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„It actually doesn’t take much to be considered a difficult woman.

That’s why there are so many of us.“

Jane Goodall

Table of Contents

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Finally, to my past self… Look! We made it!

General Introduction |

From Wolf to Dog: a domestication story

Wolves were the first species humans domesticated (Botigué et al., 2017; Clutton-Brock, 1992; Thalmann et al., 2013). Evidence suggests dogs diverged from Pleistocene wolves across multiple places sometime between 15,000 to 40,000 years ago (Bergström et al., 2020; Botigué et al., 2017; Frantz et al., 2016; Ovodov et al., 2011; Perri et al., 2021; Tancredi & Cardinali, 2023). However, for most modern domesticated plants and animals, the phenomenon happened within the last 12,000 years (Smýkal et al., 2018; Zeder, 2012) and started alongside humans becoming sedentary. Domestication of plants and animals was a key point in urbanization and generally, in the success of humankind (Diamond, 2002; Larson et al., 2014). Today, domesticated animals are still an important part of our life in a wide range of functional domains, from food to social companions (Diamond, 2002; Kotrschal, 2018).

For all that is known, the domestication process has yet to be fully elucidated. The whens, wheres, and hows are still hotly debated (Larson, 2011; Larson et al., 2012; Purugganan, 2022; Zeder, 2006, 2015). Even agreeing on a definition that could satisfy all scientific fields and scholars involved poses a challenge (Purugganan, 2022; Zeder, 2015). Nonetheless, a simple evolutionary orientated definition of domestication could be: domestication is a genetic change as compared to wildtype, due to adaptations to living with/close to humans (Clutton-Brock, 1992; Price, 1984).

There are two main hypotheses about how this domestication happened. The “commensal hypothesis” posits that some of the Pleistocene wolves started to use an accidental new ecological niche caused by hunter-gatherers accumulating refuse and carrion near their temporary camps sites. In this hypothesis, less fearful and aggressive wolves would have been left in peace to enjoy those new opportunity to scavenge and would have, over time, domesticated themselves (Coppinger & Coppinger, 2001; Driscoll et al., 2009; Grimm, 2015). More recently, the “commensal hypothesis” has been determined to be unlikely for several reasons: First, the human population was still mostly nomadic (Driscoll et al., 2009) when the first domestication event occurred and could not generate enough refuse to feed scavenging wolves (Lupo, 2019; Serpell, 2021). Second, the behaviours of modern wolves do not corroborate this hypothesis, for example, in populations that were never hunted, wolves that are deferential and submissive toward their conspecifics tend to be the shyest toward humans (Mech & Janssens, 2022). Further, there is evidence that socialized, but not habituated wolves would accept humans as cooperation partners (Klinghammer & Goodmann, 1987; Range & Marshall-Pescini, 2022a). Given the conflicting evidence, a better hypothesis may be the “cross-species adoption hypothesis”. This hypothesis states that humans would have been naturally attracted to wolf pups and adopted some of them. The more docile ones would have stayed and were bred at the human camp and, over time, a proto-dog would have emerged (Germonpré et al., 2018, 2021; Mech & Janssens, 2022; Serpell, 2021). Despite the differences, the two hypotheses have a common point: Intentional or not, over time a kind of selection for tameness (i.e. diminution of fear and potentially, aggressiveness toward humans) must have occurred (Belyaev, 1979; Darwin, 1868; Price, 1999; Trut et al., 2009).

Selection for tameness, Domestication Syndrome, and Neural Crest hypothesis

Belyaev’s silver farm fox experiment was the first serious attempt to test Charles Darwin´s idea (1868) that a range of domestication characteristics, later called “domestication syndrome” (Price, 2002; Wilkins et al., 2014) may be have been caused by selection for tameness (Belyaev, 1979;

Trut, 1999; Trut et al., 2009). Starting in 1959, Belyaev and his colleagues selectively bred foxes for low fearfulness of humans (i.e., so-called low fear line) and years later, bred another line of foxes for high fearfulness of humans. Within a few generations (but see Lord et al., 2020 for more details on the origin of the foxes), they observed a cascade of changes in the foxes unrelated to the behavioral change selected for (Belyaev et al., 1985; Trut et al., 2004). They found that as a by-product of selection for tameness, domesticated animals generally share several physiological (e.g., increased in fertility, non-seasonal oestrus), morphological (e.g., curly tail, shorten jaw), behavioural (e.g., reduced reactivity and aggressivity), and genetic traits; those changes were named the domestication syndrome (DS; Price, 1984, 1999, 2002). Later, a potential explanation was offered as a common mechanistic cause linking all the seemingly unrelated traits: The "neural crest hypothesis" (NCCH) suggests that the coappearance of seemingly unrelated traits in domesticated animals are due to mild migratory changes of the stem cells of the neural crest and of their gene expression under hormonal influence during embryonic development (Wilkins et al., 2014, 2021; Wilkins, 2017, 2020). Under the NCCH assumptions, we could also expect that the functioning of the autonomic nervous system (ANS) would be affected, relating to changes in the way dogs perceive their environment as compared to wolves.

Comparing wolves to dogs: what it taught us.

Drawing clear conclusions from comparing wild wolves, free-ranging dogs, and pet dogs is a complex endeavour (Range & Marshall-Pescini, 2022e) because they are simply not comparable in a few respects. First, life experience can affect behavioural responses, for example, wolf populations that have never been hunted by humans tend to not fear humans, unlike populations that have been hunted (Mech & Janssens, 2022). Additionally, pet dogs, free-ranging dogs, and wilds wolves have vastly different experiences with humans. Pet dogs' lives are controlled and heavily scheduled by their owners (Kotrschal, 2018; Smith & Van Valkenburgh, 2021) whereas free-ranging dogs have more agency but still get the majority of their food from humans (Bhadra & Bhadra, 2014). In contrast, most wolf populations are wary of humans and tend to avoid them. Hence, it is important to be aware of all these factors when comparing wolves and dogs (Range & Marshall-Pescini, 2022d). Second, wolves are highly sociable animals who live in packs and rely on cooperation to breed, hunt, and defend their territory from other individuals or packs (Mech & Boitani, 2003). In contrast, free-ranging dogs tend to form multi-male multi-females packs, parental care mostly relies on the mother, and they stay near human settlement to feed on human refuse (Cafazzo et al., 2010, 2014; Majumder et al., 2014; Marshall-Pescini et al., 2017). They live in different ecological niches and therefore differ behaviourally (Range & Marshall-Pescini, 2022b, 2022d). To overcome these problems, researchers need to compare animals with the same life experience (i.e., equally raised and kept individuals). Alternatively, different dog populations can be compared to ass how the environment alters their behaviours.

When all this is taken into account, the previously stated “uniqueness” of dogs' social and cooperative skills (Hare & Tomasello, 2005; Kaminski & Nitzschner, 2013; Miklósi & Topál, 2013) may not be that unique. Indeed, wolves cooperate among themselves in a fine-tuned manner, including high social attentiveness, high tolerance, and a superior ability to learn from conspecifics (Range & Virányi, 2013, 2014). Wolves follow conspecifics’ gaze even behind a barrier (Range & Virányi, 2011) and seem to be sensitive to inequity (Essler et al., 2017). All of these may be considered mental prerequisites for cooperating with humans when appropriately socialized. In certain conditions they even outperform dogs: Wolves cooperate better with each other than dogs in a string-pulling task (Marshall-Pescini, et al., 2017) and are more tolerant towards their conspecifics than dogs (Range & Virányi, 2015). Moreover, human socialized wolves are well able to cooperate with humans but in contrast to dogs, are fond of taking the lead (Range, 2019a; Range, al., 2019b; Range & Virányi, 2011, 2013, 2014; Virányi et al., 2008). Dogs form a close bond with their human caretaker, rely on humans in strange situations, and use them as a safe base (Palmer & Custance, 2008; Prato-Previde et al., 2003; Solomon et al., 2019; Topál et al., 1998). However, also wolves seem to bond with their human caretakers: When young, they greet more familiar humans than unfamiliar ones (Hall et al., 2015) and this preference for familiar people seems to persist throughout adulthood (Lenkei et al., 2020; Ujfalussy et al., 2017; Wheat et al., 2021). Like dogs, wolves benefit from positive reinforcement training sessions with a familiar caretaker as they show reduced salivary cortisol in response (Vasconcellos et al., 2016). Thus, the social-cognitive abilities of wolves and dogs – even towards humans - may be less unique than previously thought.

Domestication hypotheses pertinent to this thesis

There are many dog-related domestication hypotheses (Range & Marshall-Pescini, 2022b for a summary). In my thesis I cannot consider all of them, hence I will only present those here which are most pertinent to my work as they predict dogs' and wolves' behaviours towards humans. These hypotheses are not necessarily mutually exclusive.

The "emotional reactivity hypothesis" (Hare et al., 2012) suggests that selection for reduced aggression and fear (equivalent to tameness) towards humans is the key to dog domestication and as a result, dogs are more docile with humans (Hare & Tomasello, 2005), more tolerant with their conspecifics (Hare et al., 2012), and develop enhanced cognitive skills (Hare et al., 2002). However, recent comparative studies provide conflicting evidence as dogs were not found to be more tolerant towards each other than wolves (Range et al., 2015). Additionally, unlike wolves, dogs lack the ritualistic behaviours that permit reconciliation after conflicts (Cafazzo et al., 2021), which may be due to domestication relaxing the need for conspecific tolerance and reconciliation in dogs (Feddersen-Petersen, 2007; Frank & Frank, 1982).

Based on more comparative studies between similarly raised and kept wolves and dogs, the "canine cooperation hypothesis" (Range & Virányi, 2015) suggests that dogs' social and cooperative skills toward humans are derived from wolves' social abilities toward other wolves. As wolves are tolerant and cooperative within their packs, their emotional and cognitive skills might have been a basis for the development of dog-human cooperation during domestication. Indeed, multiple studies have demonstrated that socialized wolves can perform equally to dogs (Range, Kassis, et al., 2019; Range, Marshall-Pescini, et al., 2019; Range & Marshall-Pescini, 2022a; Range & Virányi, 2011, 2013, 2014; Virányi et al., 2008) and even outperform then in certain tasks (Marshall-Pescini, Schwarz, et al., 2017; Range & Virányi, 2014).

The "two-stage hypothesis" (Udell et al., 2010) predicts that socio-cognitive skills in dogs have dual origins: acceptance of humans as a social partner in early ontogeny and positive conditioning to follow human gestures. Any canids subjected to these two steps would demonstrate socio-cognitive skills similar to dogs', which is the case with socialized wolves (Range & Marshall-Pescini, 2022a) and also in foxes selected for low fear of humans and used to human interaction from a young age (Hare et al., 2005).

The "hypersociality hypothesis" (vonHoldt et al., 2017) suggests that similarly to the human Williams-Beuren syndrome, the genetics of dogs have been altered to increase sociability toward any kind of social partners – humans or conspecifics. As mentioned above, dogs are attached to humans (Prato-Previde et al., 2003; Solomon et al., 2019; Topál et al., 1998) but wolves also can bond with familiar humans when appropriately socialised (Lenkei et al., 2020; Ujfalussy et al., 2017; Wheat et al., 2021); even wolves that have not been thoroughly socialised can differentiate between familiar and unfamiliar human voices (Gammino et al., 2023). Concerning the hormonal mechanism of attachment, dogs seem to have increased oxytocin levels after humans interaction (Handlin et al., 2011). However, when comparing equally raised and kept wolves and dogs to pet dogs, it appeared that only pets dogs have an increase in oxytocin after an interaction with humans, which could mean that life experience also influences the oxytocin, not only domestication system (Wirobski et al., 2021).

Finally, the “deferential hypothesis” (Range, Marshall-Pescini, et al., 2019) posits that due to selection for increased social inhibition, dogs avoid conflict with higher-ranked conspecifics and humans whereas wolves do not. Indeed, in several cognitive tasks that require cooperation, unlike wolves, dogs tend to fail because submissive individuals avoid approaching a dominant one when resources such as food are involved (Dale et al., 2019; Marshall-Pescini et al., 2018). In addition, in the presence of a human, dogs show more inhibitory control than wolves (Marshall-Pescini et al., 2015; Range et al., 2020).

To conclude, all those hypotheses provide different explanations for how wolves’ and dogs’ behaviours toward their environment, and in particular humans, may have changed due to domestication, resulting in dogs increased attention and focus on humans. This is a key point of domestication I try to shed light on in my PhD project.

About the domestication of Chicken

The chicken is another good model to investigate domestication. First, with more than 50 billion individuals (Nicol, 2015), they are the most numerous domestic species worldwide (Lawler, 2016;

Nicol, 2015; Wang et al., 2020). Secondly, like dogs, their modern wild counterpart, the red junglefowl (*Gallus gallus*; RJF), is available for studies, and chicken domestication has been tracked back to 8000 years ago in Southeast Asia (Abdulwahid & Zhao, 2021; Wang et al., 2020). Current populations of RJF are located in S and SE Asia. They are living in families or mixed groups that tend to avoid humans (Schütz et al., 2001; Siegel et al., 1992). This situation allows for direct comparisons between RJF and domestic chicken. White leghorns (WL; *Gallus gallus domesticus*) are a common eggs-laying breed; comparative studies of WL and RJF have demonstrated that domestication has altered chickens behaviorally (Campler et al., 2009; Lindqvist & Jensen, 2009; Schütz et al., 2001), physiologically (Ericsson et al., 2014) and also, genetically (Kerje et al., 2003; Løtvedt et al., 2017). Third, RJF, like Belayev's farm foxes, has been subjected to a domestication replication experiment. The Avian Lab at the University of Linköping had been selectively breeding lines of high and low fear of humans RJF, which has revealed significant insights into the effects of selection for tameness in RJF (Agnvall et al., 2014, 2015; Agnvall & Jensen, 2016; Bélteky et al., 2017; Gjøen & Jensen, 2022; Katajamaa & Jensen, 2021). Taken together, it becomes clear that comparative studies between RJF and WL are invaluable for studying domestication. Although fairly comparing wolves with dogs requires more effort, the two model systems are synergic. One difference might be that as farm animals chickens have been domesticated later (Abdulwahid & Zhao, 2021; Agnvall et al., 2015; Wang et al., 2020) after humans became more sedentary and to fulfill a different purpose than wolves, therefore fit more the classical frame of domesticated animals than dogs (Germonpré et al., 2018; Russell, 2012; Uerpmann & Uerpmann, 2017).

Focus of my PhD project, methodology and chapters’ overview

The primary aim of my thesis was to draw a broad picture of behavioural and emotional adaptations of dogs toward humans and their environment. Hence, I compared how equally raised and kept socialized wolves and dogs react to a human via a series of experimental paradigms covering 1) physiological responses to the presence of a familiar human during rest, 2) overall behavioural response to human presence during daily activity, and 3) behavioural and physiological responses to the social support of a familiar human during a stressful event. The secondary aim of this thesis was to test how these reactions to human presence support or refute the domestication hypotheses cited in a precedent section of this thesis.

As mentioned above, to be conclusive, comparative studies need to compare dogs and wolves on equal footing. Hence in this thesis, I choose to compare equally raised and housed and socialized wolves and dogs, kept at the Wolf Science Center (https://www.wolfscience.at/). Wolf and dog pups were hand-raised in conspecific groups by WSC’s trainers since 10 days old. At five months they were moved to different, already established packs of conspecifics and kept in comparable situations: living in packs in outside closures with the same amount of human socialization and exposure to the environment and various scientific tests. This careful and standardized rearing process ensures that all the animals have similar life experiences and thus allows for a fair comparison of the wolves’ and dogs’ abilities and responses (for more details on the raising of the wolves and dogs see Range & Marshall-Pescini, 2022). This method also allows staff to to train and habituate the animals to various procedures and as a result, a range of biological and physiological measurements were available.

To understand the arousal and stress responses of the animals in various situations, I mainly used cardiac measurements, in particular, heart rate (HR) and heart rate variability (HRV) as they are well-known measurements, indicative of the autonomic nervous system (ANS) activity and commonly used to measure animal welfare and assess emotional state (Kovács et al., 2014; Kreibig, 2010; von Borell et al., 2007).

