "disinhibited attachment") is characterized, among other aspects, by an excessive friendliness towards strangers (Miron and Zeanah, 2017; Prato-Previde and Valsecchi, 2014; Thielke and Udell, 2020). This hypersocial behaviour is reminiscent of WBS, but in DSED it is presumed to be a consequence of insufficient care rather than a genetic disorder (Miron and Zeanah, 2017). High sociability and social flexibility could be adaptive in the shelter environment, particularly when competition for human attention is high (Prato-Previde and Valsecchi, 2014; Thielke and Udell, 2020). Research with human infants suggests that a lack of checking in with the attachment figure in anxiety-provoking situations and limited discrimination of adults based on their familiarity are key features of disinhibited attachment (Rutter et al., 2007). Accordingly, Thielke and Udell (2020) interpreted reduced proximity seeking with a familiar person after separation in an unfamiliar room (i.e., a potentially stressful situation), and increased proximity seeking with an unfamiliar human when a familiar person was also present as indicative of disinhibited attachment in dogs. However, the validity of these behaviours as measures of disinhibited attachment is unclear, and no comparison with pet dogs was made.

So far, studies comparing shelter and pet dogs (also reviewed in Duranton and Gaunet, 2016) have provided mixed evidence for the hypothesis that poor social environments might boost social motivation or result in social disinhibition. When presented with an unfamiliar human in an enclosure, shelter dogs (SD) spent less time near the door overall, and more time near the passive human than pet dogs (PD) tested in a room within their homes, but the groups did not differ in their frequency of initiation of physical contact (Barrera et al., 2010). Given that standing near the door when left alone or with a stranger in a novel environment is considered an attachment response (i.e., an attempt to reunite with the attachment figure that is absent), the fact that SD stood near the door less often than PD might actually imply a lack of attachment bond towards their caregivers. In humans, the relationship between attachment and DSED is not completely clear (Lyons-Ruth, 2015; Miron and Zeanah, 2017). Conversely, Shin and Shin (2017) did not find any significant difference in sociability between PD and SD in terms of proximity to and physical contact with an unfamiliar human. Former SD

spent less time in proximity to the experimenter than dogs that have lived with the same family since puppyhood (labelled "constant family dogs"), and less time with a stranger than their caregiver, but this difference was not present in constant family dogs (Cimarelli, Schindlbauer, et al., 2021). Moreover, contrary to one of the core behavioural features of DSED (Miron and Zeanah, 2017), current and former shelter dogs show wariness when confronted with a stranger, and to a higher degree than pet dogs and constant family dogs respectively (Barrera et al., 2010; Cimarelli, Schindlbauer, et al., 2021). Still, when given a choice between a human that provided food and one that provided petting, SD were the group that showed the highest level of preference for the latter, which suggests that social contact might constitute a stronger reward for them than for owned dogs (Feuerbacher and Wynne, 2014).

Investigation of differences between PD and SD in human-directed gazing behaviour has provided mixed findings as well. Although gazing serves different functions depending on the context, it can be a proxy for social motivation. Previously reinforced gazing behaviour is more resistant to extinction in PD than in SD, which can be interpreted as higher persistence to communicate in PD compared to SD, potentially due to increased learning opportunities (Barrera et al., 2011). In problem-solving contexts, Udell (2015) found no differences between PD and SD in gazing at a human. In another study, SD remained in proximity and gazed at the experimenter for longer than PD when presented with an empty apparatus from which they had previously been able to obtain food rewards, which was considered an indication of higher social motivation, since SD opted to seek human interaction rather than persist in searching for food in the apparatus (Barrera et al., 2015). In contrast, Wallner Werneck Mendes et al. (2021) and Gould et al. (2022) found shorter gaze durations in an unsolvable task in SD compared to PD and dogs living in a home for at least a year, respectively. These latter results do not support the hypothesis that SD's restricted social contact with humans boosts their social motivation, at least in terms of engagement in human-directed communicative behaviours, and rather suggest that a higher degree of interaction with humans increases these behaviours.

Importantly, there are some limitations when testing SD, such as the fact that many of these dogs may have probably experienced significant trauma throughout their life which can affect their social behaviour later in life (Buttner and Strasser, 2022). Further, the stressful nature of the shelter environment and a habitual lack of information about their life history should be considered when interpreting the results of these studies.

#### 3.2.2. *Free-ranging dogs*

Free-ranging dogs (FRD) are a particularly interesting population to study since they may not only have positive interactions with humans, but also frequent negative experiences, making their relationship with humans more complex (Paul et al., 2016; Sen Majumder et al., 2016). According to Miklósi (2007), we can differentiate between feral dogs, which have not been socialized, usually live far from human settlements and therefore have no individualized contact with humans; and stray or village dogs, that have been socialized to some extent and thus can establish social relationships with humans. Given that feral dogs show a strong and continuous avoidance of humans (Boitani and Ciucci, 1995), presumably the majority, if not all dogs that have been tested in the published literature, belong to this second category of FRD. It should be noted that some FRD populations have been found to be genetically distinct from pure and mixed-breed dogs (Boyko et al., 2009; Pilot et al., 2015), hence it is likely that not only developmental, but also genetic factors contribute to behavioural differences between FRD and other dog populations.

On the one hand, some studies demonstrate that FRD are predominantly timid and prefer to avoid contact with humans, despite being positively reinforced through food or social rewards (Bhattacharjee, Sau, et al., 2017; Bhattacharjee et al., 2020; Brubaker et al., 2019; Ortolani et al., 2009). On the other hand, it has been found that FRD express a strong interest to approach and establish contact with humans, even surpassing pet dogs in some circumstances (Lazzaroni, Range, et al., 2020). The location and circumstances of each population of FRD, such as food abundance and the cultural acceptance of FRD in that area, clearly play a major role in the attitude and behaviour of dogs towards humans.

Evidence in this regard comes from a recent study comparing FRD living in zones with differing human flux, which highlighted the association between degree of exposure to humans (i.e., level of socialization with humans) and the quality of interactions with them (i.e., life experiences) and free-ranging dogs' sociability levels (Bhattacharjee et al., 2021). Dogs living in zones with a low human flux were the least sociable, showing minimal tendency to approach a stranger even after being offered a food reward, and displaying more anxious behaviours. The authors proposed a lack of socialization as explanation for this less sociable and more wary behaviour, though, as the study is correlational, it is also possible that the least sociable dogs moved to these zones to avoid humans as much as possible. In contrast, dogs from intermediate flux zones were highly sociable, approaching the stranger during the initial phase in which the human only vocalized positively. A more cautious response during the vocalization phase was observed in dogs from high flux zones, which were more willing to get closer after provision of food. Although the ample exposure to humans in dogs from high human flux areas enables them to experience higher degrees of socialization, risks associated with human interaction are higher too. To avoid potential conflict, it thus becomes essential for these dogs to quickly and accurately assess humans' attitudes before approaching (Bhattacharjee et al., 2021). The fact that in the same study people from intermediate flux zones had relatively more tolerant attitudes towards FRD than those from the other zones supports this interpretation to some degree.

Remarkably, even if immediate social reward is not effective in reducing their avoidance of humans, in the long-term, social contact can have a strong effect on the formation of free-ranging dogs' trust in human beings (Bhattacharjee, Sau, et al., 2017). Simply having a human in sight frequently during the socialization period might suffice to create a primary social relationship (Scott and Fuller, 1965). Interestingly, FRD have been shown to preferentially den in proximity to humans (Sen Majumder et al., 2016). This implies that, in some circumstances, the level of exposure to humans experienced by FRD pups during their early development might be enough for some socialization to occur, and to spark dogs' motivation to interact with human beings. Moreover, dog mothers appear to favour begging from humans over direct scavenging as their main method for obtaining food resources (Sen Majumder et al., 2016). FRD also display human-directed behaviours which might denote help-seeking (but see Lazzaroni, Marshall-Pescini, et al., 2020 for an alternative interpretation) when they face an unfamiliar task in which they can obtain food, even if the human is a stranger (Bhattacharjee, Dasgupta, et al., 2017). However, PD looked longer at a human when presented with an unsolvable task, which could be due to a stronger attraction toward human beings compared to FRD or due to past reinforcement history (Lazzaroni, Marshall-Pescini, et al., 2020; Figs. 4 and 5; but see Brubaker et al., 2017). In line with this, in a food provisioning paradigm, PD and SD spent more time in proximity to the unfamiliar experimenter and gazed longer at both an attentive and an inattentive human than FRD (Brubaker et al., 2019). In this study, only FRD gazed significantly less at the inattentive human, thus the authors proposed that FRD's gazing behaviour might be linked to the likelihood of obtaining food, while for PD and SD gazing might be intrinsically rewarding.

### 3.3. *Changes across the lifespan*

Sociability is not only influenced by early life experiences and the characteristics of the environment, but it also changes across the dog's


**Fig. 4.** Test conditions presented to the dogs: social (a human present); dummy (a dummy human present); object (a big cardboard present); alone (the dog is alone). A, B, and D represent free-ranging dogs, C shows a pet dog during testing. (Reprinted from Lazzaroni, Marshall-Pescini et al., 2020; licensed under CC-BY 4.0).