The ANS ensures homeostasis within the body despite external and internal perturbations (Wehrwein et al., 2016). It is divided into three parts, the sympathetic nervous system, the parasympathetic nervous system, and the enteric nervous system. The sympathetic nervous system is often described as the “fight or flight” component of the ANS whereas the parasympathetic nervous system is described as the “rest and digest” system of the ANS. These two divisions of the ANS operate antagonistically, synergistically, or independently, to regulate the different visceral functions of the body (Shields, 1993; Wehrwein et al., 2016). The enteric nervous system is an extensive web-like structure mainly responsible for the digestive process (Furness, 2012). In addition, the ANS is also involved in the regulation of emotions (Kreibig 2010). For example, Stephen W. Porges in his “polyvagal theory” (Porges, 1995, 1997, 2001, 2003, 2009, 2011) argues that the brain and the heart are linked and that emotional states can influence heartbeats (Porges, 1995). Indeed, the ANS regulates the visceral function and therefore, also regulates the heart. Porges also claimed that the evolution of the ANS is linked to emotional expression and social behaviours (Porges, 2003), thanks to the Nervus vagus. This is the 10th cranial nerve, a major component of the ANS, and its branches regulate the striated muscles of the head, the face, and several visceral organs (Porges, 2001). To summarize, the “polyvagal theory” proposes that the different branches of the Nervus vagus are related to unique and adaptive behavioural strategies, reflecting three phylogenetic stages of the development of the mammalian ANS. However, the phylogenetic component of the polyvagal theory is now criticized because it does not sufficiently consider the existence of social behaviours in taxa other than mammals and birds (Doody et al.,

2023) and therefore, would not accurately depict the evolution of vagal control of HRV (Grossman & Taylor, 2007). Alternatively, the “neurovisceral integration model” (Thayer, 2009; Thayer & Lane, 2000) proposes that the central autonomic network (CAN; Benarroch, 1993), a functional unit of the central nervous system, regulates goal-directed behaviours and adaptability. The outputs of the CAN are mediated through the ANS neurons that also innervate peripherical organs, for the heart via the Nervus vagus. In return, peripherical organs send feedback to the CAN. Thus, the ANS is essential to cope with the environment. However, to my knowledge, the difference in ANS modulation in domesticate vs wild-type animals has not been investigated yet.

As said above, the activity of the ANS can be measured non-invasively through cardiac parameters such as heart rate (HR) and heart rate variability. HR, the number of heartbeats per unit of time, is a relevant variable for assessing mental arousal if bodily movements are taken into account (Maros et al., 2008). Indeed, body position (Maros et al., 2008) and physical activity in general (Visser et al., 2002) increased HR. HRV, the variation over time of the period between consecutive heartbeats (R-R intervals), is a simple measurement of the ANS activity, that could reflect the ability to adapt to changing circumstances (Rajendra Acharya et al., 2006) and the capacity to regulate emotions (Appelhans & Luecken, 2006). In addition, HRV is affected by cognitive processes: perceptual demands, like a discrimination task, influenced more HRV than attentional demands such as sustained attention tasks (Luque-Casado et al., 2013). In general, relaxation is paired with higher HRV values, and higher HRV reflects greater adaptive/regulatory capacity of an individual.

Hence, in chapter one (Jean-Joseph et al., 2020), I compared equally raised and kept human-socialised wolves’ and dogs’ cardiac outputs at rest. Each subject was tested in three conditions, alone, with a familiar human, and with its packs. My aims were: First, to replicate Kortekaas and Kotrschal's study (2019) on socialised wolves and dogs. In their study, dogs were found more alert than wolves at rest. However, the subjects were observed by an unfamiliar human. According to the “hypersociability hypothesis” (vonHoldt et al., 2017), dogs might have a higher drive to interact with social partners, which could mean that, unlike the wolves, dogs in Kortekaas and Kotrschal study might have been more interested in the unfamiliar human than wolves. Second, I aimed to compare socialised wolves’ and dogs' relaxation during rest and inactive wakefulness. Finally, I wanted to assess the effect of social support by a familiar human as compared to being alone or with pack members. According to the emotional reactivity hypothesis dogs would be more relaxed than wolves no matter the conditions. Under the assumption of the “hypersociability hypothesis” (vonHoldt et al., 2017), dogs would be more affected by any social condition than wolves. The “deferential hypothesis” predicted that dogs would be more affected by humans than wolves and finally, the canine cooperation hypothesis (Range & Virányi, 2015) and two-stage hypothesis (Udell et al., 2010) assume that dogs and socialized wolves would react similarly to humans and conspecifics.

In chapter two (Jean-Joseph et al., 2022), I focused on a less experimental and artificial context. I broadened my observations and assessed the daily activities of equally raised kept, and socialized wolves and dogs over a year. My aims were threefold, first established a comparative daylight time budget for socialised wolves and dogs, which had never been done before. Second, I wanted to assess the possible effects of domestication on their time budgets, taking into account that in the wild, main drivers of time budgets, such as seasonality and biological cycle, would also have an effect. Finally, in line with chapter one, I assessed humans as potential social Zeitgeber for socialised wolves and dogs by measuring the impact of visitors on their level of activity. Due to domestication, I expected dogs to be less energy-efficient and more active overall than wolves. However, I expected that natural factors, such as season and temperature, would have the same effect on them, as both our socialised wolves and dogs live outside year-round. Additionally, along the line of “hypersociability hypothesis” (vonHoldt et al., 2017) and “deferential hypothesis” (Range, Marshall-Pescini, et al., 2019), I expect dogs to react more strongly to the presense of humans than wolves.

In chapter three (Jean-Joseph et al., submitted), I took a more classical approach and assessed the other end of the relaxation/stress axis by observing physiological (i.e., cardiac outputs) and behavioural responses to fear and stress when facing a stressor in order to acquire food, i.e., a risk-taking paradigm. Due to the down-regulation of the stress system in domesticated animals, I predicted that dogs would show less reaction behaviorally and physiologically to stress and fear, as well as being bolder and taking the food sooner than wolves. Subjects were tested in two conditions, alone and with a familiar human. Under the assumption of the “hypersociability hypothesis” (vonHoldt et al., 2017) and “emotional reactivity hypothesis” (Hare et al., 2012), dogs would benefit from the presence of a familiar human and be even less stressed when wolves would not. Alternatively, the “canine cooperation hypothesis” (Range & Virányi, 2015) and the “two-stage hypothesis” (Udell et al., 2010) would predict that socialised wolves and dogs would react to, and behave, similarly to the presence of a familiar human.

Finally, faced with the somewhat uniqueness of the dogs’ case (Germonpré et al., 2018; Russell, 2012; Uerpmann & Uerpmann, 2017), I chose to broaden my investigation to another domesticated species, the chicken (Gjøen et al., 2023). In chapter four, I focused once more on comparing reactions to stress and fear during a risk-taking experiment, this time using red junglefowl (RJF), the wild counterpart of all domesticated poultry, and the white leghorn (WL), a breed of chicken selected for eggs laying. Subjects were tested in two conditions, alone and with the presence of a conspecific. In agreement with the selection for the tameness hypothesis (Darwin, 1868; Wilkins et al., 2014), I expected WL to be less affected by the risk-taking paradigm than RJF. Additionally, as domesticated might have relaxed the need for a social partner, both wild and domesticated chicks would be affected by the presence of a social partner but the effect would be stronger in RJF.

With the present studies, I add the ongoing domestication debate by testing the subtle nuances of different domestication hypotheses in regards to dogs' and socialised wolves' perception of their environment and particularly, humans, and suggest that domestication results in more complex mental and behavioral patterns than generally thought.

References

Abdulwahid, A. M., & Zhao, J. B. (2021). China as a Center of Origin and Domestication of Chicken: A Review. *Agricultural Reviews*. https://arccjournals.com/journal/agricultural-reviews/R-206

Agnvall, B., Ali, A., Olby, S., & Jensen, P. (2014). Red Junglefowl (Gallus gallus) selected for low fear of humans are larger, more dominant and produce larger offspring. *Animal*, *8*(9), 1498–1505. https://doi.org/10.1017/S1751731114001426

Agnvall, B., & Jensen, P. (2016). Effects of Divergent Selection for Fear of Humans on Behaviour in Red Junglefowl. *PLOS ONE*, *11*(11), e0166075. https://doi.org/10.1371/journal.pone.0166075

Agnvall, B., Katajamaa, R., Altimiras, J., & Jensen, P. (2015). Is domestication driven by reduced fear of humans? Boldness, metabolism and serotonin levels in divergently selected red junglefowl (Gallus gallus). *Biology Letters*, *11*(9), Article 9. https://doi.org/10.1098/rsbl.2015.0509

Appelhans, B. M., & Luecken, L. J. (2006). Heart rate variability as an index of regulated emotional responding. *Review of General Psychology*, *10*(3), Article 3. https://doi.org/10.1037/1089-2680.10.3.229

Bélteky, J., Agnvall, B., & Jensen, P. (2017). Gene expression of behaviorally relevant genes in the cerebral hemisphere changes after selection for tameness in Red Junglefowl. *PLOS ONE*, *12*(5), e0177004. https://doi.org/10.1371/journal.pone.0177004

Belyaev, D. K. (1979). Destabilizing selection as a factor in domestication. *Journal of Heredity*, *70*(5), Article 5. https://doi.org/10.1093/oxfordjournals.jhered.a109263

Belyaev, D. K., Plyusnina, I. Z., & Trut, L. N. (1985). Domestication in the silver fox (Vulpes fulvus Desm): Changes in physiological boundaries of the sensitive period of primary socialization. *Applied Animal Behaviour Science*, *13*(4), Article 4. https://doi.org/10.1016/0168-1591(85)90015-2

Benarroch, E. E. (1993). The Central Autonomic Network: Functional Organization, Dysfunction, and Perspective. *Mayo Clinic Proceedings*, *68*(10), 988–1001. https://doi.org/10.1016/S0025-6196(12)62272-1

Bergström, A., Frantz, L., Schmidt, R., Ersmark, E., Lebrasseur, O., Girdland-Flink, L., Lin, A. T., Storå, J., Sjögren, K.-G., Anthony, D., Antipina, E., Amiri, S., Bar-Oz, G., Bazaliiskii, V. I., Bulatović, J., Brown, D., Carmagnini, A., Davy, T., Fedorov, S., … Skoglund, P. (2020). Origins and genetic legacy of prehistoric dogs. *Science*, *370*(6516), 557–564. https://doi.org/10.1126/science.aba9572

Bhadra, A., & Bhadra, A. (2014). Preference for meat is not innate in dogs. *Journal of Ethology*, *32*(1), Article 1. https://doi.org/10.1007/s10164-013-0388-7

Botigué, L. R., Song, S., Scheu, A., Gopalan, S., Pendleton, A. L., Oetjens, M., Taravella, A. M., Seregély, T., Zeeb-Lanz, A., Arbogast, R.-M., Bobo, D., Daly, K., Unterländer, M., Burger, J., Kidd, J. M., & Veeramah, K. R. (2017). Ancient European dog genomes reveal continuity since the Early Neolithic. *Nature Communications*, *8*, 16082. https://doi.org/10.1038/ncomms16082

Cafazzo, S., Bonanni, R., Valsecchi, P., & Natoli, E. (2014). Social Variables Affecting Mate Preferences, Copulation and Reproductive Outcome in a Pack of Free-Ranging Dogs. *PLOS ONE*, *9*(6), Article 6. https://doi.org/10.1371/journal.pone.0098594

Cafazzo, S., Marshall-Pescini, S., Lazzaroni, M., Virányi, Z., & Range, F. (2021). The effect of domestication on post-conflict management: Wolves reconcile while dogs avoid each other. *Royal Society Open Science*, *5*(7), Article 7. https://doi.org/10.1098/rsos.171553

Cafazzo, S., Valsecchi, P., Bonanni, R., & Natoli, E. (2010). Dominance in relation to age, sex, and competitive contexts in a group of free-ranging domestic dogs. *Behavioral Ecology*, *21*(3), Article 3. https://doi.org/10.1093/beheco/arq001

Clutton-Brock, J. (1992). The process of domestication. *Mammal Review*, *22*(2), Article 2. https://doi.org/10.1111/j.1365-2907.1992.tb00122.x

Coppinger, R., & Coppinger, L. (2001). *Dogs: A Startling New Understanding of Canine Origin, Behavior & Evolution*. Simon and Schuster.

Dale, R., Palma-Jacinto, S., Marshall-Pescini, S., & Range, F. (2019). Wolves, but not dogs, are prosocial in a touch screen task. *PLOS ONE*, *14*(5), e0215444. https://doi.org/10.1371/journal.pone.0215444

Darwin, C. (1868). *The Variation of Animals and Plants Under Domestication*. O. Judd.

Diamond, J. (2002). Evolution, consequences and future of plant and animal domestication. *Nature*, *418*(6898), Article 6898. https://doi.org/10.1038/nature01019

Doody, J. S., Burghardt, G., & Dinets, V. (2023). The evolution of sociality and the polyvagal theory. *Biological Psychology*, *180*, 108569. https://doi.org/10.1016/j.biopsycho.2023.108569

Driscoll, C. A., Macdonald, D. W., & O'Brien, S. J. (2009). From wild animals to domestic pets, an evolutionary view of domestication. *Proceedings of the National Academy of Sciences*, *106*(supplement_1), 9971–9978. https://doi.org/10.1073/pnas.0901586106

Ericsson, M., Fallahsharoudi, A., Bergquist, J., Kushnir, M. M., & Jensen, P. (2014). Domestication effects on behavioural and hormonal responses to acute stress in chickens. *Physiology & Behavior*, *133*, 161–169. https://doi.org/10.1016/j.physbeh.2014.05.024

Essler, J. L., Marshall-Pescini, S., & Range, F. (2017). Domestication Does Not Explain the Presence of Inequity Aversion in Dogs. *Current Biology*, *27*(12), Article 12. https://doi.org/10.1016/j.cub.2017.05.061

Feddersen-Petersen, D. U. (2007). Social behaviour of dogs and related canids. *The Behavioural Biology of Dogs*, 105–119. https://doi.org/10.1079/9781845931872.0105

Frank, H., & Frank, M. G. (1982). On the effects of domestication on canine social development and behavior. *Applied Animal Ethology*, *8*(6), Article 6. https://doi.org/10.1016/0304-3762(82)90215-2

Frantz, L. A. F., Mullin, V. E., Pionnier-Capitan, M., Lebrasseur, O., Ollivier, M., Perri, A., Linderholm, A., Mattiangeli, V., Teasdale, M. D., Dimopoulos, E. A., Tresset, A., Duffraisse, M., McCormick, F., Bartosiewicz, L., Gál, E., Nyerges, É. A., Sablin, M. V., Bréhard, S., Mashkour, M., … Larson, G. (2016). Genomic and archaeological evidence suggest a dual origin of domestic dogs. *Science*, *352*(6290), Article 6290. https://doi.org/10.1126/science.aaf3161

Furness, J. B. (2012). The enteric nervous system and neurogastroenterology. *Nature Reviews Gastroenterology & Hepatology*, *9*(5), Article 5. https://doi.org/10.1038/nrgastro.2012.32

Gammino, B., Palacios, V., Root-Gutteridge, H., Reby, D., & Gamba, M. (2023). Grey wolves (Canis lupus) discriminate between familiar and unfamiliar human voices. *Animal Cognition*. https://doi.org/10.1007/s10071-023-01796-9

Germonpré, M., Galetova, M., Sablin, M., & Bocherens, H. (2018). *Self-domestication or human control? The Upper Palaeolithic domestication of the wolf* (pp. 39–64).

Germonpré, M., Van den Broeck, M., Lázničková-Galetová, M., Sablin, M. V., & Bocherens, H. (2021). Mothering the Orphaned Pup: The Beginning of a Domestication Process in the Upper Palaeolithic. *Human Ecology*, *49*(6), 677–689. https://doi.org/10.1007/s10745-021-00234-z

Gjøen, J., Jean-Joseph, H., Kotrschal, K., & Jensen, P. (2023). Domestication and social environment modulate fear responses in young chickens. *Behavioural Processes*, *210*, 104906. https://doi.org/10.1016/j.beproc.2023.104906

Gjøen, J., & Jensen, P. (2022). Selection for Reduced Fear of Humans Changes Intra-Specific Social Behavior in Red Junglefowl—Implications for Chicken Domestication. *Genes*, *13*(1), Article 1. https://doi.org/10.3390/genes13010043

Grimm, D. (2015). Dawn of the dog. *Science*, *348*(6232), 274–279. https://doi.org/10.1126/science.348.6232.274

Grossman, P., & Taylor, E. W. (2007). Toward understanding respiratory sinus arrhythmia: Relations to cardiac vagal tone, evolution and biobehavioral functions. *Biological Psychology*, *74*(2), 263–285. https://doi.org/10.1016/j.biopsycho.2005.11.014

Hall, N. J., Lord, K., Arnold, A.-M. K., Wynne, C. D. L., & Udell, M. A. R. (2015). Assessment of attachment behaviour to human caregivers in wolf pups (Canis lupus lupus). *Behavioural Processes*, *110*(Supplement C), Article Supplement C. https://doi.org/10.1016/j.beproc.2014.11.005

Handlin, L., Hydbring-Sandberg, E., Nilsson, A., Ejdebäck, M., Jansson, A., & Uvnäs-Moberg, K. (2011). Short-Term Interaction between Dogs and Their Owners: Effects on Oxytocin, Cortisol, Insulin and Heart Rate—An Exploratory Study. *Anthrozoös*, *24*(3), Article 3. https://doi.org/10.2752/175303711X13045914865385

Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The Domestication of Social Cognition in Dogs. *Science*, *298*(5598), Article 5598. https://doi.org/10.1126/science.1072702

Hare, B., Plyusnina, I., Ignacio, N., Schepina, O., Stepika, A., Wrangham, R., & Trut, L. (2005). Social Cognitive Evolution in Captive Foxes Is a Correlated By-Product of Experimental Domestication. *Current Biology*, *15*(3), Article 3. https://doi.org/10.1016/j.cub.2005.01.040

Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Sciences*, *9*(9), Article 9. https://doi.org/10.1016/j.tics.2005.07.003

Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour*, *83*(3), Article 3. https://doi.org/10.1016/j.anbehav.2011.12.007

Jean-Joseph, H., Dooey, G., & Kotrschal, K. (2022). Diurnal activity patterns of equally socialized and kept wolves, Canis lupus, and dogs, Canis lupus familiaris. *Animal Behaviour*, *190*, 41–52. https://doi.org/10.1016/j.anbehav.2022.05.009

Jean-Joseph, H., Kortekaas, K., Range, F., & Kotrschal, K. (2020). Context-Specific Arousal During Resting in Wolves and Dogs: Effects of Domestication? *Frontiers in Psychology*, *11*. https://www.frontiersin.org/articles/10.3389/fpsyg.2020.568199

Jean-Joseph, H., Kortekaas, K., Range, F., & Kotrschal, K. (submitted). Equally raised and kept wolves and dogs show similar risk-proneness – no matter whether alone or with a familiar human. *PLOS ONE*.