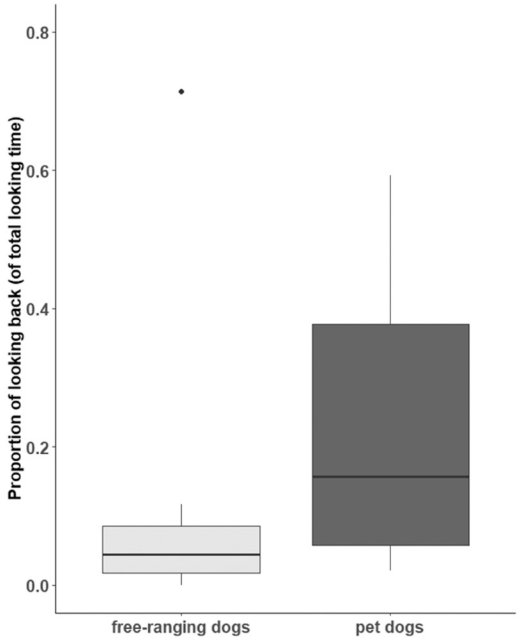


**Fig. 5.** Time spent looking back (i.e., turning head towards the experimenter) as a proportion of time spent looking up (i.e., head raised after interaction with bowl) in the social condition for free-ranging dogs (light grey, left) and pet dogs (dark grey, right). (Plot redrawn from Lazzaroni, Marshall-Pescini et al., 2020; licensed under CC-BY 4.0).

lifespan. A marked increase in behaviours related to human-directed communication and social motivation was observed from early ontogeny to young adulthood in a population of candidate assistance dogs (Bray et al., 2020). Specifically, from approximately 9 weeks to 21 months, time spent looking at a human that spoke using dog-directed speech, and in the context of an unsolvable task, significantly increased. Several studies, mostly questionnaire-based, have reported a decline with age in pet dogs' sociability (Wahlgren and Lester, 2003) and factors/facets containing items related to human-directed social behaviours, such as boldness (Kubinyi et al., 2009; Starling et al., 2013b), activity/excitability (Chopik and Weaver, 2019; Wallis et al., 2020), friendliness/aggressiveness (Bennett and Rohlf, 2007), extraversion, companionability and playfulness (Henriksson, 2016). Recently, Chapagain et al. (2020) found a linear decline of sociability and boldness with increasing age in pet dogs. The sociability component included variables such as playing with a stranger and the caregiver and remaining in proximity to the caregiver, while the boldness component included variables such as greeting a stranger. On the other hand, there is evidence that gazing behaviour during problem solving increases with age, which is probably related to learning of this response during daily life (reviewed in Cavalli et al., 2018).

A decrease in social interactions is expected as a potential consequence of sensory impairments, painful pathologies or cognitive decline in elderly dogs. Different cognitive functions, such as attention, suffer changes with aging (Chapagain et al., 2017; Wallis et al., 2014), that in turn impact the ability of dogs to engage in social interactions. Cognitive dysfunction syndrome (CDS) is a neurodegenerative disorder affecting aged dogs that includes alterations in social interactions among its classic clinical signs (Landsberg et al., 2012). These changes in social interactions comprise decreased interest in petting, avoiding contact, decreased greeting behaviour and altered relationships with people and other pets (e.g., being less sociable or becoming aggressive) (Landsberg et al., 2012). Research on the effect of age and severity of CDS on dogs' social responsiveness found that young dogs ($\leq$ 4 years) are more responsive to social stimuli and isolation than aged dogs ($\geq$ 9 years), as is the case for unimpaired aged dogs compared to dogs with CDS (Rosado et al., 2012a, 2012b; Siwak et al., 2001). Therefore, dogs' motivation to interact with humans seems to decrease, not only as a consequence of CDS, but also as part of the normal aging process. Indeed, Starling et al. (2013b) remark that, interestingly, apart from the more evident changes taking place in geriatric dogs, which could be due to different pathologies, there is a gradual reduction in boldness across the lifespan. The authors suggested that this reduction in boldness with age might be due to a cumulative effect of experiences, which might lead to a natural decline in interest for exploration of the environment

resulting in aloof or shy behaviour, such as a lower tendency to approach strangers or to engage in social interactions. The hypothesis that older animals might experience a type of desensitization process over the lifespan is supported by the finding that unimpaired aged animals still showed appropriate social responses, but these were attenuated compared to those of younger individuals (Siwak et al., 2001). Furthermore, if the accumulated experiences are aversive, it might also culminate in a decrease in the frequency of behaviours positively related to boldness, such as playful and sociable behaviours (Starling et al., 2013b). Parallel changes have been observed in humans, with cross-cultural studies showing a decline with age in the Extraversion factor of the Five Factor Model of personality (Costa et al., 2019), which could suggest that personality changes across the lifespan are the result of a biological process that is shared across dogs and humans (and potentially other species). On the other hand, although an overall decrease in sociability across age has also been found in humans, contrary to findings in dogs, it was followed by an upward trend in older adulthood (Brook and Schmidt, 2020).

### 3.4. Conclusion

To sum up, in this section we have highlighted the importance of ontogenetic experiences in shaping dogs' social motivation to interact with humans. Early life experiences are fundamental for the acceptance of humans as social partners, though limited exposure to humans might be enough, likely as a consequence of the domestication process. Still, dogs need to flexibly adapt their social responses based on their experiences and on the role humans play in their particular environment. Research on different populations of dogs can be informative in this regard. In the case of shelter dogs, it has been hypothesized that limited social contact might increase their social motivation, but evidence is mixed so far. There is suggestive evidence that the attachment bonds that dogs adopted from shelters form with their caregivers differ from those of dogs living in the same household since puppyhood. However, an important limitation of testing SD is that their life history is often unknown, and there is now research showing that, even when residing in the same shelter environment, having experienced extreme early life deficiencies alters social behaviours. In the case of free-ranging dogs, it has been proposed that in their interactions with humans they might be primarily food oriented rather than socially motivated. It should be noted that not only lifetime experiences, but also genetic factors might explain behavioural differences between FRD and other dog populations. Comparison of different FRD populations supports that there is an association between their sociability levels and both the degree of exposure to humans (i.e., level of socialization with humans) and the quality of interactions with them (i.e., life experiences). As we will discuss in the next section, there is a cost-benefit ratio in the dog-human relationship, which presumably causes adjustments in dogs' interspecific social motivation. Finally, there is a decrease in dogs' social motivation with age, which is probably related to a natural decline in interest for exploration or a process of desensitization to social stimuli across the lifespan but can also be a consequence of cognitive dysfunction in pathological aging.

## 4. Adaptive value

An important aspect to consider when studying dogs' social motivation to interact with humans is how this interspecific association can be beneficial (or harmful) to dogs and how it may increase (or decrease) their fitness. In this section we will explore the adaptive value and the cost-benefit trade-off of dogs' association with humans for different dog populations. Although the term 'fitness' specifically refers to survival and reproduction, we will also review how the different types of relationships humans establish with dogs affect canine welfare more generally.

From an ecological perspective, three main forms have been distinguished in the dog-human relationship: (1) competition/parasitism, (2) commensalism, and (3) mutualism (Coppinger and Coppinger, 2001; Miklósi and Topál, 2013). It is assumed that it was at the final stage of the domestication process when a mutualistic relationship emerged between humans and dogs, and nowadays we can find the three types of relationships depending on ecological and cultural factors (Miklósi and Topál, 2013). However, in this classification what differentiates the types of relationships is whether humans are harmed, unaffected or benefit from the association with dogs, and it assumes that this relationship is always advantageous for dogs. In this review, we are concerned with dogs' point of view, that is, we will focus on the benefits dogs obtain from, but equally important, on the costs they incur as a consequence of their interactions with humans. While dogs as we know them today would not exist without humans, and the human side of this partnership is essential to understand the domestication process and why dogs are the way they are, an analysis of how humans' fitness has been affected by their partnership with dogs during their evolutionary history is an extensive topic that is beyond the scope of this review. Obviously, the human perspective will also be relevant insofar as the cost-benefit trade-off of their relationship with dogs determines the treatment they are given. Dogs perform many different roles in human societies and their fitness and welfare are closely related to their function for humans (e.g., Chira et al., 2023). Although we will mostly speak in general terms, attitudes towards dogs are also influenced by culture (Serpell, 2017).

### 4.1. Free-ranging dogs

The majority of the global dog population is comprised of free-ranging dogs (FRD) (Hughes and Macdonald, 2013; Lord et al., 2013), representing a genetically distinct group compared to breed dogs (Pilot et al., 2015). FRD themselves are a heterogenous category that has been classified in multiple ways (e.g., Boitani and Ciucci, 1995; Bonanni and Cafazzo, 2014; Macdonald and Carr, 2017; Miklósi, 2007; Vanak and Gompper, 2009a). They vary widely in their degree of association with humans, since this category may include pets not confined or abandoned by their caregivers, lost or escaped dogs, as well as non-socialized dogs born without human care (Boitani and Ciucci, 1995; Bonanni and Cafazzo, 2014). Importantly, FRD are subject to natural selection processes and show genetic adaptations to their environment (e.g., high altitude, Wang et al., 2014).

Association with humans can have clear benefits for FRD. Some FRD populations mostly rely on food sources provided by humans, either through direct feeding or indirectly through scavenging (Bonanni and Cafazzo, 2014; Coppinger and Coppinger, 2001; Daniels and Bekoff, 1989; Macdonald and Carr, 2017; Ortolani et al., 2009; Sen Majumder et al., 2016; Vanak and Gompper, 2009b), and pregnant females have been shown to selectively choose dens close to sites of high human activity (Sen Majumder et al., 2016). Moreover, FRD can use humans as a source of information when making foraging choices, as shown in a study in which dogs matched the choice of an unfamiliar human when presented with two novel food-delivering boxes (Cimarelli et al., 2023, Figs. 6 and 7).

FRD often suffer from poor nutrition, which suggests that in some cases dogs are dependent upon direct provisioning by people to maintain an adequate health status (Morters et al., 2014). In fact, some authors suggest that the majority of dogs are in an obligatory symbiotic relationship with humans (Coppinger and Coppinger, 2001; Ortolani et al., 2009). Actually, FRD's diets probably depend on their location and ranging behaviour, as it has been observed that the farther they move into natural areas, the more they rely on wild-caught, non-anthropogenic food (Vanak and Gompper, 2009a). Dogs categorized as "feral" are completely independent of so-called human-derived materials, which include human food refuse, crops and livestock, as well as direct feeding (Vanak and Gompper, 2009a). Thus, the level of dependence on human provisions varies with each population. In addition,

**Fig. 6.** Equipment and set-up used in the study. Two boxes were placed 2 m away from each other, at ~10 m from a subject. In the figure, the unfamiliar human kneels and pretends to eat from 1 of the 2 boxes for 30 s (Demonstration group). (Reprinted from Cimarelli et al., 2023, licensed under CC-BY 4.0).