Kaminski, J., & Nitzschner, M. (2013). Do dogs get the point? A review of dog–human communication ability. *Learning and Motivation*, *44*(4), Article 4. https://doi.org/10.1016/j.lmot.2013.05.001

Katajamaa, R., & Jensen, P. (2021). Tameness correlates with domestication related traits in a Red Junglefowl intercross. *Genes, Brain and Behavior*, *20*(3), e12704. https://doi.org/10.1111/gbb.12704

Kerje, S., Carlborg, Ö., Jacobsson, L., Schütz, K., Hartmann, C., Jensen, P., & Andersson, L. (2003). The two-fold difference in adult size between the red junglefowl and White Leghorn chickens is largely explained by a limited number of QTLs. *Animal Genetics*, *34*(4), 264–274. https://doi.org/10.1046/j.1365-2052.2003.01000.x

Klinghammer, E., & Goodmann, P. A. (1987). *The Management and Socialization of Captive Wolves (Canis Lupus) at Wolf Park*. North American Wildlife Park Foundation.

Kortekaas, K., & Kotrschal, K. (2019). Does socio-ecology drive differences in alertness between wolves and dogs when resting? *Behavioural Processes*, *166*, 103877. https://doi.org/10.1016/j.beproc.2019.05.024

Kotrschal, K. (2018). How Wolves Turned into Dogs and How Dogs Are Valuable in Meeting Human Social Needs. *People and Animals: The International Journal of Research and Practice*, *1*(1), Article 1. https://docs.lib.purdue.edu/paij/vol1/iss1/6

Kovács, L., Jurkovich, V., Bakony, M., Szenci, O., Póti, P., & Tőzsér, J. (2014). Welfare implication of measuring heart rate and heart rate variability in dairy cattle: Literature review and conclusions for future research. *Animal*, *8*(2), 316–330. https://doi.org/10.1017/S1751731113002140

Kreibig, S. D. (2010). Autonomic nervous system activity in emotion: A review. *Biological Psychology*, *84*(3), Article 3. https://doi.org/10.1016/j.biopsycho.2010.03.010

Larson, G. (2011). Genetics and Domestication: Important Questions for New Answers. *Current Anthropology*, *52*(S4), S485–S495. https://doi.org/10.1086/658401

Larson, G., Karlsson, E. K., Perri, A., Webster, M. T., Ho, S. Y. W., Peters, J., Stahl, P. W., Piper, P. J., Lingaas, F., Fredholm, M., Comstock, K. E., Modiano, J. F., Schelling, C., Agoulnik, A. I., Leegwater, P. A., Dobney, K., Vigne, J.-D., Vilà, C., Andersson, L., & Lindblad-Toh, K. (2012). Rethinking dog domestication by integrating genetics, archeology, and biogeography. *Proceedings of the National Academy of Sciences*, *109*(23), Article 23. https://doi.org/10.1073/pnas.1203005109

Larson, G., Piperno, D. R., Allaby, R. G., Purugganan, M. D., Andersson, L., Arroyo-Kalin, M., Barton, L., Climer Vigueira, C., Denham, T., Dobney, K., Doust, A. N., Gepts, P., Gilbert, M. T. P., Gremillion, K. J., Lucas, L., Lukens, L., Marshall, F. B., Olsen, K. M., Pires, J. C., … Fuller, D. Q. (2014). Current perspectives and the future of domestication studies. *Proceedings of the National Academy of Sciences*, *111*(17), 6139–6146. https://doi.org/10.1073/pnas.1323964111

Lawler, A. (2016). *Why Did the Chicken Cross the World?: The Epic Saga of the Bird that Powers Civilization*. Simon and Schuster.

Lenkei, R., Újváry, D., Bakos, V., & Faragó, T. (2020). Adult, intensively socialized wolves show features of attachment behaviour to their handler. *Scientific Reports*, *10*(1), Article 1. https://doi.org/10.1038/s41598-020-74325-0

Lord, K. A., Larson, G., Coppinger, R. P., & Karlsson, E. K. (2020). The History of Farm Foxes Undermines the Animal Domestication Syndrome. *Trends in Ecology & Evolution*, *35*(2), 125–136. https://doi.org/10.1016/j.tree.2019.10.011

Løtvedt, P., Fallahshahroudi, A., Bektic, L., Altimiras, J., & Jensen, P. (2017). Chicken domestication changes expression of stress-related genes in brain, pituitary and adrenals. *Neurobiology of Stress*, *7*, 113–121. https://doi.org/10.1016/j.ynstr.2017.08.002

Lupo, K. D. (2019). Hounds follow those who feed them: What can the ethnographic record of hunter-gatherers reveal about early human-canid partnerships? *Journal of Anthropological Archaeology*, *55*, 101081. https://doi.org/10.1016/j.jaa.2019.101081

Luque-Casado, A., Zabala, M., Morales, E., Mateo-March, M., & Sanabria, D. (2013). Cognitive Performance and Heart Rate Variability: The Influence of Fitness Level. *PLoS ONE*, *8*(2), Article 2. https://doi.org/10.1371/journal.pone.0056935

Majumder, S. S., Bhadra, A., Ghosh, A., Mitra, S., Bhattacharjee, D., Chatterjee, J., Nandi, A. K., & Bhadra, A. (2014). To be or not to be social: Foraging associations of free-ranging dogs in an urban ecosystem. *Acta Ethologica*, *17*(1), Article 1. https://doi.org/10.1007/s10211-013-0158-0

Maros, K., Dóka, A., & Miklósi, Á. (2008). Behavioural correlation of heart rate changes in family dogs. *Applied Animal Behaviour Science*, *109*(2–4), Article 2–4. https://doi.org/10.1016/j.applanim.2007.03.005

Marshall-Pescini, S., Basin, C., & Range, F. (2018). A task-experienced partner does not help dogs be as successful as wolves in a cooperative string-pulling task. *Scientific Reports*, *8*(1), Article 1. https://doi.org/10.1038/s41598-018-33771-7

Marshall-Pescini, S., Cafazzo, S., Virányi, Z., & Range, F. (2017). Integrating social ecology in explanations of wolf–dog behavioral differences. *Current Opinion in Behavioral Sciences*, *16*, 80–86. https://doi.org/10.1016/j.cobeha.2017.05.002

Marshall-Pescini, S., Schwarz, J. F. L., Kostelnik, I., Virányi, Z., & Range, F. (2017). Importance of a species' socioecology: Wolves outperform dogs in a conspecific cooperation task. *Proceedings of the National Academy of Sciences*, 201709027. https://doi.org/10.1073/pnas.1709027114

Marshall-Pescini, S., Virányi, Z., & Range, F. (2015). The Effect of Domestication on Inhibitory Control: Wolves and Dogs Compared. *PLOS ONE*, *10*(2), e0118469. https://doi.org/10.1371/journal.pone.0118469

Mech, L. D., & Boitani, L. (2003). *Wolves: Behavior, Ecology, and Conservation*. University of Chicago Press.

Mech, L. D., & Janssens, L. A. A. (2022). An assessment of current wolf Canis lupus domestication hypotheses based on wolf ecology and behaviour. *Mammal Review*, *52*(2), 304–314. https://doi.org/10.1111/mam.12273

Miklósi, Á., & Topál, J. (2013). What does it take to become 'best friends'? Evolutionary changes in canine social competence. *Trends in Cognitive Sciences*, *17*(6), Article 6. https://doi.org/10.1016/j.tics.2013.04.005

Nicol, C. J. (2015). *The Behavioural Biology of Chickens*. CABI.

Ovodov, N. D., Crockford, S. J., Kuzmin, Y. V., Higham, T. F. G., Hodgins, G. W. L., & Plicht, J. van der. (2011). A 33,000-Year-Old Incipient Dog from the Altai Mountains of Siberia: Evidence of the Earliest Domestication Disrupted by the Last Glacial Maximum. *PLOS ONE*, *6*(7), Article 7. https://doi.org/10.1371/journal.pone.0022821

Palmer, R., & Custance, D. (2008). A counterbalanced version of Ainsworth's Strange Situation Procedure reveals secure-base effects in dog–human relationships. *Applied Animal Behaviour Science*, *109*(2), Article 2. https://doi.org/10.1016/j.applanim.2007.04.002

Perri, A. R., Feuerborn, T. R., Frantz, L. A. F., Larson, G., Malhi, R. S., Meltzer, D. J., & Witt, K. E. (2021). Dog domestication and the dual dispersal of people and dogs into the Americas. *Proceedings of the National Academy of Sciences*, *118*(6), e2010083118. https://doi.org/10.1073/pnas.2010083118

Porges, S. W. (1995). Orienting in a defensive world: Mammalian modifications of our evolutionary heritage. A Polyvagal Theory. *Psychophysiology*, *32*(4), Article 4. https://doi.org/10.1111/j.1469-8986.1995.tb01213.x

Porges, S. W. (1997). Emotion: An Evolutionary By-Product of the Neural Regulation of the Autonomic Nervous Systema. *Annals of the New York Academy of Sciences*, *807*(1), Article 1. https://doi.org/10.1111/j.1749-6632.1997.tb51913.x

Porges, S. W. (2001). The polyvagal theory: Phylogenetic substrates of a social nervous system. *International Journal of Psychophysiology*, *42*(2), Article 2. https://doi.org/10.1016/S0167-8760(01)00162-3

Porges, S. W. (2003). The Polyvagal Theory: Phylogenetic contributions to social behavior. *Physiology & Behavior*, *79*(3), Article 3. https://doi.org/10.1016/S0031-9384(03)00156-2

Porges, S. W. (2009). The polyvagal theory: New insights into adaptive reactions of the autonomic nervous system. *Cleveland Clinic Journal of Medicine*, *76*(Suppl 2), Article Suppl 2. https://doi.org/10.3949/ccjm.76.s2.17

Porges, S. W. (2011). *The Polyvagal Theory: Neurophysiological Foundations of Emotions, Attachment, Communication, and Self-regulation (Norton Series on Interpersonal Neurobiology)*. W. W. Norton & Company.

Prato-Previde, E., Spiezio, C., Sabatini, F., & Custance, D. M. (2003). Is the dog-human relationship an attachment bond? An observational study using Ainsworth's strange situation. *Behaviour*, *140*(2), Article 2. https://doi.org/10.1163/156853903321671514

Price, E. O. (1984). Behavioral Aspects of Animal Domestication. *The Quarterly Review of Biology*, *59*(1), 1–32. https://doi.org/10.1086/413673

Price, E. O. (1999). Behavioral development in animals undergoing domestication. *Applied Animal Behaviour Science*, *65*(3), Article 3. https://doi.org/10.1016/S0168-1591(99)00087-8

Price, E. O. (2002). *Animal domestication and behavior*. CABI Pub.

Purugganan, M. D. (2022). What is domestication? *Trends in Ecology & Evolution*, *37*(8), 663–671. https://doi.org/10.1016/j.tree.2022.04.006

Rajendra Acharya, U., Paul Joseph, K., Kannathal, N., Lim, C. M., & Suri, J. S. (2006). Heart rate variability: A review. *Medical & Biological Engineering & Computing*, *44*(12), Article 12. https://doi.org/10.1007/s11517-006-0119-0

Range, F., Brucks, D., & Virányi, Z. (2020). Dogs wait longer for better rewards than wolves in a delay of gratification task: But why? *Animal Cognition*, *23*(3), 443–453. https://doi.org/10.1007/s10071-020-01346-7

Range, F., Kassis, A., Taborsky, M., Boada, M., & Marshall-Pescini, S. (2019). Wolves and dogs recruit human partners in the cooperative string-pulling task. *Scientific Reports*, *9*(1), Article 1. https://doi.org/10.1038/s41598-019-53632-1

Range, F., & Marshall-Pescini, S. (2022a). Comparing the Behaviour and Cognition of Wolves and Dogs. In F. Range & S. Marshall-Pescini (Eds.), *Wolves and Dogs: Between Myth and Science* (pp. 19–46). Springer International Publishing. https://doi.org/10.1007/978-3-030-98411-3_2

Range, F., & Marshall-Pescini, S. (2022b). Comparing wolves and dogs: Current status and implications for human 'self-domestication.' *Trends in Cognitive Sciences*, *26*(4), 337–349. https://doi.org/10.1016/j.tics.2022.01.003

Range, F., & Marshall-Pescini, S. (2022c). Domestication Hypotheses Relating to Behaviour and Cognition: Which Are Supported by the Current Data? In F. Range & S. Marshall-Pescini (Eds.), *Wolves and Dogs: Between Myth and Science* (pp. 335–373). Springer International Publishing. https://doi.org/10.1007/978-3-030-98411-3_11

Range, F., & Marshall-Pescini, S. (2022d). Taking confounding factors and life experience seriously. *Trends in Cognitive Sciences*, *26*(9), 730–731. https://doi.org/10.1016/j.tics.2022.06.007

Range, F., & Marshall-Pescini, S. (2022e). *Wolves and Dogs: Between Myth and Science*. Springer International Publishing. https://doi.org/10.1007/978-3-030-98411-3

Range, F., Marshall-Pescini, S., Kratz, C., & Virányi, Z. (2019). Wolves lead and dogs follow, but they both cooperate with humans. *Scientific Reports*, *9*(1), Article 1. https://doi.org/10.1038/s41598-019-40468-y

Range, F., Ritter, C., & Virányi, Z. (2015). Testing the myth: Tolerant dogs and aggressive wolves. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1807), Article 1807. https://doi.org/10.1098/rspb.2015.0220

Range, F., & Virányi, Z. (2011). Development of Gaze Following Abilities in Wolves (Canis Lupus). *PLOS ONE*, *6*(2), Article 2. https://doi.org/10.1371/journal.pone.0016888

Range, F., & Virányi, Z. (2013). Social learning from humans or conspecifics: Differences and similarities between wolves and dogs. *Frontiers in Psychology*, *4*. https://doi.org/10.3389/fpsyg.2013.00868

Range, F., & Virányi, Z. (2014). Wolves Are Better Imitators of Conspecifics than Dogs. *PLOS ONE*, *9*(1), Article 1. https://doi.org/10.1371/journal.pone.0086559

Range, F., & Virányi, Z. (2015). Tracking the evolutionary origins of dog-human cooperation: The “Canine Cooperation Hypothesis.” *Frontiers in Psychology*, *5*. https://doi.org/doi.org/10.3389/fpsyg.2014.01582

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

Sánchez-Villagra, M. R., Geiger, M., & Schneider, R. A. (2016). The taming of the neural crest: A developmental perspective on the origins of morphological covariation in domesticated mammals. *Royal Society Open Science*, *3*(6), 160107. https://doi.org/10.1098/rsos.160107

Schütz, K. E., Forkman, B., & Jensen, P. (2001). Domestication effects on foraging strategy, social behaviour and different fear responses: A comparison between the red junglefowl (Gallus gallus) and a modern layer strain. *Applied Animal Behaviour Science*, *74*(1), 1–14. https://doi.org/10.1016/S0168-1591(01)00156-3

Serpell, J. A. (2021). Commensalism or Cross-Species Adoption? A Critical Review of Theories of Wolf Domestication. *Frontiers in Veterinary Science*, *8*. https://www.frontiersin.org/articles/10.3389/fvets.2021.662370

Shields, R. W. J. (1993). Functional Anatomy of the Autonomic Nervous System. *Journal of Clinical Neurophysiology*, *10*(1), Article 1.

Siegel, P. B., Haberfeld, A., Mukherjee, T. K., Stallard, L. C., Marks, H. L., Anthony, N. B., & Dunnington, E. A. (1992). Jungle fowl–domestic fowl relationships: A use of DNA fingerprinting. *World’s Poultry Science Journal*, *48*(2), 147–155. https://doi.org/10.1079/WPS19920014

Smith, T. D., & Van Valkenburgh, B. (2021). The dog–human connection. *The Anatomical Record*, *304*(1), Article 1. https://doi.org/10.1002/ar.24534

Smýkal, P., Nelson, M. N., Berger, J. D., & Von Wettberg, E. J. B. (2018). The Impact of Genetic Changes during Crop Domestication. *Agronomy*, *8*(7), Article 7. https://doi.org/10.3390/agronomy8070119

Solomon, J., Beetz, A., Schöberl, I., Gee, N., & Kotrschal, K. (2019). Attachment security in companion dogs: Adaptation of Ainsworth’s strange situation and classification procedures to dogs and their human caregivers. *Attachment & Human Development*, *21*(4), Article 4. https://doi.org/10.1080/14616734.2018.1517812

Tancredi, D., & Cardinali, I. (2023). Being a Dog: A Review of the Domestication Process. *Genes*, *14*(5), Article 5. https://doi.org/10.3390/genes14050992

Thalmann, O., Shapiro, B., Cui, P., Schuenemann, V. J., Sawyer, S. K., Greenfield, D. L., Germonpré, M. B., Sablin, M. V., López-Giráldez, F., Domingo-Roura, X., Napierala, H., Uerpmann, H.-P., Loponte, D. M., Acosta, A. A., Giemsch, L., Schmitz, R. W., Worthington, B., Buikstra, J. E., Druzhkova, A., … Wayne, R. K. (2013). Complete Mitochondrial Genomes of Ancient Canids Suggest a European Origin of Domestic Dogs. *Science*, *342*(6160), Article 6160. https://doi.org/10.1126/science.1243650

Thayer, J. F. (2009). Heart Rate Variability: A Neurovisceral Integration Model. In *Encyclopedia of Neuroscience* (pp. 1041–1047). Elsevier. https://doi.org/10.1016/B978-008045046-9.01991-4

Thayer, J. F., & Lane, R. D. (2000). A model of neurovisceral integration in emotion regulation and dysregulation. *Journal of Affective Disorders*, *61*(3), Article 3. https://doi.org/10.1016/S0165-0327(00)00338-4

Topál, J., Miklósi, Á., Csányi, V., & Dóka, A. (1998). Attachment behavior in dogs (Canis familiaris): A new application of Ainsworth's (1969) Strange Situation Test. *Journal of Comparative Psychology*, *112*(3), Article 3. https://doi.org/10.1037/0735-7036.112.3.219

Trut, L. (1999). Early Canid Domestication: The Farm-Fox Experiment. *American Scientist*, *87*(2), Article 2. https://doi.org/10.1511/1999.2.160

Trut, L. N., Plyusnina, I. Z., & Oskina, I. N. (2004). An Experiment on Fox Domestication and Debatable Issues of Evolution of the Dog. *Russian Journal of Genetics*, *40*(6), Article 6. https://doi.org/10.1023/B:RUGE.0000033312.92773.c1

Trut, L., Oskina, I., & Kharlamova, A. (2009). Animal evolution during domestication: The domesticated fox as a model. *BioEssays*, *31*(3), Article 3. https://doi.org/10.1002/bies.200800070

Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2010). What did domestication do to dogs? A new account of dogs' sensitivity to human actions. *Biological Reviews*, *85*(2), Article 2. https://doi.org/10.1111/j.1469-185X.2009.00104.x

Uerpmann, H.-P., & Uerpmann, M. (2017). The "Commodification" of Animals. In A. Tsuneki, S. Yamada, & K. Hisada (Eds.), *Ancient West Asian Civilization: Geoenvironment and Society in the Pre-Islamic Middle East* (pp. 99–113). Springer. https://doi.org/10.1007/978-981-10-0554-1_7

Ujfalussy, D. J., Kurys, A., Kubinyi, E., Gácsi, M., & Virányi, Z. (2017). Differences in greeting behaviour towards humans with varying levels of familiarity in hand-reared wolves (Canis lupus). *Royal Society Open Science*, *4*(6), Article 6. https://doi.org/10.1098/rsos.160956

Vasconcellos, A. da S., Virányi, Z., Range, F., Ades, C., Scheidegger, J. K., Möstl, E., & Kotrschal, K. (2016). Training Reduces Stress in Human-Socialised Wolves to the Same Degree as in Dogs. *PLOS ONE*, *11*(9), Article 9. https://doi.org/10.1371/journal.pone.0162389

Virányi, Z., Gácsi, M., Kubinyi, E., Topál, J., Belényi, B., Ujfalussy, D., & Miklósi, Á. (2008). Comprehension of human pointing gestures in young human-reared wolves (Canis lupus) and dogs (Canis familiaris). *Animal Cognition*, *11*(3), Article 3. https://doi.org/10.1007/s10071-007-0127-y

Visser, E. K., van Reenen, C. G., van der Werf, J. T. N., Schilder, M. B. H., Knaap, J. H., Barneveld, A., & Blokhuis, H. J. (2002). Heart rate and heart rate variability during a novel object test and a handling test in young horses. *Physiology & Behavior*, *76*(2), Article 2. https://doi.org/10.1016/S0031-9384(02)00698-4

von Borell, E., Langbein, J., Després, G., Hansen, S., Leterrier, C., Marchant-Forde, J., Marchant-Forde, R., Minero, M., Mohr, E., Prunier, A., Valance, D., & Veissier, I. (2007). Heart rate variability as a measure of autonomic regulation of cardiac activity for assessing stress and welfare in farm animals—A review. *Physiology & Behavior*, *92*(3), Article 3. https://doi.org/10.1016/j.physbeh.2007.01.007

vonHoldt, B. M., Shuldiner, E., Koch, I. J., Kartzinel, R. Y., Hogan, A., Brubaker, L., Wanser, S., Stahler, D., Wynne, C. D. L., Ostrander, E. A., Sinsheimer, J. S., & Udell, M. A. R. (2017). Structural variants in genes associated with human Williams-Beuren syndrome underlie stereotypical hypersociability in domestic dogs. *Science Advances*, *3*(7), Article 7. https://doi.org/10.1126/sciadv.1700398

Wang, M.-S., Thakur, M., Peng, M.-S., Jiang, Y., Frantz, L. A. F., Li, M., Zhang, J.-J., Wang, S., Peters, J., Otecko, N. O., Suwannapoom, C., Guo, X., Zheng, Z.-Q., Esmailizadeh, A., Hirimuthugoda, N. Y., Ashari, H., Suladari, S., Zein, M. S. A., Kusza, S., … Zhang, Y.-P. (2020). 863 genomes reveal the origin and domestication of chicken. *Cell Research*, *30*(8), Article 8. https://doi.org/10.1038/s41422-020-0349-y

Wang, X., Pipes, L., Trut, L. N., Herbeck, Y., Vladimirova, A. V., Gulevich, R. G., Kharlamova, A. V., Johnson, J. L., Acland, G. M., Kukekova, A. V., & Clark, A. G. (2018). Genomic responses to selection for tame/aggressive behaviors in the silver fox (Vulpes vulpes). *Proceedings of the National Academy of Sciences*, *115*(41), 10398–10403. https://doi.org/10.1073/pnas.1800889115

Wehrwein, E., Orer, H. S., & Barman, S. (2016). Overview of the Anatomy, Physiology, and Pharmacology of the Autonomic Nervous System. In *Comprehensive Physiology* (Vol. 6, pp. 1239–1278). https://doi.org/10.1002/cphy.c150037

Wheat, C. H., Larsson, L., Berner, P., & Temrin, H. (2021). *Hand-reared wolves show attachment comparable to dogs and use human caregiver as a social buffer in the Strange Situation Test* (p. 2020.02.17.952663). bioRxiv. https://doi.org/10.1101/2020.02.17.952663

Wilkins, A. S. (2017). Revisiting two hypotheses on the "domestication syndrome" in light of genomic data. *Vavilov Journal of Genetics and Breeding*, *21*(4), Article 4. https://doi.org/10.18699/VJ17.262

Wilkins, A. S. (2020). A striking example of developmental bias in an evolutionary process: The "domestication syndrome." *Evolution & Development*, *22*(1–2), 143–153. https://doi.org/10.1111/ede.12319

Wilkins, A. S., Wrangham, R., & Fitch, W. T. (2021). The neural crest/domestication syndrome hypothesis, explained: Reply to Johnsson, Henriksen, and Wright. *Genetics*, *219*(1), iyab098. https://doi.org/10.1093/genetics/iyab098

Wilkins, A. S., Wrangham, R. W., & Fitch, W. T. (2014). The "Domestication Syndrome" in Mammals: A Unified Explanation Based on Neural Crest Cell Behavior and Genetics. *Genetics*, *197*(3), Article 3. https://doi.org/10.1534/genetics.114.165423

Wirobski, G., Range, F., Schaebs, F. S., Palme, R., Deschner, T., & Marshall-Pescini, S. (2021). Life experience rather than domestication accounts for dogs' increased oxytocin release during social contact with humans. *Scientific Reports*, *11*(1), 14423. https://doi.org/10.1038/s41598-021-93922-1

Zeder, M. A. (2006). Central questions in the domestication of plants and animals. *Evolutionary Anthropology: Issues, News, and Reviews*, *15*(3), 105–117. https://doi.org/10.1002/evan.20101

Zeder, M. A. (2012). The Domestication of Animals. *Journal of Anthropological Research*, *68*(2), 161–190. https://doi.org/10.3998/jar.0521004.0068.201

Zeder, M. A. (2015). Core questions in domestication research. *Proceedings of the National Academy of Sciences*, *112*(11), 3191–3198. https://doi.org/10.1073/pnas.1501711112

Chapter 1|

Context-Specific Arousal During Resting in Wolves and Dogs: Effects of Domestication?

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Context-Specific Arousal During Resting in Wolves and Dogs: Effects of Domestication?

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Due to domestication, dogs differ from wolves in the way they respond to their environment, including to humans. Selection for tameness and the associated changes to the autonomic nervous system (ANS) regulation have been proposed as the primary mechanisms of domestication. To test this idea, we compared two low-arousal states in equally raised and kept wolves and dogs: resting, a state close to being asleep, and inactive wakefulness, which together take up an important part in the time budgets of wolves and dogs. We measured arousal via cardiac output in three conditions: alone, with a familiar human partner, or with pack members (i.e., conspecifics). Specifically, we compared heart rate (HR) and heart rate variability (HRV) of six wolves and seven dogs. As patterns of resting can vary adaptively, even between closely related species, we predicted that dogs would be generally more aroused than wolves, because living with humans may come with less predictable contexts than living with conspecifics; hence, dogs would need to be responsive at all times. Furthermore, we predicted that due to the effects of domestication, emotional social support by familiar people would reduce arousal more in dogs than in equally human-socialized wolves, leading to more relaxed dogs than wolves when away from the pack. Overall, we found a clear effect of the interactions between species (i.e., wolf versus dog), arousal state (i.e., resting or awake inactive) and test conditions, on both HR and HRV. Wolves and dogs were more aroused when alone (i.e., higher HR and lower HRV) than when in the presence of conspecifics or a familiar human partner. Dogs were more relaxed than wolves when at rest and close to a familiar human but this difference disappeared when awake. In conclusion, instead of the expected distinct overall differences between wolves and dogs in ANS regulation, we rather found subtle context-specific responses, suggesting that such details are important in understanding the domestication process.

Keywords: heart rate, heart rate variability, dogs, wolves, domestication, dog-human relationship

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INTRODUCTION

Domesticated species differ systematically from their wild conspecifics ("domestication syndrome," Darwin, 1859; Wilkins et al., 2014). As the primary domestication mechanism seems to be selection for tameness (Belyaev, 1979; Trut et al., 2004), domesticated animals have been suggested to be hypersocial – defined as "a heightened propensity to initiate social contact that often extends to members of others species" – toward other individuals, including humans, compared to their wild counterparts (vonHoldt et al., 2017). The dog-wolf model is a great system to investigate potential differences due to domestication. Dogs began to diverge genetically from wolves some 35,000 years ago (Frantz et al., 2016; Botigué et al., 2017). Domestication has affected the ecology and behavior of dogs (Axelsson et al., 2013; Miklósi and Topál, 2013; Range and Virányi, 2015; Marshall-Pescini et al., 2017; Kotrschal, 2018). Wolves are cooperative hunters and breeders which generally avoid close contact with humans (Mech and Boitani, 2003). Still, equally human-socialized wolves and dogs behave relatively similar in experimental situations. For example, they are attentive toward humans (Range and Virányi, 2013) and cooperate with them (Range et al., 2019b), greet familiar and unfamiliar humans (Hall et al., 2015; Ujfalussy et al., 2017), and like in dogs, their salivary cortisol decreases during training sessions (Vasconcellos et al., 2016). Human-socialized adult wolves maintain social bonds with their early caretakers and other familiar people (preprint; Wheat et al., 2020) and, hence, may benefit from their presence in stressful situations via emotional social support. Still, wolves may not depend on humans as much as dogs that are raised and kept in a similar way (Topál et al., 2005) because dogs usually live in human environments (Coppinger and Coppinger, 2001) and may be selected for attaching easily and strongly to their human caretakers (Palmer and Custance, 2008; Gácsi et al., 2013; Solomon et al., 2019).

Previous studies have shown a clear interaction between dogs' physiology and their emotional bonds with humans. For example, kennel dogs exposed to a novel environment in the presence of their human caretaker showed no increase in glucocorticoids, which was in contrast to when they were tested alone or with a familiar dog in a novel environment (Tuber et al., 1996). A study of pet dogs found that when dogs were petted by their owner during a veterinary examination dogs' heart rate and ocular surface temperature increased less than when facing examination alone (Csoltova et al., 2017). Furthermore, another study of pet dogs showed that dogs' heart rate variability (HRV) generally increased in response to being pet by their owners (Katayama et al., 2016), which suggests that this is experienced as a positive and rewarding situation. In humans also, heart rate and HRV is linked to emotional responses (Porges, 1995; Appelhans and Luecken, 2006).

The autonomic nervous system (ANS) regulates the heart and other visceral functions (Shields, 1993), including the expression of emotions in the social context (Porges, 2003). As domesticated animals differ from their wild ancestors mainly in their emotional responses to human contexts, domestication may have affected ANS modulations, the more as the neural crest hypothesis suggests that 'initial selection for tameness leads to a change in the neural-crest-derived tissues' (Wilkins et al., 2014), which includes the ANS. In turn, this leads to the changes observed trough all domesticated species, the so called "domestication syndrome" (Darwin, 1859; Wilkins et al., 2014).

The modulation of the ANS can be estimated via cardiac activity (Porges, 1995, 2001, 2003, 2009; Rajendra Acharya et al., 2006; Kreibig, 2010). Useful parameters are HR, i.e., the number of heartbeats per time unit, and HRV, i.e., the variation over time of the period between consecutive heartbeats (R-R intervals). While both physical activity and mental states modulate HR (Visser et al., 2002; Maros et al., 2008), HRV is less dependent on physical activity than HR, but generally decreases via psychological stress and increases during relaxation (Luque-Casado et al., 2013). A way to avoid the effect of physical activity on ANS modulation and thus, cardiac outputs, and test the emotional effect of social support by a social partner on wolves and dogs is to compare their arousal at rest.

Rest is considered as an intermediate state of the sleep-wakefulness continuum (Campbell and Tobler, 1984) defined as, "a state of reduced activity without the loss of consciousness or greatly reduced responsiveness" (Lesku et al., 2006; Siegel, 2008). At rest, parasympathetic activity increases, resulting in a comparatively low HR and high HRV. In addition, respiration deepens in association with a sinusoid pattern of HR, which is caused by the rhythmic breathing of the animal. This is called respiratory sinus arrhythmia (RSA, Oken et al., 2006). As RSA is present in both wolves (Kreeger et al., 1990) and dogs (Hamlin et al., 1966), we used it as a marker of a deep state of relaxation, i.e., resting (Kortekaas and Kotrschal, 2019). In the present study, we focused on the resting state but we also included a state in which an animal is more aroused and alert than during rest, i.e., the awake inactive state in which an animal is paying close attention to its environment (Oken et al., 2006) but is still physically inactive. With the term "arousal," we integrate correlated mental and physiological states; low arousal such as during rest is equivalent to decreased consciousness toward environmental stimuli, with relatively low HR and high HRV.