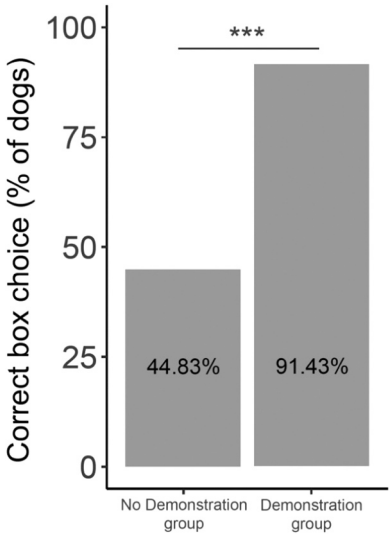


**Fig. 7.** Percentage of dogs approaching the correct box (i.e., box approached by the experimenter in the Demonstration group, randomly chosen yellow box in the No Demonstration group) as first in the 2 groups. ***P<0.001. (Reprinted from Cimarelli et al., 2023, licensed under CC-BY 4.0).

populations of FRD have elevated rates of pup/juvenile mortality (Butler and Bingham, 2000; Pal, 2001; Paul et al., 2016), and in some cases might not be reproductively self-sustaining, but depend upon an influx of co-optable individuals (Boitani and Ciucci, 1995). It has been reported that dogs that do not have a "referral household" have the lowest rates of reproduction and pup survival (Jackman and Rowan, 2007).

On the other hand, humans can also constitute a considerable threat for the FRD population. Humans may kill entire litters and selectively cull females (Macdonald and Carr, 2017). A study conducted in India estimated that 63 % of early life mortality in FRD was human-induced (including poisoning, beating, malnutrition, road accidents and being taken away from the population) (Paul et al., 2016; see also Pal, 2001). In some parts of the world, dogs are shunned, maltreated and killed due to their status as potential carriers of zoonotic diseases (Dalla Villa et al., 2010; Majumder et al., 2014). Additionally, overpopulation of FRD is problematic not only for human populations, but also wildlife species (e.g., see Young et al., 2011 for a review), and some dog-control programmes incorporate lethal methods (Dalla Villa et al., 2010).

Overall, many populations of FRD exhibit extremely poor welfare levels and high rates of mortality, given that they suffer from diseases, and are continuously at risk of starvation, malnutrition and dehydration (see Jackman and Rowan, 2007 for a review). As discussed above, dogs' degree of association with humans and human's attitudes towards dogs are important mediators of FRD's fitness and welfare. However, whether benefits derived from approaching humans (which is presumably linked to sociability) are enough to impact adaptation and welfare at the population level requires large-scale quantification of costs and benefits comparing FRD populations that vary in their degrees of association with humans. In the case of owned dogs, those that are allowed to roam freely have a higher risk of contracting diseases and being exposed to fights and are less likely to receive veterinary care than those that are restricted or kept in the house (Jackman and Rowan, 2007). To conclude, while associating with humans may not entirely mitigate the high rates of malnutrition, disease, and mortality in FRD, it nonetheless seems to represent an adaptive strategy that has allowed some FRD populations to persist despite challenging conditions. In the next subsection we will focus on owned dogs that are not free-roaming and will explore how humans impact their reproduction, health and welfare.

### 4.2. *Owned dogs*

#### 4.2.1. *Breeding*

How do humans affect the survival and reproduction of the dogs they own? Regarding reproduction, as with other domestic animals, humans are typically in control of whether their dogs procreate, who they mate with, when, and for what purpose. Dawson et al. (2019) distinguished three main breeder groups: (1) commercial breeders, (2) hobby breeders and (3) the general public. Though they recognize that these categories are not exhaustive or mutually exclusive, they propose some defining characteristics for each group.

Generally, the main goal of commercial breeders is gaining economic profit, and they frequently breed dogs in large-scale facilities specifically to supply the pet market (Dawson et al., 2019). Facilities with intensive dog breeding have received different names, such as "puppy farms/-mills" or "commercial breeding establishments" (Wauthier et al., 2018). In these facilities, dogs are often bred intensively neglecting genetic, prenatal and developmental factors that are fundamental for the pups' physical and behavioural health, and can lead to long-term adverse effects (Wauthier et al., 2018). There is evidence that dogs acquired from pet stores and/or bred in high-volume commercial breeding establishments have more behavioural and health issues than dogs from other sources (McMillan, 2017; Wauthier et al., 2018). Given that dogs bred in these facilities are more likely to present behavioural problems, and that undesirable behaviours are one of the most common reasons for dog relinquishment (e.g., Jensen et al., 2020; Patronek et al., 1996; but see Patronek et al., 2022 for a critical review), intensive breeding might worsen the situation of overcrowding in shelters by supplying dogs that are not suitable as companions. Importantly, this can result in the death of an elevated number of animals, since dogs that are not adopted are often euthanised (e.g., Arbe Montoya et al., 2017; Bartlett et al., 2005; Hubrecht et al., 2017).

Hobby breeders are usually members of kennel clubs or similar groups that aim to "improve the breed" by following the written standards closely (Dawson et al., 2019). This goal, however, has led to the appearance of major health problems in certain breeds and a reduced lifespan as a consequence of inbreeding and selection based solely on aesthetic criteria (Asher et al., 2009; Collins et al., 2011; Hubrecht et al., 2017; Rooney and Sargan, 2010; Summers et al., 2010; Yordy et al., 2020). Decreased longevity has been found in pure breed dogs in comparison with mixed breed dogs in various studies (Inoue et al., 2018; O'Neill et al., 2013; Patronek et al., 1997; Proschowsky et al., 2003; Wallis et al., 2018, but see McMillan et al., 2024; Urfer et al., 2020). Furthermore, inbreeding in dogs can reduce fecundity (Chu et al., 2019),

litter size and longevity (Leroy et al., 2015). Some breeds have an increased risk of dystocia or other periparturient diseases and often need veterinary assistance to give birth (O'Neill et al., 2017). Thus, humans not only control reproduction of the domestic dog, but they often use strategies that have detrimental impacts on dogs' biological fitness.

The third group of dog breeders distinguished by Dawson et al. (2019) is the general public. It is important to note that these "breeders" might be less likely to consider fundamental factors for optimal puppy development, such as testing for genetic disorders or even assessing if their dog is suitable as a pet and therefore if it is advisable to let them reproduce (Dawson et al., 2019). In fact, in many countries responsible dog ownership is linked to the practice of neutering. Ironically, widespread neutering might imply that many dogs that possess good qualities to be a companion are excluded from the gene pool (see Dawson et al., 2019 for a review). Furthermore, although neutering might help to control dog population size, it is likely that most pet dogs in Europe and North America are sufficiently controlled to largely prevent unwanted reproduction (Palmer et al., 2012). In addition, even if neutering can be beneficial for individual dogs as it reduces or eliminates the risk for certain pathologies, recently attention has been drawn to possible negative associations between gonadectomy and health (see Oberbauer et al., 2019 for a review). Therefore, routine neutering raises ethical concerns, and it is now recommended that decisions on neutering are taken on a case-by-case basis, considering the lifestyle and circumstances of each dog (Hart et al., 2024; Palmer et al., 2012).

#### 4.2.2. *Types of dog-owner relationships*

There are several ways in which owned dogs' health and welfare can be compromised, which depends, among others, on the relationship with the owner[1] and the role the dog fulfils. Indeed, in a global sample the function of the dog predicted how they were treated (Chira et al., 2023). Here we focus on WEIRD societies and two broad categories of owned dogs: working and pet dogs.

*4.2.2.1. Working dogs.* Working dogs perform a wide variety of roles in our society and there are huge differences regarding the breeding, rearing, housing, training and assessment procedures used in each sector. Selection of working dogs varies with the activities the dogs must perform and with the different agencies involved (Burghardt, 2003; Rooney et al., 2016). For example, while large assistance dog agencies often breed their own dogs, most military dog programs purchase adult dogs from different breeders (Rooney et al., 2016), and in some cases working dogs are even recruited from the shelter dog population (Weiss and Greenberg, 1997). As we have previously discussed, certain breeding practices can result in predisposition to various disorders in different breeds.

Working dogs must be raised and housed in appropriate environments (Rooney et al., 2009). Indeed, these dogs often encounter a high number of stressful stimuli in their working environments, which makes it extremely important that they are reared in optimal circumstances and gradually exposed to diverse stimuli in a positively-reinforced way using controlled protocols (Rooney et al., 2016). Yet, methods employed in working dog programmes are not always adequate, and some protocols even increase the risk of behavioural problems (see Rooney et al., 2016 for a review). For example, some programmes might not have proper weaning protocols, which is important since maternal separation affects resilience to stressors later in life (Rooney et al., 2016). In addition, housing environments and transport conditions are sometimes inappropriate (Cobb et al., 2015; Leadon and Mullins, 1991; Orr et al., 2019; Skånberg et al., 2018).

Working dogs must also be motivated and rewarded for performing the required tasks. Although nowadays the majority of working dogs are trained using reward-based methods, aversive training techniques are still used (Orr et al., 2019; Rooney et al., 2016), despite their association with indicators of compromised welfare (reviewed in Guilherme Fernandes et al., 2017; Ziv, 2017; see also De Castro et al., 2020). Importantly, the sense of wellbeing a working dog obtains from a task likely depends on the suitability of the job to their capacities (Hens, 2009). In some cases, for example in hunting, herding or sled dogs, selection has favoured individuals that are predisposed to perform the requested task and seem to enjoy it (Coppinger and Coppinger, 2001). In other cases, such as therapy dogs in animal assisted interventions, it remains uncertain how and to what extent participation in these activities affects dogs' welfare (reviewed in Glenk, 2017; see also McCullough et al., 2018).

Working dogs are at greater risk than pet dogs of experiencing certain lesions or conditions (e.g., traumas, exposure to toxins) due to the nature of their occupations (Iddon et al., 2014; Orr et al., 2019; Otto, 2018). Moreover, dogs that do not meet the operational standards and are not deemed suitable as companion animals might be euthanised (Cobb et al., 2015; Orr et al., 2019). Something similar happens in the case of racing dogs (Houpt et al., 2007; Thomas et al., 2017).

To sum up, the cost-benefit trade-off for working dogs probably depends on the environments in which they are raised, live and work, the methods used for their training, the rewards given for their performance, as well as on the alignment between the type of tasks they are expected to perform and their intrinsic motivation and personality (see Hall et al., 2021 for a review on working dog training).