Not much is known about dog resting patterns; they probably change with age, environment, and social context as it has been observed with sleep patterns. For example, living conditions affected the length of dog sleep cycles and the time they spent sleeping (Adams and Johnson, 1993) as shelter dogs slept more but with shorter sleep cycles than dogs living with owners. Interestingly, if more than one dog lived in the same household, the dogs tended to show asynchronous sleep-wake cycles (Adams and Johnson, 1993), meaning that at least one of them was awake at any time. Other studies have shown that after an active day, dogs are drowsier earlier and sleep more (Bunford et al., 2018) and older dogs sleep more during the day and less at night than younger dogs (Takeuchi and Harada, 2002; Bódizs et al., 2020). Also, the frequency of sleep spindles (i.e., a burst of brain activity) has been shown to vary with age, physical activity, social pre-sleep activity, sex, and reproductive status (Kis et al., 2014, 2017; Iotchev et al., 2019), factors which also have been shown to affect the HR and HRV of dogs before falling asleep (Varga et al., 2018). In adaptation to different ecologies and lifestyles, sleep patterns may vary substantially, even among closely related species (Siegel, 2005; Lesku et al., 2008; Aulsebrook et al., 2016). For example, birds (gadwall and black-tailed Godwit) had their eyes open for longer periods of time during rest/sleep when in large groups or in the center of the flock (Gauthier-Clerc et al., 2000; Dominguez, 2003). Whereas in yellow baboons, individuals in smaller groups were resting higher above ground than individuals in bigger groups (Stacey, 1986). Socialized wolves, were found to be more relaxed than dogs and have lower HR and higher HRV during periods of rest and inactive wakefulness (Kortekaas and Kotrschal, 2019). This has been suggested to be a specific adaptation of dogs for living in a human environment, which is presumably less predictable than the pack environment of wolves and hence, would necessitate a greater basic alertness. However, in this study, an unfamiliar human was present during the recording of the animals' behavior, which might have influenced the results.

In our present study we assessed the effect of domestication on the modulation of dogs' ANS by comparing wolves' and dogs' ANS modulation in three different social conditions: alone, with a familiar human, and with the other pack members. Similar to Kortekaas and Kotrschal (2019), we investigated two behavioral states with minimal physical activity and sensory stimulation: resting (animal is lying immobile and eyes closed) and inactive wakefulness (animal is lying with its head in an upward position with the eyes open). We compared cardiac output in similarly raised and kept, and therefore fully comparable, group-living wolves and dogs. We selected periods of respiratory sinus arrhythmia for analysis, as this is indicative of rest (Kortekaas and Kotrschal, 2019).

As human-socialized wolves form social bonds with familiar humans, we expected that emotional support by humans would modulate their ANS. However, due to dogs' adaptation to the human environment during domestication, the proposed emotional support effect should be more pronounced in dogs than wolves. Different predictions can be generated from the major dog domestication hypotheses. If selection for tameness as primary mechanism of domestication (Belyaev, 1979; Wilkins et al., 2014) shaped dogs' ANS's modulation, we predicted they would be generally more relaxed (i.e., less reactive to stressful events and with lower HR and higher HRV) than their wild ancestors (Darwin, 1868; Price, 1999; Hare et al., 2012). Based on the hypersociality hypothesis (vonHoldt et al., 2017), we expected that dogs would benefit more (i.e., be more relaxed at rest and with lower HR and higher HRV compared to a control condition where the animals are alone) in the presence of a human and possibly also in the presence of conspecifics than wolves. Alternatively, the intention to interact with the familiar person or pack member – due to the proposed higher sociability of dogs as compared to wolves – might result in increased arousal (higher HR and lower HRV). However, this was not expected to be the case once the animals has settled down to rest.

In contrast to the precedent domestication hypotheses, the canine cooperation hypothesis (Range and Virányi, 2015) suggests that dogs' social and cooperative skills toward humans are not a by-product of domestication but rather a direct wolf heritage originating from the wolves' social orientation toward pack members. This hypothesis suggests that during domestication dogs shifted their cooperative orientation to humans. Based on this hypothesis we predicted that wolves as well as dogs would relax in the presence of both a familiar human and a conspecific pack member. This is in alignment with the deferential hypothesis (Range et al., 2019b), which predicts that dogs should benefit more from the human presence than wolves, dogs should gain a greater support effect from humans (i.e., lower HR and higher HRV with a human compared to being with other dogs) whereas wolves would gain great support effect from conspecifics (i.e., lower HR and higher HRV with their conspecifics). In contrast to the hypersociability hypothesis (vonHoldt et al., 2017), the deferential hypothesis would not predict that dogs can benefit more from the presence of other dogs.

MATERIALS AND METHODS

Ethical Approval

This research was approved by the institutional ethics committee at the University of Veterinary Medicine, Vienna, in accordance with GSP guidelines and national legislation (ETK-11/11/2018).

All study animals were housed at the Wolf Science Center (WSC) located in the Game Park Ernstbrunn in Austria. Their participation in the experimental sessions was voluntary. If they were not motivated to leave their home enclosure, the session was canceled and repeated on a different day. In nine cases, trials had to be repeated for this reason. If the subject did not rest in the test enclosure during the session, the condition was repeated on another day, in total this situation happened 53 times. If they did not rest in five sessions, the subject was tested in its home enclosure while its pack mates were brought to the test enclosure ($n = 2$). Via these adjustments we also achieved a homogenous motivational basis for our experiments. Only animals in a positive/relaxed mood would participate, because temporarily wary or anxious animals would not leave their enclosure to participate. All animals at the WSC are well habituated to being shifted to and from their home enclosure and also to experimental procedures.

Subjects

Subjects were six wolves, *Canis lupus* (three males and three females) and seven dogs, *Canis lupus familiaris* (four males and three females; see **Table 1**). All wolves and dogs were born in captivity and were hand-raised from 10 days old by humans following a standardized procedure to produce trustful and workable partners for research (Klinghammer and Goodman, 1987). At 5 months of age they were integrated into preexisting conspecific packs. For more details on the raising of the animals see Range and Virányi (2014).

All animals were kept in small groups in outside enclosures ranging between 2,000 and 8,000 m^2 in size with natural landscape including trees, bushes, shelters, and natural objects such as stones, branches, and tree trunks. The subjects were between 5 and 11 years of age when tested – wolves: median (range) = 7 (6–10); dogs: median (range) = 4 (4–8) and had between 20.8 and 48.9 kg – wolves: median (range) = 40 (37.5–48.9); dogs: median (range) = 24.5 (20.8–35). The wolves were fed with carcasses of deer, rabbit, or chicken 3–4 times a week, while the dogs were fed with commercial dog food daily. As the dogs could not be provided carcasses, like the wolves, the dogs were regularly provided food enrichment, such as small pieces of deer, rabbit, or chicken, to make wolf and dog feeding as similar as possible. Water was available *ad libitum* to all wolves

TABLE 1 | List of the subjects.

Individual	Species	Sex	Date of birth	Weight*	Pack size
Amarok	Wolf	♂	4.04.2012	39.82	2
Aragorn	Wolf	♂	4.05.2008	48.50	3
Chitto	Wolf	♂	4.04.2012	46.72	2
Shima	Wolf	♀	4.05.2008	39.50	2
Tala	Wolf	♀	4.04.2012	39.15	2
Yukon	Wolf	♀	2.05.2009	37.82	3
Enzi	Dog	♂	2.04.2014	29.00	4
Gombo	Dog	♂	21.03.2014	28.67	2
Hiari	Dog	♂	21.03.2014	24.13	3
Imara	Dog	♀	21.04.2014	21.39	3
Meru	Dog	♂	1.10.2010	24.18	2
Panya	Dog	♀	2.04.2014	25.20	4
Zuri	Dog	♀	24.05.2011	20.80	4

**Weights displayed here are the weights of the subjects over the three testing days in kilograms.*

and dogs, including during training and test situations. Wolves and dogs had the same amount of contact with humans and both received veterinary and obedience training from puppyhood and cooperated in a number of behavioral tests on a weekly basis. As a result, all animals were accustomed to participating in research while separated from their pack members.

Data Collection

Overall, we tried to keep our methods as similar as possible to Kortekaas and Kotrschal (2019). Heart rate (HR) was measured via the Polar® RS800CX system designed for human usage. The accuracy of the Polar system has been validated for dogs via a comparison with a conventional electrocardiogram (ECG; Jonckheer-Sheehy et al., 2012; Essner et al., 2013, 2015). The system consists of a chest belt with electrodes, which are fastened around the animals' chest behind the shoulders. From there the data are sent to a watch-like data logger attached to a neck collar. As the belt was designed for humans, the fur of the wolves and dogs impedes the belt electrodes. Hence, the fur under the electrodes in the belt was wetted with 70% ethanol to enhance signal conductivity. The entire procedure was trained beforehand via positive reinforcement.

HR data were first checked for the presence of respiratory sinus arrhythmia as an indicator of deep rest (i.e., a sleep-like condition). Video recordings of these sessions were coded with Solomon Coder©. HR and behavioral data were manually synchronized. Specifically, when the watch started recording data, the experimenter said loudly "start," which was used as a signal for synchronizing the video and the HR recording. For the resting condition, all HR data showing a respiratory sinus arrhythmia pattern and the matching resting behaviors was kept. For analyses, HR and HRV recording are required to be the same length of time to be comparable (von Borell et al., 2007). Most of our animals rested for more than 80 s but for one wolf (Amarok resting with a familiar human) and one dog (Enzi resting alone) 80 s was the shortest maximum time they spend resting. Hence, we selected 80 s HR strands for analysis and all bouts shorter than 80 s were excluded from further analyses. One resting bout was randomly selected per animal and conditions. For the inactive wakefulness, no specific HR pattern has been described (in analogy to RSA during rest), hence we selected any strand of HR data longer than 80 s that corresponded to awake but inactive behaviors (i.e., laying down immobile with eyes open). If the animal moved (i.e., changed the position of its body or its head) or closed its eyes for more than a blink (i.e., eyes closed for more than 1 s and opening again, 1 s corresponded to five frames on Solomon Coder) the HR strand was discarded. One strand of HR per animal and activity (i.e., resting or inactive wakefulness) was randomly selected. As we only had one HR recording per animal and condition, we avoided selecting multiple strands of the same activity (i.e., resting or inactive wakefulness) to avoid dependent data points.

HR measurements collected with the Polar system can contain artifacts, leading to the need for editing (von Borell et al., 2007). Accordingly, the HRs measured were corrected using the algorithm-supported visual error correction (AVEC) method (Schöberl et al., 2015), applying a confidence interval for the outliers of 95%. HR measurements with more than 5% of errors were excluded. Heart rate variability (HRV) in this study was expressed as the root mean square of successive differences (RMSSD), normally used for short-term HRV analysis (for RMSSD details see von Borell et al., 2007). Mean HR and RMSSD were calculated with Kubios©. Resting HRs and awake inactive HRs were taken from the same recording but were not time adjacent.

Procedure

The experimental sessions were conducted during a quiet period of the day when the animals were resting (normally between 12 am and 2 pm). Depending on the condition, the focal subject was taken out of the pack and brought to a test enclosure with some distance to its home pack or was accommodated in the shifting system immediately adjacent to the pack enclosure (i.e., the subject was only separated from the pack mates by a single wire mesh). Before the onset of the experimental phase, an animal trainer applied the Polar-belt to the subject for the recording of the HR. During the test period (1 h), no human was present around the enclosure (i.e., keeping away from the enclosure and out of sight of the animal tested) except for the human company condition. Each session was recorded with one or two cameras (depending on the size and configuration of the enclosure).

The animals were tested in the following three conditions: (1) alone: the subject was alone in its enclosure; (2) human company: The subject was alone in its enclosure while a familiar human was sitting just outside the fence of the enclosure (minimal distance 50 cm). The subject was free to approach the human or to stay away. The familiar human was instructed to not interact with the subject, but instead was reading a book or working on a laptop; (3) conspecific company: The subject and its pack members (1–3) stayed in visual contact during the test hour but were separated by a fence.

We analyzed cardiac outputs in two different behavioral conditions, resting and inactive wakefulness. We used the same behavioral criteria as Kortekaas and Kotrschal (2019) to define two conditions.

1. Resting: The body touching the ground either with caudal, dorsal, or lateral side. The position of the paws varies, e.g., folded (under body) or stretched out. The head is in a downward position, either lying on paws, ground, or tucked under the body. The eyes are generally closed but may repeatedly open and close (peeking). Parts of the body occasionally twitching.
2. Inactive wakefulness: The subject is awake, body touching the ground either with caudal, dorsal, or lateral side. The position of the paws varies, e.g., folded (under body) or stretched out. The head is in an upward position and can be moved around. The eyes are open, but increased blinking can occur.

Statistical Analyses

All models were fitted in R (version 3.6.1; R Core Team, 2019) using the function lmer of the R package lme4 (version 1.1-21; Bates et al., 2014). To test whether the cardiac parameters would differ depending on species, activity of the subject, and condition of the test, the response variables "mean" HR and RMSSD (a common measure for HRV) were both analyzed in separate linear mixed effect models (LME, Baayen, 2008). Species (wolf or dog), activity (resting or inactive wakefulness), condition of the test (alone, with a human, or with conspecifics) included as fixed effects factors. We also included in the model a three-way interaction between species, activity and condition (and also all three two-way interactions this encompasses) in order to understand how cardiac outputs changed as a function of activities and conditions and how these differences in cardiac outputs varied between wolves and dogs. To control for the effects of temperature, body mass, age, and sex, these factors were also included as fixed effects. Subject identity was included as a random intercept to account for individual differences and to avoid pseudo replication, as all subject were tested in each condition. To keep type I error rates at the nominal level of 5%, we included random slopes of condition and activity and also the correlation parameters among the random intercept and random slopes terms of the HR model (Schielzeth and Forstmeier, 2009; Barr et al., 2013). However, we chose to exclude those correlations from the HRV model because many of them were estimated to be close to 1 or −1 which is indicative of them to be unidentifiable (Matuschek et al., 2017). This led to an only moderate decrease in model fit (HRV model with correlations: logLik = −440.3498 (*df* = 32) and HRV model without correlations: logLik = −446.6024 (*df* = 22). Body mass, age, and temperature were z-transformed (to a mean of zero and a standard deviation of one). Activity, condition, and species were manually dummy-coded (i.e., the categorical predictors were replaced by one or several dummy variables, one for each level of the factor except its reference category, each consisting solely of 0 and 1 s to facilitate model computation) and then centered to a mean of zero before including them in the random slopes in the model.

We checked whether the residuals were normally distributed and homogeneous by visually inspecting a qqplot and the residuals plotted against fitted values. Both indicated no obvious deviations from these assumptions. We checked for model stability by excluding subjects one at a time from the data and comparing the model estimates derived for these subsets of the data with those derived for the full data set. Both models were unstable for the factor species (see **Supplementary Tables 1**, **2**). To check for potential collinearity issues, we inspected Variance Inflation Factors (VIF, Field, 2005) which we derived using the function VIF of the R-package car (Fox and Weisberg, 2018), applied to a standard linear model excluding the random effects and interactions. This revealed that species and body mass were slightly collinear with a VIF of 11.57 and 10.21, respectively. However, there was considerable variation of body mass within both species and, hence, the results obtained for these two predictors should not be distorted by collinearity among them.

To avoid cryptic multiple testing and keep type I error rate at the nominal level of 0.05 (Forstmeier and Schielzeth, 2011) we tested the significance of the full model as compared to the null model (comprising only age, body mass, sex, temperature, and the random effects) by means of a likelihood ratio test (R function anova with argument test set to "Chisq"; Dobson and Barnett, 2018). To allow for a likelihood ratio test we fitted the models using maximum likelihood (rather than Restricted Maximum Likelihood; Bolker et al., 2009). *P*-values for the individual effects were based on likelihood ratio tests comparing the full with the respective reduced models (Barr et al., 2013; R function drop1).

The sample size for both these models was 73 observations made on 13 individuals (seven dogs, six wolves). Six data points were missing as the animals did not display the behaviors measured in this study (rest/inactive wakefulness). Four data points were included despites displaying bad RSA pattern to enhance model stability (Meru alone, Zuri alone and with human company, Hiari alone).

RESULTS

Mean Heart Rate

Overall, species, activity, and condition had a clear effect on HR (full-null comparison likelihood ratio test: $\chi^2 = 57.22$, $df = 11$, $P < 0.001$). More specifically, we found that the interaction between species, activity, and condition had an effect on HR ($\chi^2 = 10.60$, $df = 2$, $P = 0.005$; **Table 2**) and that the HR differences between dogs and wolves varied depending on the combination of test conditions and activities.

Overall, HR in wolves and dogs was lower when resting, as compared to being awake but inactive (**Figures 1A,B**). During rest, dogs in proximity of a social partner (human or conspecific) had lower HRs than when alone (**Figure 1A** and **Table 3**). In contrast, during inactive wakefulness, dogs' HRs in proximity of a familiar human were higher than in the two other conditions (**Figure 1B**) and dogs' HRs when alone or with conspecifics was similar. During rest, the HRs of wolves were lower in proximity to their pack members as compared to being close to a familiar human or alone (**Figure 1A**). In addition, wolf HRs seemed

TABLE 2 | Results of the HR Model.

	Estimate	SE	χ^2	F	P[1]
Intercept	97.245	6.440			
Species (0, dog; 1, wolf)	−25.237	9.604			
Human	9.908	4.123			
Conspecifics	3.002	5.315			
Activity (0, awake; 1, rest)	−11.773	3.560			
Body mass[2]	10.706	3.585	5.187	1	**0.023**
Temperature[2]	−2.027	1.016	3.378	1	0.066
Age[2]	15.248	2.402	14.648	1	**<0.001**
Sex (0, F; 1, M)	−5.251	2.470	3.015	1	0.082
Wolf:Human	−21.823	6.053			
Wolf:Conspecifics	−16.729	7.465			
Wolf:Rest	−7.956	4.942			
Human:Rest	−9.627	4.448			
Conspecifics:Rest	−7.030	4.361			
Wolf:Human:Rest	22.889	6.490	10.601	2	**0.005**[3]
Wolf:Conspecifics:Rest	10.030	6.185			

Statistically significant p-value are in bold.

[1] *Not indicated in the case where p-value had a limited interpretation.*

[2] *Predictors were z-transformed to a mean of zero and a standard deviation of one; original means (SD) were weight: 32.98 (9.49) kg, temperature: 22.41 (7.18)°C and age 2440.23 (801.93) days.*

[3] *Overall test of the three-way interaction between species, activity and conditions.*

similar when resting alone or in proximity of a familiar human (**Figure 1A** and **Table 3**). When awake and inactive, wolf HRs near a pack member were lower as compared to being alone or close to a familiar human (**Figure 1B**). Furthermore, HRs of wolves and dogs were roughly similar when resting near their pack members whereas they differed in the two other conditions (**Figure 1A**): Dog HRs were lower than those of wolves when alone or close to a human partner (**Figure 1A**). During inactive wakefulness wolves had higher HRs than dogs when alone whereas in the social conditions the HRs of wolves and dogs were similar (**Figure 1B**). HRs also increased with age (estimate ± SE = 15.24 ± 2.40, $\chi^2 = 14.65$, $P < 0.001$) and body mass (estimate ± SE = 10.71 ± 3.59, $\chi^2 = 5.19$, $P = 0.023$), whereas sex and temperature had no significant effect (**Table 3** and **Supplementary Table 1**).

We found distinct inter-individual differences in HR in both dogs and wolves (see **Supplementary Figure 1**). In the dogs, two subjects seemed to drive the decrease in HR at rest, whereas two other animals had the highest HR during the pack condition. In the inactive but awake state, two individuals had the highest HRs in presence of a familiar human (**Supplementary Figure 1A**). Similarly, in the wolves, two animals displayed a higher HR when resting with a familiar human than when alone, whereas one female had a substantially lower HR in presence of a familiar human than when alone. Only one wolf had a higher HR when with her pack than when alone. During inactive wakefulness, two individuals had very high HRs when alone and for both of them the presence of a familiar human seemed to lead to a lower HR. Compared to the alone condition, all wolves displayed lower HRs in the presence of their pack mates; however, when compared to the human condition, two wolves had higher HRs and two lower HRs in the pack condition (**Supplementary Figure 1B**).

Heart Rate Variability (RMSSD)

Overall, the full model was significant as compared to the null model (likelihood ratio test: $\chi^2 = 40.15$, $df = 11$, $P < 0.001$), i.e., species, activity, condition, or their interaction(s) affected the root mean square of successive differences (RMSSD, which expresses heart rate variability; HRV) in wolves and dogs. However, since the three-way interaction between species, activity, and condition was not significant (likelihood ratio test: $\chi^2 = 3.47$, $df = 2$, $P = 0.18$, **Figures 1C,D** and **Table 3**), we removed it from the model to explore the significance of the two-way interactions between our factors of interest: species, activity and condition. The two-way interaction between species and condition was significant (likelihood ration test: $\chi^2 = 8.48$, $df = 2$, $P = 0.014$); wolf and dog RMSSDs were similar in the alone condition, but in presence of a social partner dogs had higher HRVs than wolves (**Supplementary Figure 2**). Also, the two-way interaction between species and activity was significant (likelihood ration test: $\chi^2 = 8.27$, $df = 1$, $P = 0.004$), meaning that both wolves and dogs had similar RMSSDs when awake and inactive while at rest dogs had higher RMSSDs (**Supplementary Figure 3**). Finally, the two-way interaction between activity and condition was also significant (likelihood ratio test: $\chi^2 = 7.99$, $df = 2$, $P = 0.018$). When alone RMSSDs of wolves and dogs did not differ much between being awake or resting, whereas when with a social partner (human or conspecifics) RMSSDs where higher at rest than when awake (**Figures 1C,D**). RMSSDs decreased with age (estimate ± SE = −103.54 ± 41.19, $\chi^2 = 5.07$, $df = 1$, $P = 0.024$) whereas body mass, sex, and temperature had no significant effect on the RMSSD (**Table 4** and **Supplementary Table 2**).

As the case with HR, we also found considerable individual differences in RMSSD. In two dogs it was overall lower than in the other dogs at rest. Also, individual dogs differed in their response to the presence of their pack; when resting two individuals had substantially lower RMSSDs close to their pack as compared to being alone, while during inactive wakefulness three individuals had higher RMSSDs with their pack as compared to the alone condition (**Supplementary Figure 1C**). At rest, two wolves, did not vary in their RMSSD, regardless of condition. During inactive wakefulness, the RMSSD of three wolves reached lowest values in the presence of the familiar human, whereas it peaked in two others in this condition (**Supplementary Figure 1D**).

DISCUSSION

Our results show than dogs and wolves' cardiac output varies with degree of activity, social environment, and also quite substantially between individuals in the different contexts. Across all three conditions, both wolves and dogs were less aroused, showing lower heart rates (HR) and higher heart rate variation (HRV) when resting, as compared to inactive wakefulness. This aligns with previous results (Varga et al., 2018; Kortekaas and Kotrschal, 2019). However, in contrast to Kortekaas and Kotrschal (2019),

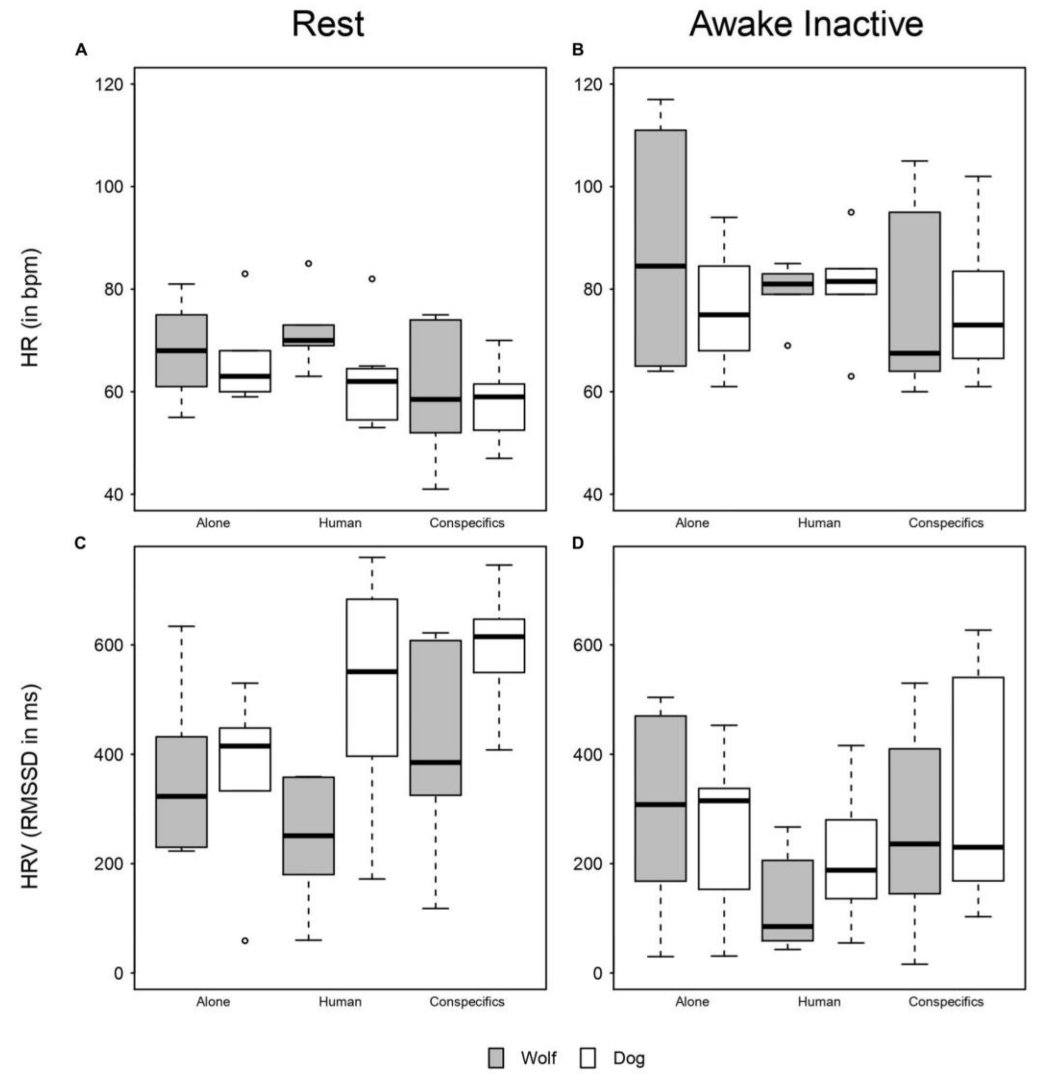

FIGURE 1 | Boxplot of mean HR and HRV. **(A)** Mean HR of wolves and dogs when resting across conditions. **(B)** Mean HR of wolves and dogs when awake and inactive across conditions. **(C)** HRV of wolves and dogs when resting across conditions. **(D)** HRV of wolves and dogs when awake and inactive across conditions.

dogs at rest were generally less aroused (i.e., had lower HR and higher HRV) than wolves but showed roughly the same cardiac parameters as wolves when awake and inactive. This discrepancy may be explained by the different social context in the two studies. Kortekaas and Kotrschal (2019) had an unfamiliar human filming all the experimental sessions, while in our study we controlled for familiarity by having either no human, a familiar human, or conspecifics nearby. The presence of an unfamiliar human could have been more arousing than soothing for the dogs than the presence of a familiar human. However, we also need to note that as we found a substantial individual variation in our data, the differences between the two studies might also be explained by small samples sizes, as discussed below.

Interestingly, we found that dogs at rest seemed to respond to the presence of a familiar human in a similar way as to

TABLE 3 | Descriptive statistics for the mean HR and RMSSD values.

			HR					RMSSD				
Species	**Condition**	**Activity**	**Mean**	**SD**	**Min**	**Max**	**Median**	**Mean**	**SD**	**Min**	**Max**	**Median**
Dog	Alone	Rest	66.60	9.81	55	81	63	357.00	180.94	59	530	415
Dog	Alone	Awake	76.43	12.80	64	117	75	254.28	152.96	31	453	315
Dog	Human	Rest	62.14	10.09	53	82	62	520.43	225.84	172	760	551
Dog	Human	Awake	80.67	10.33	63	95	81.5	210.50	128.53	55	416	188
Dog	Conspecific	Rest	57.71	8.03	47	70	59	594.57	113.53	408	746	615
Dog	Conspecific	Awake	76.57	14.73	61	102	73	339.71	222.21	103	627	230
Wolf	Alone	Rest	68.00	10.08	59	83	68	360.84	155.22	223	634	323
Wolf	Alone	Awake	87.67	23.15	61	94	84.5	298.00	189.20	30	504	308
Wolf	Human	Rest	72.00	8.12	63	85	70	241.60	126.68	60	359	251
Wolf	Human	Awake	79.40	6.23	69	85	81	132.00	98.94	43	267	85
Wolf	Conspecific	Rest	59.84	13.23	41	75	58.5	407.17	189.96	118	622	385
Wolf	Conspecific	Awake	76.50	18.81	60	105	67.5	262.17	185.56	16	530	236

Descriptive statistics of dogs and wolves mean HR and RMSSD values grouped by conditions and activity.

TABLE 4 | Results for the HRV model.

	Estimate	**SE**	**χ^2**	***df***	**P[1]**
Intercept	270.451	88.462			
Species (0: dog; 1: wolf)	80.431	133.413			
Human	−24.868	57.153			
Conspecifics	122.402	44.987			
Activity (0: awake; 1: rest)	149.889	43.636			
Body mass[2]	80.874	60.934	1.567	1	0.211
Temperature[2]	−5.988	14.578	0.162	1	0.688
Age[2]	−103.540	41.188	5.072	1	**0.024**
Sex (0: F; 1:M)	−68.764	69.425	0.973	1	0.324
Wolf:Human	−163.474	76.643	8.478	2	**0.014[3]**
Wolf:Conspecifics	−168.204	53.965			
Wolf:Rest	−130.650	42.885	8.266	1	**0.004**
Human:Rest	150.712	53.755	7.994	2	**0.018[4]**
Conspecifics:Rest	114.564	51.403			

Significant p-value are in bold.

[1] *Not indicated in the case where p-value had a limited interpretation.*

[2] *Predictors were z-transformed to a mean of zero and a standard deviation of one; original means (SD) were weight: 32.98 (9.49) kg, temperature: 22.41 (7.18)°C and age 2440.23 (801.93) days.*

[3] *Overall test of the two-way interaction between species and conditions.*

[4] *Overall test of the two-way interaction between activity and conditions.*

the presence of their pack members (i.e., lower HR and higher HRV than when alone), whereas in our human-socialized wolves, pack members seemed to be more effective at being emotional social support than familiar humans. When dogs and wolves were awake, the differences between their cardiac parameters decreased, probably because both were more alert (increased HR and lower HRV) as compared to resting with eyes closed. More specifically, when awake and close to a familiar human, the HRs of our human-socialized wolves and dogs were similar, whereas the HRVs were still lower in wolves. Also, during inactive wakefulness, the dogs had distinctly higher HRs and lower HRVs in the presence of a familiar human than when alone or with pack members, whereas differences between conditions were less clear in the wolves. It seems that the presence of humans affected dogs differently depending on if the dogs were awake, where multiple other stimuli may influence them and reduce the effect of the human, or asleep when there were fewer external stimuli to distract the dogs. We suggest that when awake, the dogs anticipated interacting with the familiar human, which may have increased their arousal. Wolves showed similar arousal levels than dogs in the presence of familiar humans as indicated by similar HR but HRV in this condition was lower in wolves than in dogs. As HRV has been linked to cognitive processes (Maros et al., 2008; Luque-Casado et al., 2013), we speculate that the presence of familiar humans might have been cognitively more stimulating for the wolves than for the dogs. Alternatively, due to the presence of a close human partner, our socialized wolves could have also anticipated interesting events, such as a test situation, training session, or a social interaction, whereas the dogs may have responded with relatively unspecific excitement. In other words, our socialized wolves may attribute a different meaning or valence (HRV is frequently used to assess affective state; Kreibig, 2010) to the presence of a human than the dogs. Still, these wolves are similarly attentive to humans than the dogs (Range and Virányi, 2011), benefit from training interactions with them in a similar way (Vasconcellos et al., 2016), and interact socially with their hand-raiser (Ujfalussy et al., 2017). Our socialized wolves also differed in their HRV responses to the presence of a familiar person, which hints at the importance of the quality of social relationships and personality.

Rather than dogs being overall calmer than wolves due to domestication (Hare et al., 2012) or being "hypersocial" (vonHoldt et al., 2017), our results support the idea that pack members act as social support in wolves and that dogs use humans similarly as social support (Range and Virányi, 2015). This seemingly minor shift in the social significance of conspecific pack members versus socialized humans may have far-reaching implications. Support by a familiar human – in most cases the owner – can indeed help dogs to cope with a task or an unfamiliar situation (Topál et al., 1997; Gácsi et al., 2013; Horn et al., 2013). Comparable studies with human-socialized wolves are essentially lacking: Topál et al. (2005) found that, unlike

16 weeks old dogs, 16 weeks old hand-reared wolves did not show a preference for a human caretaker in an Ainsworth's strange situation test. However, these wolves were not intensively in contact with their caretaker at the period the test was conducted (Virányi et al., 2008). Hence, as the wolves' and dogs' socialization substantially differed between research groups, results are hard to compare. Hall et al. (2015) found that socialized wolf puppies at 3, 5, and 7 weeks of age showed attachment behavior to a human caregiver. However, proper comparisons of wolves with dogs require similarly socialized and reared animals, as, for example, available at the WSC. A recent preprint, and hence not peer-reviewed study, comparing similarly reared wolves and dogs found that both species showed attachment toward their caretakers as adults (preprint; Wheat et al., 2020).