*4.2.2.2. Pet dogs.* Dogs kept as companion animals (i.e., pet or family dogs) are often considered friends or even family members by their owners and fulfil the role of children (see Blouin, 2013; Houpt et al., 2007; Serpell and Paul, 2012 for reviews). Even though most dog owners probably have a strong emotional bond with their dogs and try to ensure they have a good quality of life, on many occasions the relationship is focused on the owner's desires and needs, rather than the best interests of the dog (Beverland et al., 2008; Blouin, 2013; Serpell, 2019). Indeed, as outlined below, owners frequently fail to meet some of the basic needs of their companion dogs. The reasons for this are complex, as there are several factors involved in compliance with responsible ownership behaviours, including owner demographic, attitudinal and dog-owner relationship variables (e.g., Lue et al., 2008; Park et al., 2021; Rohlf et al., 2012; Rohlf et al., 2010).

As with other animals under human care, the Five Freedoms (Farm Animal Welfare Council, 2009; see also the Five Domains model: Mellor and Beausoleil, 2015) can be a useful framework to discuss the welfare of companion dogs (e.g., Houpt et al., 2007). The first freedom states that animals must be free from hunger and thirst, having access to water and a healthy diet. In relation to this, obesity is one of the most commonly reported companion dog welfare concerns (Hubrecht et al., 2017; Philpotts et al., 2019). While obesity can have a negative impact on dogs' health, longevity and quality of life (e.g., German, 2006; Yam et al., 2016), many owners might not see it as a health problem (Freeman et al., 2006).

The second freedom is from discomfort, that is, animals must live in an appropriate environment which includes secure and comfortable areas. This is probably true for most companion dogs, although it is possible that owners who have an utilitarian view of their dogs neglect this aspect since they provide them with less comforts (Blouin, 2013). Indeed, many dogs are used as guard animals and are regularly left outdoors and even permanently tethered (e.g., Denko, 2008).

The third freedom refers to pain, injury, and disease, and promotes prevention or a rapid diagnostics and treatment in case thereof. Again, research on the variables that affect owners' health care behaviour toward their pets has revealed that there are multiple factors involved (Lue

[1] Throughout this review we have used the term 'caregiver' rather than 'owner' to emphasize companionship rather than ownership in the human-dog relationship; however, as this section explores explicitly the differences between 'owned' and free-ranging dogs, we opted to use the term 'owner' here.

et al., 2008; Park et al., 2021; Rohlf et al., 2012), that might lead to a lack of basic veterinary care in some dogs. Furthermore, as commented above, current breeding practices have resulted in numerous congenital disorders, and demand for certain breeds based on their looks without consideration of these health issues, which are often not seen as a problem by owners, sustains these practices (Packer et al., 2019).

The fourth freedom declares that animals should be free to express normal behaviour and is probably one of the most forgotten aspects of pet dog welfare. This ties in with the fifth freedom, which is freedom from fear and distress and emphasizes the avoidance of mental suffering. Behavioural problems in the pet dog population are extremely common, with a recent international survey revealing a prevalence of 85 %, with almost half belonging to the fear/anxiety category (Dinwoodie et al., 2019). Importantly, on some occasions what owners consider a problematic behaviour might be a normal behaviour for dogs, but not acceptable in our society. Owners often fail to meet their dogs' physical and social needs, which can lead to behavioural disorders. For example, although seemingly there are no evidence-based recommendations on the frequency and/or duration of exercise for dogs (Kinsman et al., 2022), some owners rarely walk their dogs (see Westgarth et al., 2022 for a study on factors associated with regular dog walking). Even dogs that are walked daily might have limited or no opportunities to interact with other conspecifics (Westgarth et al., 2008, 2010). Furthermore, dogs are often left alone for extended periods of time, up to 9–12 hours/day, which suggests that the elimination needs of some dogs might not be met (Chung et al., 2016; Norling and Keeling, 2010). Additionally, absence of the owner can lead to separation anxiety, a behavioural disorder with a high prevalence in the companion dog population (Dinwoodie et al., 2019), that might increase the risk of other behavioural problems (Col et al., 2016).

### 4.3. Conclusion

Dogs' relationships with humans are full of paradoxes, especially in the case of companion dogs (McGreevy and Bennett, 2010). If we compare the population size of companion animals to that of their wild ancestors, association with humans has greatly benefitted domestic species (Serpell, 2003). Furthermore, as we have seen, establishing a partnership with humans is fitness-enhancing for populations of FRD, which otherwise have high rates of mortality and poor welfare. Overall, populations of FRD carved out a highly successful existence alongside humans and thus dogs may be considered one of the most successful mammal species worldwide. Yet, as dogs' reproduction becomes controlled by humans, they start facing new selection pressures. As Serpell (2003) put it, the selection exerted on breed dogs by humans is similar to the phenomenon of "female choice" in sexual selection. Indeed, humans select dogs based on physical and behavioural traits of their liking, even if these are not favourable for the individual's health and survival (e.g., extremely brachycephalic breeds). In conclusion, although association with humans is a driving factor for the extraordinary evolutionary success of dogs worldwide, the artificial selection some breeds have been subjected to in recent decades has had detrimental consequences for the wellbeing of the species as well. From this perspective, dogs might be considered "victims of their own success" (McGreevy and Bennett, 2010), as some have become trapped in relationships that are not beneficial anymore at the species and at the individual level.

## 5. Mechanisms

In this section we will review some of the cognitive, neurophysiological, and genetic mechanisms underlying dog-human interactions, which are consequently relevant for dogs' social motivation.

### 5.1. Cognitive mechanisms

Cognitive mechanisms relate to how dogs perceive, make sense of, and remember social interactions with human partners. Dogs' social motivation to seek contact with humans is coupled with a complex set of socio-cognitive skills that allow them to successfully navigate their interactions with humans. Dogs' socio-cognitive abilities have received substantial scientific attention and the literature on the topic is ever-expanding. Here we will only provide a brief overview and interested readers can find more extensive reviews elsewhere (e.g., Bensky et al., 2013; Benz-Schwarzburg et al., 2020; Huber and Lonardo, 2023; Jardat and Lansade, 2022; Marshall-Pescini and Kaminski, 2014; Range and Virányi, 2017; Udell and Wynne, 2008; Wynne, 2021).

#### 5.1.1. Human-directed attention

In tandem with dogs' motivation to interact with humans comes their motivation to pay attention to humans and their actions. In some studies dogs were more attentive towards a human than towards a conspecific or toy (Chapagain et al., 2017; Range et al., 2009; Wallis et al., 2014; but see Bognár et al., 2018) and showed preferential attention towards their caregiver over a stranger (Mongillo et al., 2010). In a visual cue-response association task, dogs found a task-irrelevant human visual stimulus more distracting than a non-social stimulus (Galambos et al., 2021). Interestingly, the distracting effect of the social stimulus was positively linked to dogs' social competence levels, which were measured through a questionnaire that included factors reflecting contact seeking and synchronization, behaviour towards strangers and attention to human communicative signals. Indeed, sociability is known to modulate dogs' human-directed gazing behaviour. Specifically, more sociable animals might remain attentive to humans for longer durations. Dogs with higher sociability scores (based on proximity to and physical contact with a stranger) showed longer spontaneous gazes at a human's face when food was out of reach (Boada, 2024; Putrino et al., 2014), and persisted longer in the behaviour when it was no longer reinforced (Jakovcevic et al., 2012). In a more recent study, more playful individuals established eye contact faster, whereas greeting behaviour had no effect on latency (Bognár et al., 2021). Caregiver-rated sociability was positively associated with dogs' preferential attention to a point-light display of a frontal view of an approaching person over a lateral view, which is an arguably less socially salient stimulus (Ishikawa et al., 2018).

#### 5.1.2. Communication with humans

From an early age, dogs show a notable motivation to seek contact with humans, but also a sophisticated capacity to understand human communicative cues (Salomons et al., 2021). Dogs reliably follow various human communicative signals, including pointing, head turns and gazing, are able to generalize this behaviour to relatively novel cues (e.g., "cross-pointing" or leg pointing), and are sensitive to ostensive cues (reviewed in Bensky et al., 2013; Benz-Schwarzburg et al., 2020; Jardat and Lansade, 2022; Topál et al., 2014; Wynne, 2021). Social signals provided by a human have proven to be more salient and effective than non-social cues for dogs solving object choice tasks (OCTs) (Agnetta et al., 2000; Udell, Giglio, et al., 2008). An interesting question is whether there is an association between dogs' sociability and these socio-cognitive skills. To our knowledge, few studies have addressed this question, and findings are mixed so far. Most studies find no association between dogs' human-directed social behaviours in different contexts and their ability to follow human gestures (Boada, 2024; Lazarowski et al., 2020; MacLean, Herrmann, et al., 2017; Sundman et al., 2018). In contrast, success in a pointing test correlated with the reinforcer efficacy of petting and verbal praise, but this finding was not replicated in subsequent studies (Brown, 2019).

Dogs are not only able to comprehend human gestures, but they are also capable of learning numerous words. Besides early studies reporting this ability in dogs (Griebel and Oller, 2012; Kaminski et al., 2004; Pilley

and Reid, 2011), there has been a recent upsurge in research on object label learning, a skill that only a few "gifted" individuals seem to possess (e.g., Dror et al., 2021, 2023, 2024; Fugazza et al., 2022; Fugazza, Andics, et al., 2021; Fugazza, Dror, et al., 2021). These dogs can quickly acquire large vocabularies of object labels, which they can recall for at least 2 years (Dror et al., 2024). Interestingly, an association between this ability and dogs' personality has been found, with "gifted" Border collies being rated as more playful than regular ones (Fugazza et al., 2022). In contrast, the groups did not differ in companionability, a facet reflecting how affectionate dogs are and their interest in spending time with people.

Dogs are also adept at communicating with humans, using vocalizations, body positioning and gaze alternations, from a very early age (Riemer et al., 2024), and they also take into account humans' attentional states, as we will see below (reviewed in Bensky et al., 2013; Jardat and Lansade, 2022; Udell and Wynne, 2008). Gazing is perhaps the most studied behaviour in research on dog-human communication, and is often interpreted as a help-requesting behaviour (but see for alternative explanations Lazzaroni, Marshall-Pescini, et al., 2020; Marshall-Pescini, Rao, et al., 2017; Udell, 2015). Dogs resort to humans when confronted with problems they are unable to solve on their own (e.g., Carballo et al., 2020; Gaunet, 2008; Heberlein et al., 2016; Marshall-Pescini et al., 2009; Miklósi et al., 2000; Miklósi et al., 2003; Passalacqua et al., 2011; Sommese et al., 2019). In fact, dogs show poorer performance in problem-solving tasks compared to wolves (Frank and Frank, 1982b, 1985; Udell, 2015), and it has been hypothesized that this might be due to the domestication process (Frank and Frank, 1985; Miklósi et al., 2003; Udell, 2015) and/or to their strong relationship with humans (Topál et al., 1997), which may have resulted in decreased persistence and increased dependency on us (Brubaker et al., 2017; Marshall-Pescini, Rao, et al., 2017; Rao et al., 2018; Topál et al., 1997; Udell, 2015).

#### 5.1.3. Understanding humans' attention, perspective and mental states

Researchers have also tried to discern whether dogs take humans' attentional states and perspectives into account, and whether they can infer knowledge and beliefs (reviewed in Bensky et al., 2013; Benz-Schwarzburg et al., 2020; Bräuer, 2014; Huber and Lonardo, 2023; Jardat and Lansade, 2022; Range and Virányi, 2017; Udell and Wynne, 2008; Wynne, 2021). Dogs are sensitive to humans' gaze direction, can follow humans' gaze into distant space and show geometrical gaze-following (i.e., they track humans' gaze direction geometrically behind visual barriers). They are also sensitive to attentional states, discriminating between attentive and inattentive humans based on cues such as head and body orientation, visibility of the eyes and whether they are open or closed, and adjusting their behaviour accordingly in different contexts, including begging for food, seeking interaction, communicating, obeying a command, playing fetch, following communicative gestures and stealing food. Moreover, dogs have some understanding of human's visual and auditory perspective, mainly demonstrated in stealing contexts. To our knowledge, only one study has investigated how dogs' sociability might be associated with their sensitivity to human's perspectives, with unconclusive findings (Boada, 2024). Finally, there is still no convincing evidence that dogs can attribute knowledge or false beliefs to humans (reviewed in Huber and Lonardo, 2023; Range and Virányi, 2017; Wynne, 2021).

#### 5.1.4. Social learning from humans

Dogs learn from humans in a variety of contexts, as indicated by studies in which dogs' performance in different tasks improves after observing a human demonstration (see Pongrácz, 2014; Range and Virányi, 2017 for reviews). Research, predominantly using the "Do-As-I-Do" paradigm, has also found that dogs are able to copy human actions, even showing deferred imitation (i.e., matching demonstrated actions after a time delay) (e.g., Fugazza et al., 2016; Fugazza and Miklósi, 2014). Remarkably, dogs show overimitation (i.e., copying another's unnecessary or causally irrelevant actions) (Huber et al., 2018, 2022; Mackie and Huber, 2023; but see Johnston et al., 2017), previously thought to be a uniquely human phenomenon. It has been hypothesized that this behaviour might be driven by social motivation and there is suggestive evidence that it is affected by the relationship quality with the human demonstrator (Huber et al., 2022). Finally, several studies have demonstrated social referencing in dog-human dyads. Social referencing is a process in which one's understanding of a situation and one's subsequent actions are based on the interpretation of such situation by another individual (Feinman, 1982). Dogs show referential looks (i.e., gaze alternations between the social partner and the stimulus) and adjust their behaviour based on the human partner's reaction when presented with an unfamiliar object or person (Duranton et al., 2016; Fugazza et al., 2018; Merola et al., 2012a, 2012b, 2013; Salamon et al., 2020; but see Duranton et al., 2017).

#### 5.1.5. Human emotion recognition in dogs

How well dogs can use humans as social references depends on their ability to recognize and respond appropriately to human emotions. Dogs readily integrate bimodal information of a person's emotional state (e.g., vocalization and facial expression) and they distinguish between positive and negative emotional valence (Albuquerque et al., 2016). Using eye-tracking technology, several studies have investigated dogs' looking behaviour when it comes to human emotional faces (Barber et al., 2016; Karl et al., 2020; Müller et al., 2015). Karl and colleagues (2020) report an increase in dogs' pupil size in response to watching angry human faces. Pupil dilation has been linked to emotional arousal associated with increased sympathetic activity (Bradley et al., 2008). Dogs' distinctive physiological and behavioural responses to human emotions is the focus of another line of research that investigates how emotional information may be transferred between humans and dogs. For instance, dogs reacted differently to 'chemosignals' in human sweat representing different emotional conditions (happiness vs. fear) (D'Aniello et al., 2018). Whereas they were more likely to approach a stranger in the happy odour condition, they sought out proximity with their caregivers more in the fearful condition. On average, dogs' heart rates (HR) remained elevated throughout the fearful condition compared to the happy and control conditions suggesting a transfer of emotional information between human and dog, in line with previous work (Siniscalchi et al., 2016).

Despite these highly interesting results warranting further exploration, not much is known about how dogs' social motivation mediates their perception of and reaction to human emotions. Recently, oxytocin, a neuropeptide involved in many aspects of social behaviour including social motivation, was found to modulate how dogs look at familiar human faces, i.e. decreasing their interest angry faces but also eliminating their preference for the eye region in happy faces (Kis, Hernádi, et al., 2017; but see Somppi et al., 2017 for different findings).

#### 5.1.6. Social evaluation of humans

Dogs' motivation to engage in social interactions with humans may also depend on their previous experiences with humans. We have devoted the section on the importance of life experiences and socialization history to this topic. However, dogs may also modulate their social behaviour more flexibly and rapidly depending on recent direct and indirect experiences with a human, as is the case in reputation formation. Previous studies on the topic have yielded mixed findings. Dogs distinguished between a cooperative and a competitive partner in a food-showing paradigm (Heberlein et al., 2017) and preferred a generous over a selfish person both in a food-providing context (Carballo et al., 2015) and during problem solving (Carballo, Cavalli, Martínez, et al., 2020), but in other studies dogs did not seem to form reputations after direct experience (McGetrick et al., 2021; Piotti et al., 2017). Indirect reputation formation, or eavesdropping on third-party interactions, appears to be even more challenging for dogs and, although a few studies reported it (Kundey et al., 2011; Marshall-Pescini

et al., 2011), recent studies failed to show it (Jim et al., 2020, 2022; see Anderson et al., 2017 for a review). An interesting, yet understudied aspect emerging from this line of work relates to the possible link between human-directed sociability and reputation formation in dogs.

As we have seen, cognitive mechanisms such as paying attention to and understanding human communicative cues and emotions, translating them into appropriate responses, and forming reputations based on previous interactions, could all be mediated by social motivation. Next, we will look more closely at the physiological mechanisms that contribute to dogs' social motivation.

### 5.2. Neurophysiological mechanisms

#### 5.2.1. The rewarding value of food vs. affection

One might wonder whether the affection dogs show towards people is simply based on their dependency on humans to obtain resources. In other words, we could hypothesize that dogs are motivated to interact with humans merely because they provide them with food. Scott and Fuller (1965) referred to several studies that seem to refute this idea. In these studies, dog pups that were never fed by hand still had a high motivation to establish contact with a person, even after having been punished for approaching (Brodbeck, 1954; Fisher, 1955; as cited by Scott and Fuller, 1965). Therefore, the authors concluded that feeding is not necessary for socialization of dog pups to humans (Scott and Fuller, 1965), and apparently dogs are attracted to humans independently of food provisioning. This is reminiscent of Harlow's and Bowlby's assertions that "feeding, in contrast to contact comfort, is neither necessary nor a sufficient condition for affectional development" (Harlow and Zimmermann, 1959; p. 428) and that "even in mammals, food plays only a marginal part in the development and maintenance of attachment behaviour" (Bowlby, 1969; p. 224).

More recent research has tried to discern whether social interaction with humans is rewarding for dogs, and if it is, whether it is a primary or conditioned reinforcer (Feuerbacher and Wynne, 2012, 2014; Feuerbacher, 2014). Although social interaction appears to be a relatively ineffective reinforcer compared to food (Feuerbacher and Wynne, 2012), it was preferred over food rewards under some circumstances (Feuerbacher and Wynne, 2014). Interestingly, when presented with a choice between social interaction and food, there are clear individual differences (Cook et al., 2016; Feuerbacher and Wynne, 2014; Lazzaroni, Range, et al., 2020). Cook et al. (2016) showed that choices in a behavioural test were predicted by the relative caudate activation to stimuli predicting food or praise in the fMRI scan. Caudate activation in dogs, as in other species, has been associated with reward processes (Berns et al., 2012). The preference for social over food rewards displayed by some dogs in the behavioural test was linked to individual differences in caudate responses (Cook et al., 2016). That is, dogs that consistently favoured social interaction over food rewards in the choice test, also showed higher caudate activation to stimuli predicting praise compared to stimuli predicting food, which would imply that for these individuals social rewards are indeed more valuable (Cook et al., 2016). Jakovcevic et al. (2012) found that more sociable dogs (based on proximity to and physical contact with an unfamiliar human) gazed longer at an experimenter during extinction (i.e., when gazing behaviour was no longer reinforced with food). A possible explanation could be that sociability modulates the reinforcing value of visual contact with humans, so that the presence of a human gazing at them might have been sufficient for more sociable individuals to maintain the gazing behaviour in the absence of food reinforcement (Jakovcevic et al., 2012). In contrast to shelter and pet dogs, FRDs might be mainly food oriented when interacting with humans (Brubaker et al., 2019), but it has also been demonstrated that social contact is more effective than food rewards for FRDs to build trust in humans on the long term (Bhattacharjee, Sau, et al., 2017). At the neurological level, caudate nucleus activation observed in fMRI studies suggests that merely seeing a human face or smelling a familiar human can be rewarding for dogs (Berns et al., 2015; Cuaya et al., 2016; Karl et al., 2020). For example, caudate activation was stronger in response to the scent of a familiar human compared with that of a familiar dog (Berns et al., 2015; Fig. 8).