Our data also conforms to our daily experience with the WSC wolves and dogs; both show signs of attachment to familiar persons/their hand raisers and dogs tend to be generally more excited in the presence of such a person, while wolves behave in a relatively calm and focused way. Therefore, we suggest that the different ways dogs and wolves relate to humans as social partners also influences the way they cooperate with them but wolves and similarly raised dogs have probably more in common than they would differ in this respect. For example, in both wolves and dogs, attentiveness and willingness of the animal partners to cooperate seems to depend on relationship quality (Auer et al., 2011) and in both, successful cooperation generates a positive feedback on the social relationships between a human and a companion animal and reduces salivary cortisol (Vasconcellos et al., 2016). In fact, it has been demonstrated in a range of experiments that human-socialized wolves do cooperate with humans in a similar way than dogs (Range et al., 2019a,b) but subtle differences remain. For example, when given the choice, wolves tend to initiate and lead in such interspecies-cooperation, whereas dogs rather tend to follow the leading human and in general, the willingness of wolves to cooperate with humans seems to depend even more on relationship quality in wolves than in dogs (Range et al., 2019b).

Our data indicate strong potential effects of social relationships (with the human or the conspecifics present) as well as age, weight, and previous experience on the cardiac responses in the different contexts. This is not surprising, as individual bonds with both different humans and conspecifics differ in quality (Cimarelli et al., 2019). We suggest that this is an important underlying factor for much of the inter-individual variation found. In addition, personality is likely to be important. For example, during a safe haven test, reactive dogs (i.e., dogs prone to vocalizing when separated from their owner or growl and bark when approach by a threatening stranger) displayed HR and HRV changes during the test whereas the non-reactive dogs did not (Gácsi et al., 2013). Our moderate sample sizes in combination with relatively complex modeling did not allow us to include these potential causes of variability as factors but they should be kept in mind for future studies.

As age and weight may affect cardiac parameters, we will shortly discuss them here. In humans, HR generally increases in old age (Landowne et al., 1955; Umetani et al., 1998) but evidence for this in animals across their "normal" adult age range is rare, even more so in canids (Hezzell et al., 2013). As generally true for mammals, HR will decrease from puppyhood into adulthood in wolves and dogs, and may increase again in old age animals, mainly due to deteriorating health (Mosier, 1989; Strasser et al., 1997; Ferasin et al., 2010; Hezzell et al., 2013). Even less clear are the potential interactions between weight and cardiac responses in dogs. As HR in mammals is generally negatively correlated with body mass (Brody, 1945), this may also be true for dogs (Kirkwood, 1985; Sutter et al., 2007). However, most previous studies in dogs failed to demonstrate this (Ferasin et al., 2010; Lamb et al., 2010; Nganvongpanit et al., 2011; Rishniw et al., 2012). Hezzell et al. (2013) indeed found that HR scaled negatively with body mass, whereas Hamlin et al. (1967) reported that Great Danes HR frequencies exceeded that of miniature poodles. A recent study contributes to these contrasting results by reporting only a limited effect of body mass on HR (Cruz Aleixo et al., 2017). We presently controlled for body mass and age by adding them into the statistical model and found an influence of body mass on HR, while age affected both HR and HRV. Since wolves were heavier and older than the dogs in our study, the two variables could also have a confounding effect, e.g., if HR would increase with increasing age, this would also explain the body mass effect on HR. This is supported by Kortekaas and Kotrschal (2019), who also controlled for age and weight effects on cardiac output and found none. In their study, wolves were heavier but dogs and wolves were similar in age. Hence, in our study a confounding effect of age and weight is likely. We have no reason to assume a linear increase of HR with age over adulthood (Mosier, 1989; Strasser et al., 1997), the more as all our experimental animals were adults in good health, receiving regular veterinary care. Although we controlled for age and weight, we still found an effect of species, condition, and activity on HR and HRV. Hence, age and weight do not seem to explain much of the variability in our data. We therefore conclude that despite the differences in wolf and dog body mass and age, our comparisons of HR over different contexts are still valid. Such concerns do not affect HRV in a similar way as this parameter seems even more independent of body size or motor activity than HR (Cruz Aleixo et al., 2017).

We are aware that our relatively moderate sample sizes of six wolves and seven dogs, in combination with rather complex statistical models, do not allow us to draw final conclusion on the nature of wolves' and dogs' context-specific cardiac outputs. However, the cardiac parameters measured hint at a potential domestication-related difference in context-specific ANS modulation between wolves and dogs. Whether these results in our pack-kept dogs are representative also for pet dogs remains unclear but we suggest that the patterns we found are probably generic for human-socialized wolves and dogs and hence, would also be valid for pet dogs.

To conclude, wolves' and dogs' alertness and relaxation levels partially differed according to context. When resting, dogs more than wolves seemed to rely on human as social support, whereas when awake we measured similar cardiac responses to human proximity. This suggests that ANS modulation of dogs may be affected by domestication in a more complex way than suggested by simplistic interpretations of the selection-for-tameness hypothesis of domestication.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by the institutional ethics committee at the University of Veterinary Medicine, Vienna, in accordance with GSP guidelines and national legislation (ETK-11/11/2018).

AUTHOR CONTRIBUTIONS

HJ-J, KKor, and KKot designed the experiments. HJ-J wrote the manuscript, collected the data, and analyzed them. KKor, FR, and KKot revised the manuscript. All authors have contributed to, seen, and approved the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2020.568199/full#supplementary-material

REFERENCES

Adams, G. J., and Johnson, K. G. (1993). Sleep-wake cycles and other night-time behaviours of the domestic dog *Canis familiaris*. *Appl. Anim. Behav. Sci.* 36, 233–248. doi: 10.1016/0168-1591(93)90013-F

Appelhans, B. M., and Luecken, L. J. (2006). Heart rate variability as an index of regulated emotional responding. *Rev. Gen. Psychol.* 10, 229–240. doi: 10.1037/1089-2680.10.3.229

Auer, M., Wedl, M., Range, F., Virányi, Z., Belényi, B., and Kotrschal, K. (2011). Leash walking as a model for cooperation between humans and wolves: the effects of personality and intensity of contact. *J. Vet. Behav.* 6, 100–101. doi: 10.1016/j.jveb.2010.08.002

Aulsebrook, A. E., Jones, T. M., Rattenborg, N. C., Roth, T. C., and Lesku, J. A. (2016). Sleep ecophysiology: integrating neuroscience and ecology. *Trends Ecol. Evol.* 31, 590–599. doi: 10.1016/j.tree.2016.05.004

Axelsson, E., Ratnakumar, A., Arendt, M.-L., Maqbool, K., Webster, M. T., Perloski, M., et al. (2013). The genomic signature of dog domestication reveals adaptation to a starch-rich diet. *Nature* 495, 360–364. doi: 10.1038/nature11837

Baayen, R. H. (2008). *Analyzing Linguistic Data: a Practical Introduction to Statistics Using R.* Cambridge: Cambridge University Press.

Barr, D. J., Levy, R., Scheepers, C., and Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: keep it maximal. *J. Mem. Lang.* 68, 255–278. doi: 10.1016/j.jml.2012.11.001

Bates, D., Mächler, M., Bolker, B., and Walker, S. (2014). *Fitting Linear Mixed-Effects Models using lme4. arXiv:1406.5823 [stat].* Available online at: http://arxiv.org/abs/1406.5823 (accessed April 5, 2020).

Belyaev, D. K. (1979). Destabilizing selection as a factor in domestication. *J. Heredity* 70, 301–308. doi: 10.1093/oxfordjournals.jhered.a109263

Bódizs, R., Kis, A., Gácsi, M., and Topál, J. (2020). Sleep in the dog: comparative, behavioral and translational relevance. *Curr. Opin. Behav. Sci.* 33, 25–33. doi: 10.1016/j.cobeha.2019.12.006

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., et al. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* 24, 127–135. doi: 10.1016/j.tree.2008.10.008

Botigué, L. R., Song, S., Scheu, A., Gopalan, S., Pendleton, A. L., Oetjens, M., et al. (2017). Ancient European dog genomes reveal continuity since the early neolithic. *Nat. Commun.* 8:16082. doi: 10.1038/ncomms16082

Brody, S. (1945). *Bioenergetics and Growth.* (New York, NY: Reinhold Publ. Co.), 1023.

Bunford, N., Reicher, V., Kis, A., Pogány, Á, Gombos, F., Bódizs, R., et al. (2018). Differences in pre-sleep activity and sleep location are associated with variability in daytime/nighttime sleep electrophysiology in the domestic dog. *Sci. Rep.* 8:7109. doi: 10.1038/s41598-018-25546-x

Campbell, S. S., and Tobler, I. (1984). Animal sleep: a review of sleep duration across phylogeny. *Neurosci. Biobehav. Rev.* 8, 269–300. doi: 10.1016/0149-7634(84)90054-X

Cimarelli, G., Marshall-Pescini, S., Range, F., and Virányi, Z. (2019). Pet dogs' relationships vary rather individually than according to partner's species. *Sci. Rep.* 9, 1–9. doi: 10.1038/s41598-019-40164-x

Coppinger, R., and Coppinger, L. (2001). *Dogs: A Startling New Understanding of Canine Origin, Behavior & Evolution.* New York, NY: Simon and Schuster.

Cruz Aleixo, A. S., Alfonso, A., Oba, E., Ferreira de Souza, F., Salgueiro Cruz, R. K., Fillippi, M. G., et al. (2017). Scaling relationships among heart rate, electrocardiography parameters, and body weight. *Topics Comp. Anim. Med.* 32, 66–71. doi: 10.1053/j.tcam.2017.06.002

Csoltova, E., Martineau, M., Boissy, A., and Gilbert, C. (2017). Behavioral and physiological reactions in dogs to a veterinary examination: owner-dog interactions improve canine well-being. *Physiol. Behav.* 177, 270–281. doi: 10.1016/j.physbeh.2017.05.013

Darwin, C. R. (1859). *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life John Murray.* London: Google Scholar.

Darwin, C. R. (1868). *The Variation of Animals and Plants under Domestication. Second Issue*, 1st Edn, Vol. 1. London: John Murray.

Dobson, A. J., and Barnett, A. G. (2018). *An Introduction to Generalized Linear Models*. Boca Raton, FL: CRC Press.

Dominguez, J. (2003). Sleeping and vigilance in Black-tailed Godwit. *J. Ethol.* 21, 57–60. doi: 10.1007/s10164-002-0074-7

Essner, A., Sjöström, R., Ahlgren, E., Gustås, P., Edge-Hughes, L., Zetterberg, L., et al. (2015). Comparison of Polar$^{®}$RS800CX heart rate monitor and electrocardiogram for measuring inter-beat intervals in healthy dogs. *Physiol. Behav.* 138, 247–253. doi: 10.1016/j.physbeh.2014.10.034

Essner, A., Sjöström, R., Ahlgren, E., and Lindmark, B. (2013). Validity and reliability of Polar$^{®}$RS800CX heart rate monitor, measuring heart rate in dogs during standing position and at trot on a treadmill. *Physiol. Behav.* 11, 1–5. doi: 10.1016/j.physbeh.2013.03.002

Ferasin, L., Ferasin, H., and Little, C. J. L. (2010). Lack of correlation between canine heart rate and body size in veterinary clinical practice. *J. Small Anim. Pract.* 51, 412–418. doi: 10.1111/j.1748-5827.2010.00954.x

Field, A. (2005). *Discovering Statistics Using SPSS*. London: Sage Publications.

Forstmeier, W., and Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. *Behav. Ecol. Sociobiol.* 65, 47–55. doi: 10.1007/s00265-010-1038-5

Fox, J., and Weisberg, S. (2018). *An R Companion to Applied Regression*. Thousand Oaks, CA: SAGE Publications.

Frantz, L. A. F., Mullin, V. E., Pionnier-Capitan, M., Lebrasseur, O., Ollivier, M., Perri, A., et al. (2016). Genomic and archaeological evidence suggest a dual origin of domestic dogs. *Science* 352, 1228–1231. doi: 10.1126/science.aaf3161

Gácsi, M., Maros, K., Sernkvist, S., Faragó, T., and Miklósi, Á (2013). Human analogue safe haven effect of the owner: behavioural and heart rate response to stressful social stimuli in dogs. *PLoS One* 8:e58475. doi: 10.1371/journal.pone.0058475

Gauthier-Clerc, M., Tamisier, A., and Cézilly, F. (2000). Sleep-vigilance trade-off in gadwall during the winter period. *Condor* 102, 307–313. doi: 10.1093/condor/102.2.307

Hall, N. J., Lord, K., Arnold, A.-M. K., Wynne, C. D. L., and Udell, M. A. R. (2015). Assessment of attachment behaviour to human caregivers in wolf pups (*Canis lupus* lupus). *Behav. Process.* 110, 15–21. doi: 10.1016/j.beproc.2014.11.005

Hamlin, R., Smith, C., and Smetzer, D. (1966). Sinus arrhythmia in the dog. *Am. J. Physiol. Legacy Content* 210, 321–328. doi: 10.1152/ajplegacy.1966.210.2.321

Hamlin, R. L., Olsen, I., Smith, C. R., and Boggs, S. (1967). Clinical relevancy of heart rate in the dog. *J. Am. Vet. Med. Assoc.* 151, 60–63.

Hare, B., Wobber, V., and Wrangham, R. (2012). The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. *Anim. Behav.* 83, 573–585. doi: 10.1016/j.anbehav.2011.12.007

Hezzell, M. J., Humm, K., Dennis, S. G., Agee, L., and Boswood, A. (2013). Relationships between heart rate and age, bodyweight and breed in 10,849 dogs. *J. Small Anim. Pract.* 54, 318–324. doi: 10.1111/jsap.12079

Horn, L., Huber, L., and Range, F. (2013). The importance of the secure base effect for domestic dogs – evidence from a manipulative problem-solving task. *PLoS One* 8:e65296. doi: 10.1371/journal.pone.0065296

Iotchev, I. B., Kis, A., Turcsán, B., Tejeda Fernández de Lara, D. R., Reicher, V., and Kubinyi, E. (2019). Age-related differences and sexual dimorphism in canine sleep spindles. *Sci. Rep.* 9:10092. doi: 10.1038/s41598-019-46434-y

Jonckheer-Sheehy, V. S. M., Vinke, C. M., and Ortolani, A. (2012). Validation of a Polar$^{®}$human heart rate monitor for measuring heart rate and heart rate variability in adult dogs under stationary conditions. *J. Vet. Behav. Clin. Appl. Res.* 7, 205–212. doi: 10.1016/j.jveb.2011.10.006

Katayama, M., Kubo, T., Mogi, K., Ikeda, K., Nagasawa, M., and Kikusui, T. (2016). Heart rate variability predicts the emotional state in dogs. *Behav. Process.* 128, 108–112. doi: 10.1016/j.beproc.2016.04.015

Kirkwood, J. K. (1985). The influence of size on the biology of the dog. *J. Small Anim. Pract.* 26, 97–110. doi: 10.1111/j.1748-5827.1985.tb02090.x

Kis, A., Gergely, A., Galambos, Á, Abdai, J., Gombos, F., Bódizs, R., et al. (2017). Sleep macrostructure is modulated by positive and negative social experience in adult pet dogs. *Proc. R. Soc. B Biol. Sci.* 284:20171883. doi: 10.1098/rspb.2017.1883

Kis, A., Szakadát, S., Kovács, E., Gácsi, M., Simor, P., Gombos, F., et al. (2014). Development of a non-invasive polysomnography technique for dogs (*Canis familiaris*). *Physiol. Behav.* 130, 149–156. doi: 10.1016/j.physbeh.2014.04.004

Klinghammer, E., and Goodman, P. A. (1987). "Socialization and management of wolves in captivity," in *Man and Wolf: Advances, Issues, and Problems in Captive Wolf Research*, ed. H. Frank (Dordrecht: W. Junk), 31–61.

Kortekaas, K., and Kotrschal, K. (2019). Does socio-ecology drive differences in alertness between wolves and dogs when resting? *Behav. Process.* 166, 103877. doi: 10.1016/j.beproc.2019.05.024

Kotrschal, K. (2018). How wolves turned into dogs and how dogs are valuable in meeting human social needs. *People Anim. Int. J. Res. Pract.* 1:6.