#### 5.2.2. Involvement of neuromodulators

Numerous studies provide evidence for changes in various physiological parameters and neurochemicals during positive interactions between humans and dogs. A decrease in blood pressure and increases in plasma concentrations of β-endorphin, oxytocin, prolactin, β-phenylethylamine and dopamine, all linked with pleasurable sensations and social bonding, were found in both species after an interaction involving talking, stroking and playing (Odendaal and Meintjes, 2003). Pack-living dogs showed lower cortisol concentrations following a training session with their caregivers (Vasconcellos et al., 2016). Interestingly, this effect was also observed in hand-raised wolves, which indicates that participating in positive social interactions with bonded humans is linked to relaxation in a similar way in both species, provided the animals receive adequate socialization with humans from an early age. Human interaction or merely human presence can reduce dogs'

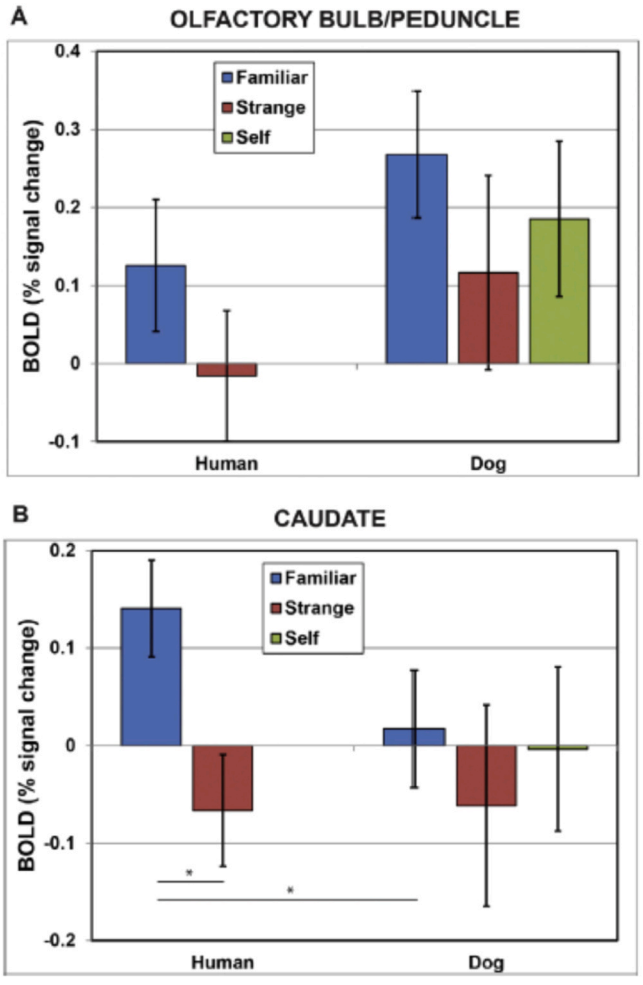


**Fig. 8.** Activation within olfactory bulb and caudate regions of interest (ROIs) to different scents. Estimated grand means for each scent are shown ±1 s.e. (adjusted for subject wise mean). (A) The olfactory bulb/peduncle was activated, on average, to all of the scents, but ANOVA indicated no significant difference between the scents [$F(4,13.0) = 1.28$, $p = 0.327$]. (B) The caudate, however, showed a significant difference between scents [$F(4,15.4) = 3.55$, $p = 0.031$]. Post hoc contrasts indicated that the scent of a familiar human activated the caudate significantly more than strange human (*$p = 0.019$) and familiar dog (*$p = 0.043$). (Reprinted from Berns et al., 2015; licensed under CC-BY-NC-ND: http://creativecommons.org/licenses/by-nc-nd/3.0/).

stress response and arousal levels, as demonstrated by measuring HR and heart rate variability (HRV) during resting alone or with a familiar human partner (Jean-Joseph et al., 2020). Other studies have analysed dogs' plasma or salivary cortisol concentrations in response to aversive situations, such as veterinary procedures (Csoltova et al., 2017; Hennessy et al., 1998), shelter housing (Coppola et al., 2006; Shiverdecker et al., 2013), exposure to an unfamiliar environment (Tuber et al., 1996) or to a threatening person (Schöberl et al., 2016). Remarkably, human presence might be more effective in reducing stress in dogs than that of conspecifics (Pettijohn et al., 1977; Tuber et al., 1996; but see Cimarelli et al., 2019, 2024). Evidently, the effects derived from human interaction depend on the individual dogs' sociability (Cainzos et al., 2018; Shin and Shin, 2017) and the type of interaction (Kuhne et al., 2014).

As mentioned above, the nonapeptide oxytocin, which, among other functions, modulates the HPA axis, has received considerable attention from researchers studying dogs' human-directed social behaviour. Oxytocin has been suggested as the main mediator of the social buffering effects of human presence on the stress response of dogs (see Buttner, 2016; Kikusui et al., 2019; Kis, Ciobica, et al., 2017; Powell, Guastella, et al., 2019; Thielke and Udell, 2017 for reviews). Several hypotheses regarding oxytocin's effect on social behaviour have been posited, including a reduction in general anxiety, augmentation of the existing emotional or psychological state, enhancement of social salience or increase of reward sensitivity (Buttner, 2016; Powell, Guastella, et al., 2019). Positive interactions with humans increase dogs' endogenous levels of peripheral oxytocin, as demonstrated by several studies (Handlin et al., 2011; MacLean, Gesquiere, et al., 2017; Mitsui et al., 2011; Nagasawa et al., 2015; Odendaal and Meintjes, 2003; Rehn et al., 2014; Wirobski et al., 2021a). In fact, the mere sight of a familiar person returning after a separation period was enough to elicit oxytocin release in pet dogs (Rehn et al., 2014). However, other studies have not found this effect (Marshall-Pescini et al., 2019; Powell et al., 2019; Romero et al., 2014), or reported differences based on socialisation history, housing and relationship strength (Wirobski et al., 2021a). Specifically, enclosure-living dogs housed with conspecifics did not show an increase in oxytocin levels following an affiliative interaction with their human hand-raisers nor with a familiar human, whereas in pet dogs elevated oxytocin concentrations were linked to interaction with their caregivers only. This suggests an important role of life experiences and the characteristics of the dog-human bond on the modulation of the oxytocin response (Wirobski et al., 2021a). Furthermore, the oxytocinergic system seems to influence dogs' sociability and attachment style. After receiving intranasal oxytocin dogs displayed higher social orientation, affiliation, and proximity seeking towards humans (Barrera et al., 2018; Nagasawa et al., 2015; Pedretti et al., 2021; Romero et al., 2014), suggesting that oxytocin enhances social motivation. However, other studies did not find any or only limited effects of intranasal oxytocin on dogs' human-directed social behaviours (Barrera et al., 2018; Dzik et al., 2020; Thielke et al., 2017). Importantly, the effects of exogenous oxytocin on dogs' social behaviour are strongly moderated by individual (e.g., breed, sex, reproductive status) and contextual (e.g., interaction partner, bond strength) factors (Dzik et al., 2020; Kis et al., 2014; Kovács et al., 2016; Kubinyi et al., 2017; Nagasawa et al., 2015; Turcsán et al., 2017). In conclusion, findings to date are mixed, hence the role of oxytocin in the dog-human relationship might be currently overestimated (Marshall-Pescini et al., 2019; Powell, Edwards, et al., 2019). Future research needs to carefully account for confounding factors and employ standardised methods for better cross-study comparability.

#### 5.2.3. *Stress buffering: the role of the attachment system*

The social buffering of stress is one of the defining characteristics of an attachment bond (i.e., "safe haven effect") (Buttner, 2016). Studies have shown that pet dogs form an attachment bond with their caregiver similar to that observed in human infants towards their mothers (see Nagasawa et al., 2009; Payne et al., 2015; Prato-Previde and Valsecchi, 2014; Rehn and Keeling, 2016 for reviews). Indeed, in addition to the "safe haven effect" (Gácsi et al., 2013; Schöberl et al., 2016), dogs exhibit other behavioural components distinctive of the attachment system. Dogs stay close to and avoid separation from their caregiver, they experience discomfort when isolated from him/her, and greet him/her enthusiastically when reunited (Gácsi et al., 2013; Konok et al., 2011; Mariti et al., 2013; Mongillo et al., 2013; Palestrini et al., 2005; Prato-Previde et al., 2003; Ryan et al., 2019; Scandurra et al., 2016; Topál et al., 1998, 2005). Specifically, during separation from their owner, dogs' HRV increased significantly (Gácsi et al., 2013). Furthermore, in novel environments or situations the caregiver provides a secure base, as demonstrated by studies in which dogs explored and played more when the caregiver was present than in the presence of a stranger or alone (Horn et al., 2013; Mariti et al., 2013; Palestrini et al., 2005; Palmer and Custance, 2008; Prato-Previde et al., 2003; Scandurra et al., 2016; Topál et al., 1998). For example, dogs experienced a significantly less pronounced HR increase in the presence of their owner during a threatening approach of a stranger than when alone (Gácsi et al., 2013).Although dogs can display a preference for and greater responsiveness to their caregiver, confirming that they indeed constitute the attachment figure (e.g., Horn et al., 2013; Kerepesi et al., 2015; Mariti et al., 2013; Palmer and Custance, 2008; Prato-Previde et al., 2003; Scandurra et al., 2016; Topál et al., 1998, 2005), in other cases they do not seem to discriminate between their caregivers and other humans (Rehn et al., 2013; Topál et al., 1998) or quickly shift these attachment behaviours to a novel human (Gácsi et al., 2001). Pet dogs have even been shown to display a high level of trust towards complete strangers (Tan et al., 2018). As Solomon et al. (2019) pointed out, even if there are similarities between the canid and primate attachment behaviour systems, species and individual differences such as exclusivity and longevity of bonds may also exist.

Attempts have been made to classify the different patterns of dog-owner attachment and typically include the categories secure, insecure-avoidant, insecure-ambivalent, insecure-disorganized and unclassified (Riggio et al., 2021; Ryan et al., 2019; Schöberl et al., 2016; Solomon et al., 2019; Thielke et al., 2017; Topál et al., 1998; Wanser and Udell, 2019). Importantly, the security of the attachment bond differs between individual dog-human dyads (e.g., Fallani et al., 2006) and is related to caregivers' expectations and patterns of response towards their dog (Brubaker and Udell, 2022; Solomon et al., 2019), similarly to what is described in the human attachment style literature. It is likely that the failure to find a secure base effect in some cases, for example, does not imply a lack of attachment but might simply reflect a different attachment style or pattern (Rehn et al., 2013).

Recently, Buttner and colleagues (2023) studied the impact of early-life adversity on dogs' ability to accept and benefit from the stress-buffering effect of their owner's presence in a threatening situation. They found that dogs from adverse backgrounds showed more fear towards the stranger – regardless of their owner's presence or absence – but also exhibited a larger decrease in cortisol levels throughout the test than the control group. Dogs from adverse backgrounds engaged in more gaze alternations between their owners and the threatening stranger, likely attempting to gather information from their owners. While this study did not classify the dogs' attachment style, they demonstrate how early-life adversity impacts dogs' human-directed behaviour throughout life. Previously, it was reported that dogs classified as insecurely attached showed increasing cortisol levels during the ASST more often than securely attached dogs (Riggio et al., 2022) suggesting that securely attached dogs may be better able to benefit from their owners' stress-buffering presence.

### 5.3. *Genetic mechanisms implicated in dogs' sociability*

Research on gene-behaviour associations in dogs has been reviewed elsewhere (e.g., Berg, 2017; Hall and Wynne, 2012) and in this subsection we will only highlight findings specifically related to dogs' human-directed sociability. The genetic basis of dogs' human-directed

sociability has been probed repeatedly, perhaps most famously by the researchers of the Farm Fox Experiment (Trut et al., 2021). Jensen and colleagues (2016) report on their approach of studying the genetics of dogs' human-directed behaviour using the unsolvable-task paradigm and dogs' propensity to seek human assistance. The heritability of this behaviour was found to be as high as 23 % in Beagles bred and kept under standard conditions (Persson et al., 2015). Further, a genome-wide association study (GWAS), conducted also on laboratory Beagles, identified several candidate genomic regions containing five possible candidate genes underlying dogs' sociability (Persson et al., 2016). Specifically, the authors report a genetic marker on chromosome 26 within the SEZ6L gene that was significantly linked to the time dogs spent close to and interacting with humans. Interestingly, the SEZ6L gene has been associated with autism spectrum disorder in humans (Chapman et al., 2015). These results were later confirmed in other dog breeds (Labrador retriever and golden retriever, Persson et al., 2018).

More recently, Morrill et al. (2022) surveyed caregivers of over 18, 000 dogs and sequenced the DNA of more than 2000 dogs, including purebred and mixed-breed. Exploratory factor analysis of the survey data yielded eight factors that captured different facets of behaviour, including human sociability (i.e., how comfortable the dog is around people, especially strangers) and proximity seeking (i.e., how readily the dog solicits human contact and closeness). Human sociability was the factor with the highest heritability ($h^2 = 67.3 \pm 13$ %) and the strongest association in a genome-wide association study (GWAS). After regions associated with toy-directed motor patterns, those associated with proximity seeking had the strongest enrichments in brain-expressed genes. Despite most behavioural traits being heritable, breed explained only 9 % of behavioural variation in individuals, hence offering little predictive value.

Breed differences in sociability-related traits have been reported in several studies based on behavioural tests and questionnaires (e.g., Jakovcevic et al., 2010; Junttila et al., 2021; Lenkei et al., 2019; Maglieri et al., 2019; Marshall-Pescini et al., 2016; Starling et al., 2013a; Sundman et al., 2016; Svartberg, 2006; Turcsán et al., 2011). A large proportion of behavioural variance across breeds was attributable to genetic factors in a study by MacLean et al. (2019), which combined questionnaire-based behavioural data from more than 14,000 dogs from 101 breeds with breed-averaged genotypic data. Among the traits with the highest among-breed heritability was the "attachment and attention-seeking" factor of the C-BARQ ($h^2 = 0.56$). Differences between breed groups in sociability-related behaviours have also been documented (Bognár et al., 2021; Konno et al., 2016; Passalacqua et al., 2011; Starling et al., 2013a; Turcsán et al., 2011), but comparability across studies is limited and interpretation of results is complicated due to dissimilar criteria used for breed categorization. In this context, how selection for particular working purposes and genetic relatedness to wolves might influence dogs' human-directed social behaviour has been investigated (Konno et al., 2016). For example, findings suggest that more 'ancient' breeds – which are more genetically similar to wolves (Larson et al., 2012; Parker et al., 2004) – and 'non-cooperative breeds' – which don't work in visual contact with humans – show less human-directed gazing behaviour than other breed groups (Bognár et al., 2021; Konno et al., 2016; Passalacqua et al., 2011).

A gene that repeatedly emerges in studies on the genetic mechanisms of dogs' human-directed sociability is the oxytocin receptor gene (OXTR). A couple of studies have shown that the effect of exogenous oxytocin on dogs' social behaviour is modulated by OXTR gene polymorphisms (Kis et al., 2014; Persson et al., 2017). Single nucleotide polymorphisms (SNPs) of the OXTR and the opioid receptor gene also affect human-directed greeting behaviour, although apparently breed differences occur (Kubinyi et al., 2017). Further, OXTR polymorphisms were associated with proximity-seeking and greeting behaviours towards both a stranger and the caregiver, friendliness towards strangers (Oláh et al., 2017; Turcsán et al., 2017; but see Ottenheimer-Carrier et al., 2017), attachment behaviours toward caregivers (Kovács et al., 2018) and gazing behaviour in an unsolvable task (Tonoike et al., 2022). Lastly, epigenetic modulation of the OXTR gene was related to dogs' owner-directed behaviour during a threatening approach demonstrating that environmental and developmental factors play a role as well (Cimarelli et al., 2017).

Finally, this section must also include the potential genetic basis for dogs' hypersocial behaviour as shown by vonHoldt and colleagues (2010, 2017). Their GWAS study on more than 700 dogs from over 80 breeds and 92 grey wolves, reported a top-ranking outlier site located within a gene region typically deleted in WBS (see also Section 2.2.2. Sociability). WBS in humans is a neurodevelopmental disorder characterized – among other symptoms – by unusually gregarious, 'hypersocial' behaviour and a lack of social inhibition (Toth, 2019). In a subsequent study, they found that the region around the WBS critical region was under positive selection in domestic dog breeds thus suggesting a significant role in the domestication process (vonHoldt et al., 2017). A recent study confirmed the relevance of this region for the evolution of dogs' hypersocial behaviour linking it to chromatin architecture (Tandon et al., 2024).

### 5.4. Conclusion

In summary, in this section we reviewed some of the most relevant cognitive mechanisms involved in dog-human interactions such as attention to humans, social learning, human emotion recognition, and reputation formation, but there are surprisingly few studies directly investigating how sociability affects these and other aspects of social cognition in dogs. We then looked at the rewarding effects of food and affection, the roles of neuromodulators such as oxytocin and dopamine, and reviewed the stress-buffering effect of an attachment figure. Especially in the field of peripheral oxytocin research, findings are mixed and there is a lack of standardized methods which makes comparison across studies difficult. Lastly, we provided a brief, non-exhaustive overview of the genetic basis of dogs' human-directed social behaviours, highlighting the OXTR gene and the genetic variants related to WBS and hypersocial behaviour which appear to be promising targets for future investigations of gene-behaviour associations.

## 6. Future directions

Examining dogs' social motivation towards humans from the perspective of Tinbergen's four questions has revealed that although we already know much about its evolution, development, function, and immediate causation there are many mixed findings, controversial hypotheses, or simply results in need of replication, which we will briefly allude to in this section. Furthermore, we will suggest additional approaches that could be used in future studies to improve our understanding of dogs' human-directed sociability.

### 6.1. Effects of domestication on social motivation

#### 6.1.1. Comparison with other domesticated species

From an evolutionary perspective, the domestication process is usually presented as the main explanation for dogs' social motivation towards humans. The results of the renowned Siberian farm fox experiment (Trut et al., 2009), as well as of studies comparing dogs and wolves' sociability (e.g., Lazzaroni, Range, et al., 2020), seem to support this view. However, to learn more about the effect of domestication on human-directed sociability it is necessary to also study the motivation to interact with humans in other domesticated species. Considerable research has been done on human-animal interactions in domestic animals (e.g., farm animals: reviewed in Waiblinger et al., 2006; Zulkifli, 2013; dairy animals: reviewed in Napolitano et al., 2020; dairy cows: Ebinghaus et al., 2018; Schmitz et al., 2020; goats: reviewed in Celozzi et al., 2022; Nawroth, 2017; horses: reviewed in Hausberger et al., 2008; Kelly et al., 2021; Merkies and Franzin, 2021; Payne et al., 2016; horses

and donkeys: Dalla Costa et al., 2015; cats: reviewed in Vitale Shreve and Udell, 2015; see also Eriksson et al., 2017; Vitale et al., 2019; Vitale and Udell, 2019; Vitale Shreve et al., 2017), but studies directly comparing the human-directed sociability of other domesticated species and dogs (e.g., cats: Miklósi et al., 2005; companion pigs: Gerencsér et al., 2019; Pérez Fraga et al., 2020, 2021, 2023: horses (comparative review): Payne et al., 2016), as well as their wild counterparts whenever possible (e.g., ferrets: Hernádi et al., 2012), would be useful. This is particularly pertinent in the case of other domestic species that are kept as companion animals, and thus live in similar environments with similar experiences as dogs. Such a comparative approach would help to clarify whether being domesticated and living in close association with humans is sufficient to elicit a social interest towards humans as strong as that seen in dogs. Still, comparing species with different domestication pathways, particularly those selected for direct cooperation or companionship with humans, with those domesticated for other purposes (e.g., meat production), would elucidate if enhanced social motivation towards humans is a general result of domestication or if it depends on the particular selection process that each domestic species has undergone. In short, a comparative approach in which the social motivation towards humans is assessed in domestic species which either differ or coincide in the purpose for which they were domesticated, the environments in which they live and/or the experiences they have with humans would be highly valuable and provide insight into the relative importance of domestication and ontogenetic experiences (Table 1). In these comparisons, factors such as the socioecology of the ancestral species or the length of the domestication process should also be considered.

#### 6.1.2. *Self-domestication: comparison with synanthropic species*

It is hypothesized that domestication not only reduced dogs' fearfulness, but also enhanced sociability (Zimen, 1987). Importantly, this implies that dogs' ancestor not only tolerated human presence but also actively sought it. A useful approach could be to study populations of wild animals that come into contact with human settlements and begin to take advantage of urban environments (i.e., synanthropic species) (see Bateman and Fleming, 2012 for a review on urban carnivores), since they might be experiencing a process of self-domestication (e.g., coyotes: Breck et al., 2019; Brooks et al., 2020; deer: Peterson et al., 2005; squirrels: Uchida et al., 2019; birds: Carrete and Tella, 2011, 2017; see Ritzel and Gallo, 2020; Ryan and Partan, 2014; Schell et al., 2021; Sol et al., 2013 for reviews on behavioural changes in urban wildlife), as has been hypothesized for the beginning of dog domestication (the 'commensal scavenger' or 'garbage dump hypothesis', Coppinger and Coppinger, 2001; Hare et al., 2012; but see Mech and Janssens, 2022; Serpell, 2021). Interestingly, though, what is often described in these urban populations after a reduction of fearfulness and an increased tolerance to human presence is an escalation of aggressive behaviour towards humans, rather than heightened sociability (e.g., Schmidt and Timm, 2007). Research into how fearfulness, aggressiveness and sociability towards humans change in urban animals compared with their rural counterparts could be beneficial for a better understanding of dog domestication.

**Table 1**
Comparative approach in the study of social motivation towards humans.

| Question | Groups to compare | | Controls |
|---|---|---|---|
| How did domestication affect social motivation? | Domestic animals | Wild counterparts | Must have similar experiences with humans |
| How did domestication purpose affect social motivation? | Animals domesticated for cooperation with humans/ companionship | Other domestic animals | Must have similar experiences with humans |
| How does experience with humans affect social motivation? | Domestic animals with intensive socialization | Domestic animals with limited exposure to humans | Must have similar domestication purpose |
| | Wild animals with intensive socialization | Wild animals with limited exposure to humans | |

#### 6.1.3. *Wolf-dog comparisons and breed differences*

Although domestication involved a reduction in fearfulness, it is unclear exactly *how* domestication affected dogs' fear response. Initially, it was proposed that domestication delayed the onset of this response (Trut et al., 2009), but more recent research suggest that this is not the case, and that there is instead a gradual reduction of fear with age in dogs (Hansen Wheat et al., 2019). Furthermore, comparative studies on neophobia in adult individuals have yielded mixed results (Jean-Joseph, 2023; Moretti et al., 2015). Thus, future research should aim to clarify this subject. Similarly, the involvement of the HPA axis and other neuroendocrine factors in the domestication process still remains to be studied more rigorously, since previous work has demonstrated that – in contrast to other domesticated species – dogs do not show a reduction in systemic cortisol levels compared to wolves (Vasconcellos et al., 2016; Wirobski et al., 2021b). The hypersociability hypothesis postulates that dogs were selected for enhanced social responses (vonHoldt et al., 2017). To test this hypothesis, it would be necessary to study dogs' social behaviour towards other non-human species (as mentioned by Lazzaroni, Range, et al., 2020) and to examine whether it is generally easier for dogs to create strong social bonds in comparison to wolves. However, some evidence points to the contrary at least at the intraspecific level: although free-ranging dogs can form stable groups similar to wolf packs (Bonanni and Cafazzo, 2014), wolves outperform dogs in their intraspecific cooperative skills (Marshall-Pescini, Schwarz, et al., 2017). On the other hand, wolf-dog differences in human-directed sociability may reflect increased deferential behaviour and submissiveness towards human partners in dogs (Range et al., 2019: 'deferential behaviour' hypothesis; Wynne, 2021: 'super-dominance' hypothesis). In addition, human-directed play behaviour might have also been a relevant factor in dog domestication (Hansen Wheat et al., 2018; Hansen Wheat and Temrin, 2020). Further research to corroborate these hypotheses is warranted. On a related note, more research is needed to confirm the presence of attachment bonds between wolves and their human caregivers, since previous results are contradictory (Hansen Wheat et al., 2020; Topál et al., 2005), and to clarify how these bonds might differ from those of dogs.

Finally, the comparison between dog breeds could provide more information on how past and current selection processes have affected social motivation towards humans. The hypothesis that "ancient" breeds might be more behaviourally similar to wolves than other dog breeds has received limited support so far (Konno et al., 2016; Smith et al., 2017; Tonoike et al., 2015, 2022) and deserves further exploration. More generally, although there are a number of studies comparing dog breeds or breed groups with regards to their neuroanatomy (Hecht et al., 2019) and human-directed behaviour (e.g., Eken Asp et al., 2015; Jakovcevic et al., 2010; Lenkei et al., 2019; Starling et al., 2013a; Sundman et al., 2016; Svartberg, 2006; Turcsán et al., 2011), usually only a small number of breeds are included (but see MacLean et al., 2019; Morrill et al., 2022) and interpretation of results and comparation across studies are hindered by the dissimilar criteria used to categorize breeds. Lastly, future studies could also examine breed differences during the socialization period (e.g., Morrow et al., 2015).

### 6.2. *Effects of ontogeny on social motivation*

For a comprehensive understanding of dogs' social motivation towards humans one must not only consider the evolutionary history of the species but also the developmental history of the individual. In this

sense, maternal care might have an important influence on the development of pups' human-directed social behaviour (Bray et al., 2017; Guardini et al., 2017; but see Guardini et al., 2016) with effects that might persist well into adulthood (Foyer et al., 2016). Further research on this subject is of great importance and can inform dog breeding practices. On the other hand, social deprivation in adult animals might boost social motivation or result in social disinhibition. To date, studies comparing shelter and pet dogs' human-directed behaviour have provided mixed findings (Barrera et al., 2010, 2011, 2015; Cimarelli, Schindlbauer, et al., 2021; Feuerbacher and Wynne, 2014; Gould et al., 2022; Shin and Shin, 2017; Udell, 2015; Wallner Werneck Mendes et al., 2021), hence future investigations should seek to elucidate this issue. Moreover, a decline in dogs' sociability with age has been revealed and various explanations have been presented (Starling et al., 2013b). Future studies can help to discern whether any or all these explanations are supported. One possible approach to test whether this decreased interest in social interactions with humans observed in older dogs is due to a process of habituation throughout life is to compare human-directed social behaviour in aged dogs that have been socially deprived and aged dogs that have had adequate social experiences. Lastly, studies of FRD populations will also be essential to obtain more insight into dogs' motivation to interact with humans.

### 6.3. *Adaptive value of human-dog associations and dog welfare*

Studies on different dog populations are indispensable to understand the adaptive value of dogs' relationship with humans. Research on the fitness of FRD populations with different degrees of association with humans is required. In this review we have discussed how, relationships with humans may also be harmful for dogs. With regards to working dogs, investigating the conditions in which they are raised, kept, trained, and perform is crucial to ensure that the welfare of these dogs is respected. Finally, also the welfare of companion dogs should not be taken for granted and further research might continue to reveal that some of the habitual practices in pet dog breeding and keeping are detrimental to dogs' welfare and require us to find alternatives.

### 6.4. *Mechanisms underlying social motivation*

Lastly, although much effort has gone into revealing the mechanisms underlying dogs' social motivation towards humans, many questions remain unsettled. The question of how dogs' human-directed sociability relates to cognitive processes involved in dog-human interactions, such as attention to humans, comprehension of humans' gestures, sensitivity to humans' perspectives and attentional states, social learning, human emotion recognition, and reputation formation, deserves more attention (e.g., Boada, 2024). Early studies suggested that dogs' bonds with humans are not dependent upon food provisioning (Brodbeck, 1954; Fisher, 1955; as cited by Scott and Fuller, 1965), but it would be interesting to evaluate further the role of feeding in dog-human socialization and bond formation. It would also be important to elaborate on previous works on the reinforcing value of social interaction with humans and potential reasons for individual differences in the preference for either affection or food (Cook et al., 2016; Feuerbacher and Wynne, 2012, 2014; Feuerbacher, 2014; Lazzaroni, Range, et al., 2020). In this sense, more studies on the neural response to different types of social and non-social stimuli would be fruitful. In the search for the proximate mechanisms underlying dogs' social motivation towards humans, abundant research has focused on the role of oxytocin. However, some authors have recently argued that its influence on dogs' social behaviour has been overestimated and oversimplified (Marshall-Pescini et al., 2019; Powell, Edwards, et al., 2019). Consequently, further studies are necessary to clarify whether and to what extent this might be true. Other hormonal (gonadal steroids, thyroid hormones) and neurotransmitter (serotonin, dopamine) systems involved in dogs' social interactions with humans remain understudied. Looking ahead, the interest in using artificial intelligence (AI) and modern technology to investigate dogs' emotional responses and underlying motivations is rising rapidly (see Koyasu et al., 2024 for a review). In combination with the knowledge gained from previous ethological work, these new technologies may offer an exciting approach to studying dogs' inner worlds. Lastly, research is only beginning to unravel the genetic basis of dogs' human-directed social behaviours, and the OXTR gene and the genetic variants related to WBS and hypersocial behaviour appear to be promising targets for future investigations of gene-behaviour associations.

## 7. Conclusions

This review aims to provide an overview of the current knowledge about dogs' human-directed sociability using Tinbergen's four questions as a guiding framework. Dogs' social motivation is a product of their evolutionary history, which involves a domestication process that altered basic features of the socialization process, possibly resulting in a genetic predisposition to form interspecific social bonds (Persson et al., 2018; vonHoldt et al., 2017). Ontogenetic experiences determine whether and how these hypersocial tendencies are expressed in the individual dog. Dogs can flexibly adapt their social responses depending on the role humans play in their environment. Throughout their lifetime, their social motivation decreases with age. Association with humans made dogs an extraordinarily successful species, but recent artificial selection on some breeds had detrimental consequences for the health and welfare of the species. Lastly, in tandem with their social motivation dogs possess a complex set of cognitive abilities that allow them to successfully navigate their social interactions with humans, which have a series of positive neurophysiological effects. We also identified some gaps in the literature and suggested potential avenues to fill them, which we hope will ignite further research. As postulated by the Tinbergian approach, only by exploring dogs' human-oriented social motivation from multiple perspectives will we gain a comprehensive understanding of this fascinating topic.

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