Kreeger, T. J., Kuechle, V. B., Mech, L. D., Tester, J. R., and Seal, U. S. (1990). Physiological monitoring of gray wolves (*Canis lupus*) by radiotelemetry. *J. Mammal.* 71, 258–261. doi: 10.2307/1382180

Kreibig, S. D. (2010). Autonomic nervous system activity in emotion: a review. *Biol. Psychol.* 84, 394–421. doi: 10.1016/j.biopsycho.2010.03.010

Lamb, A. P., Meurs, K. M., and Hamlin, R. L. (2010). Correlation of heart rate to body weight in apparently normal dogs. *J. Veter. Cardiol.* 12, 107–110. doi: 10.1016/j.jvc.2010.04.001

Landowne, M., Brandfonbrener, M., and Shock, N. W. (1955). The relation of age to certain measures of performance of the heart and the circulation. *Circulation* 12, 567–576. doi: 10.1161/01.CIR.12.4.567

Lesku, J. A., Roth, T. C. II, Amlaner, C. J., and Lima, S. L. (2006). A phylogenetic analysis of sleep architecture in mammals: the integration of anatomy, physiology, and ecology. *Am. Naturalist* 168, 441–453. doi: 10.1086/506973

Lesku, J. A., Roth, T. C., Rattenborg, N. C., Amlaner, C. J., and Lima, S. L. (2008). Phylogenetics and the correlates of mammalian sleep: a reappraisal. *Sleep Med. Rev.* 12, 229–244. doi: 10.1016/j.smrv.2007.10.003

Luque-Casado, A., Zabala, M., Morales, E., Mateo-March, M., and Sanabria, D. (2013). Cognitive performance and heart rate variability: the influence of fitness level. *PLoS One* 8:e56935. doi: 10.1371/journal.pone.0056935

Maros, K., Dóka, A., and Miklósi, Á (2008). Behavioural correlation of heart rate changes in family dogs. *Appl. Anim. Behav. Sci.* 109, 329–341. doi: 10.1016/j.applanim.2007.03.005

Marshall-Pescini, S., Cafazzo, S., Virányi, Z., and Range, F. (2017). Integrating social ecology in explanations of wolf–dog behavioral differences. *Curr. Opin. Behav. Sci.* 16, 80–86. doi: 10.1016/j.cobeha.2017.05.002

Matuschek, H., Kliegl, R., Vasishth, S., Baayen, H., and Bates, D. (2017). Balancing type I error and power in linear mixed models. *J. Mem. Lang.* 94, 305–315. doi: 10.1016/j.jml.2017.01.001

Mech, L. D., and Boitani, L. (2003). *Wolves: Behavior, Ecology, and Conservation*. Chicago, IL: University of Chicago Press.

Miklósi, Á, and Topál, J. (2013). What does it take to become 'best friends'? Evolutionary changes in canine social competence. *Trends Cogn. Sci.* 17, 287–294. doi: 10.1016/j.tics.2013.04.005

Mosier, J. E. (1989). Effect of aging on body systems of the dog. *Vet. Clin. North Am. Small Anim. Pract.* 19, 1–12. doi: 10.1016/S0195-5616(89)50001-9

Nganvongpanit, K., Kongsawasdi, S., Chuatrakoon, B., and Yano, T. (2011). Heart rate change during aquatic exercise in small, medium and large healthy dogs. *Thai J. Vet. Med.* 41, 455–461.

Oken, B. S., Salinsky, M. C., and Elsas, S. M. (2006). Vigilance, alertness, or sustained attention: physiological basis and measurement. *Clin. Neurophysiol.* 117, 1885–1901. doi: 10.1016/j.clinph.2006.01.017

Palmer, R., and Custance, D. (2008). A counterbalanced version of Ainsworth's strange situation procedure reveals secure-base effects in dog–human relationships. *Appl. Anim. Behav. Sci.* 109, 306–319. doi: 10.1016/j.applanim.2007.04.002

Porges, S. W. (1995). Orienting in a defensive world: mammalian modifications of our evolutionary heritage. A Polyvagal Theory. *Psychophysiology* 32, 301–318. doi: 10.1111/j.1469-8986.1995.tb01213.x

Porges, S. W. (2001). The polyvagal theory: phylogenetic substrates of a social nervous system. *Int. J. Psychophysiol.* 42, 123–146. doi: 10.1016/S0167-8760(01)00162-3

Porges, S. W. (2003). The Polyvagal Theory: phylogenetic contributions to social behavior. *Physiol. Behav.* 79, 503–513. doi: 10.1016/S0031-9384(03)00156-2

Porges, S. W. (2009). The polyvagal theory: new insights into adaptive reactions of the autonomic nervous system. *Cleve Clin. J. Med.* 76, S86–S90. doi: 10.3949/ccjm.76.s2.17

Price, E. O. (1999). Behavioral development in animals undergoing domestication. *Appl. Anim. Behav. Sci.* 65, 245–271. doi: 10.1016/S0168-1591(99)00087-8

R Core Team (2019). *R: A Language and Environment for Statistical Computing.* Vienna: R Foundation for Statistical Computing.

Rajendra Acharya, U., Paul Joseph, K., Kannathal, N., Lim, C. M., and Suri, J. S. (2006). Heart rate variability: a review. *Med. Biol. Eng. Comput.* 44, 1031–1051. doi: 10.1007/s11517-006-0119-0

Range, F., Kassis, A., Taborsky, M., Boada, M., and Marshall-Pescini, S. (2019a). Wolves and dogs recruit human partners in the cooperative string-pulling task. *Sci. Rep.* 9, 1–10. doi: 10.1038/s41598-019-53632-1

Range, F., Marshall-Pescini, S., Kratz, C., and Virányi, Z. (2019b). Wolves lead and dogs follow, but they both cooperate with humans. *Sci. Rep.* 9:3796. doi: 10.1038/s41598-019-40468-y

Range, F., and Virányi, Z. (2011). Development of Gaze Following Abilities in Wolves (*Canis Lupus*). *PLoS One* 6:e16888. doi: 10.1371/journal.pone.0016888

Range, F., and Virányi, Z. (2013). Social learning from humans or conspecifics: differences and similarities between wolves and dogs. *Front. Psychol.* 4:868. doi: 10.3389/fpsyg.2013.00868

Range, F., and Virányi, Z. (2014). Wolves are better imitators of conspecifics than dogs. *PLoS One* 9:e86559. doi: 10.1371/journal.pone.0086559

Range, F., and Virányi, Z. (2015). Tracking the evolutionary origins of dog-human cooperation: the "canine cooperation hypothesis. *Front. Psychol.* 5:1582. doi: 10.3389/fpsyg.2014.01582

Rishniw, M., Ljungvall, I., Porciello, F., Häggström, J., and Ohad, D. G. (2012). Sleeping respiratory rates in apparently healthy adult dogs. *Res. Vet. Sci.* 93, 965–969. doi: 10.1016/j.rvsc.2011.12.014

Schielzeth, H., and Forstmeier, W. (2009). Conclusions beyond support: overconfident estimates in mixed models. *Behav. Ecol.* 20, 416–420. doi: 10.1093/beheco/arn145

Schöberl, I., Kortekaas, K., Schöberl, F. F., and Kotrschal, K. (2015). Algorithm-supported visual error correction (AVEC) of heart rate measurements in dogs *Canis lupus* familiaris. *Behav. Res.* 47, 1356–1364. doi: 10.3758/s13428-014-0546-z

Shields, R. W. J. (1993). Functional anatomy of the autonomic nervous system. *J. Clin. Neurophysiol.* 10, 2–13. doi: 10.1097/00004691-199301000-00002

Siegel, J. M. (2005). Clues to the functions of mammalian sleep. *Nature* 437, 1264–1271. doi: 10.1038/nature04285

Siegel, J. M. (2008). Do all animals sleep? *Trends Neurosci.* 31, 208–213. doi: 10.1016/j.tins.2008.02.001

Solomon, J., Beetz, A., Schöberl, I., Gee, N., and Kotrschal, K. (2019). Attachment security in companion dogs: adaptation of Ainsworth's strange situation and classification procedures to dogs and their human caregivers. *Attach. Hum. Dev.* 21, 389–417. doi: 10.1080/14616734.2018.1517812

Stacey, P. B. (1986). Group size and foraging efficiency in yellow baboons. *Behav. Ecol. Sociobiol.* 18, 175–187. doi: 10.1007/BF00290821

Strasser, A., Simunek, M., Seiser, M., and Hofecker, G. (1997). Age-dependent changes in cardiovascular and metabolic responses to exercise in beagle dogs. *J. Vet. Med. Series A* 44, 449–460. doi: 10.1111/j.1439-0442.1997.tb01130.x

Sutter, N. B., Bustamante, C. D., Chase, K., Gray, M. M., Zhao, K., Zhu, L., et al. (2007). A single *IGF1* allele is a major determinant of small size in dogs. *Science* 316, 112–115. doi: 10.1126/science.1137045

Takeuchi, T., and Harada, E. (2002). Age-related changes in sleep-wake rhythm in dog. *Behav. Brain Res.* 136, 193–199. doi: 10.1016/S0166-4328(02)00123-7

Topál, J., Gácsi, M., Miklósi, Á, Virányi, Z., Kubinyi, E., and Csányi, V. (2005). Attachment to humans: a comparative study on hand-reared wolves and differently socialized dog puppies. *Anim. Behav.* 70, 1367–1375. doi: 10.1016/j.anbehav.2005.03.025

Topál, J., Miklósi, Á, and Csányi, V. (1997). Dog-human relationship affects problem solving behavior in the dog. *Anthrozoös* 10, 214–224. doi: 10.2752/089279397787000987

Trut, L. N., Plyusnina, I. Z., and Oskina, I. N. (2004). An experiment on fox domestication and debatable issues of evolution of the dog. *Russian J. Genet.* 40, 644–655. doi: 10.1023/B:RUGE.0000033312.92773.c1

Tuber, D. S., Hennessy, M. B., Sanders, S., and Miller, J. A. (1996). Behavioral and glucocorticoid responses of adult domestic dogs (*Canis familiaris*) to companionship and social separation. *J. Comp. Psychol.* 110, 103–108. doi: 10.1037/0735-7036.110.1.103

Ujfalussy, D. J., Kurys, A., Kubinyi, E., Gácsi, M., and Virányi, Z. (2017). Differences in greeting behaviour towards humans with varying levels of familiarity in hand-reared wolves (*Canis lupus*). *R. Soc. Open Sci.* 4:160956. doi: 10.1098/rsos.160956

Umetani, K., Singer, D. H., McCraty, R., and Atkinson, M. (1998). Twenty-four hour time domain heart rate variability and heart rate: relations to age and gender over nine decades. *J. Am. Coll. Cardiol.* 31, 593–601. doi: 10.1016/S0735-1097(97)00554-8

Varga, B., Gergely, A., Galambos, Á, and Kis, A. (2018). Heart rate and heart rate variability during sleep in family dogs (*Canis familiaris*). Moderate effect of pre-sleep emotions. *Animals* 8:107. doi: 10.3390/ani8070107

Vasconcellos, A., da, S., Virányi, Z., Range, F., Ades, C., Scheidegger, J. K., et al. (2016). Training reduces stress in human-socialised wolves to the same degree as in dogs. *PLoS One* 11:e0162389. doi: 10.1371/journal.pone.0162389

Virányi, Z., Gácsi, M., Kubinyi, E., Topál, J., Belényi, B., Ujfalussy, D., et al. (2008). Comprehension of human pointing gestures in young human-reared wolves (*Canis lupus*) and dogs (*Canis familiaris*). *Anim. Cogn.* 11, 373–387. doi: 10.1007/s10071-007-0127-y

Visser, E. K., van Reenen, C. G., van der Werf, J. T. N., Schilder, M. B. H., Knaap, J. H., Barneveld, A., et al. (2002). Heart rate and heart rate variability during a novel object test and a handling test in young horses. *Physiol. Behav.* 76, 289–296. doi: 10.1016/S0031-9384(02)00698-4

von Borell, E., Langbein, J., Després, G., Hansen, S., Leterrier, C., Marchant-Forde, J., et al. (2007). Heart rate variability as a measure of autonomic regulation of cardiac activity for assessing stress and welfare in farm animals — a review. *Physiol. Behav.* 92, 293–316. doi: 10.1016/j.physbeh.2007.01.007

vonHoldt, B. M., Shuldiner, E., Koch, I. J., Kartzinel, R. Y., Hogan, A., Brubaker, L., et al. (2017). Structural variants in genes associated with human Williams-Beuren syndrome underlie stereotypical hypersociability in domestic dogs. *Sci. Adv.* 3:e1700398. doi: 10.1126/sciadv.1700398

Wheat, C. H., Larsson, L., and Temrin, H. (2020). Hand-reared wolves show similar, or stronger, attachment toward human caregivers compared to hand-reared dogs. *bioRxiv* [Preprint]. doi: 10.1101/2020.02.17.952663

Wilkins, A. S., Wrangham, R. W., and Fitch, W. T. (2014). The "Domestication Syndrome" in mammals: a unified explanation based on neural crest cell behavior and genetics. *Genetics* 197, 795–808. doi: 10.1534/genetics.114.165423

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Chapter 2|

Diurnal activity patterns of equally socialized and kept wolves, Canis lupus, and dogs, Canis lupus familiaris

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Diurnal activity patterns of equally socialized and kept wolves, *Canis lupus*, and dogs, *Canis lupus familiaris*

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Owing to domestication, dog behaviour differs from wolf behaviour, which should also affect time budgets. At the Wolf Science Center, wolves and mongrel dogs are raised and kept in a similar way; thus, it is an ideal place to compare the time budgets of wolves and dogs in search of potential domestication-related shifts. Seven wolf packs and four dog packs were observed over a full year. We focused on major behavioural categories, such as resting and foraging, and calculated the proportion of time they spent on each of these activities. Based on mainstream domestication hypotheses we predicted dogs to be generally more active than wolves because domestication would have relaxed the need for behavioural efficiency. As expected, wolves and dogs differed in their time budgets. Wolves slept, walked and vocalized more than dogs, whereas dogs foraged, sat and manipulated objects more. Human presence around the enclosure increased the activity of both, but dogs were more active than wolves in this situation. Season and time of day had the same effect on dogs and wolves. We conclude that dogs are not too different from wolves in intrinsic motivation affecting their time budgets, except for the increased responses of dogs to humans. This suggests that humans are more important as social Zeitgeber for dogs than for equally socialized wolves.

In general, domesticated animals share a ‘domestication syndrome’ (Darwin, 1859; Wilkins et al., 2014), featuring a number of linked anatomical and behavioural features. This syndrome is thought to be caused by selection for tameness (Belyaev, 1979; Trut et al., 2004), rendering domesticated animals gentler and more tractable than their wild ancestors and affecting their anatomy and physiology (Trut et al., 2009; Agnvall et al., 2015; Fam et al., 2018; Hecht et al., 2021). Hence, domestication affects the way animals relate to their environment and should also modulate the intrinsic motivational factors of domesticated animals and their responses to external Zeitgeber (i.e. an environmental agent or event that provides the stimulus to trigger the biological clock of an organism, Aschoff, 1954). This in turn, could affect their time budgets (Künzl & Sachser, 1999; Robert et al., 1987; Troxell-Smith et al., 2016).

All dogs originated from wolves through the process of domestication, which began in the Palaeolithic some 35 000 years ago (Botigué et al., 2017; Thalmann et al., 2013). Although the nature of this process is still discussed (Hare & Tomasello, 2005; Hare et al., 2012; Range & Virányi, 2014, 2015; Wilkins et al., 2014; Marshall-Pescini et al., 2017), its outcomes are becoming clearer from an increasing number of experimental studies (Frank & Frank, 1982, 1985; Frank, 1987; Kubinyi et al., 2007; Range & Virányi, 2015; Kaminski et al., 2019). For example, dogs do not fear humans as wolves do (Klinghammer & Goodman, 1987), they are more attentive and attracted to humans (Miklósi et al., 2003; Gácsi et al., 2009) and more willing to respect both conspecific and human hierarchies (Range et al., 2015, 2019b). As a result, they are good at cooperating with humans.

Given the large influence of ecology and a number of potential Zeitgeber, including social factors, on the time budgets of wolves and dogs, a direct comparison in search of potential intrinsic changes due to domestication seems virtually impossible if the animals do not share the same environment and the same experiences from early on. At the Wolf Science Center (WSC), Ernstbrunn, Austria, wolves and dogs are similarly raised and kept. This allows fair comparisons of wolves' and dogs' cognitive skills and social and cooperative orientation towards conspecifics or humans (Cafazzo et al., 2018; Range et al., 2015, 2019a, 2019b). This also

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offers a unique opportunity for comparing time budgets of wolves and dogs in the absence and presence of humans.

Wolf packs consist of a breeding pair and their offspring (Packard, 2003). Within-pack cooperation allows for hunting large prey, defending territory and raising young (Mech & Peterson, 2003; Mech & Boitani, 2003). Wolves in the wild show a bimodal activity pattern with crepuscular activity peaks (Vilà et al., 1995; Ciuccie et al., 1997; Merrill & Mech, 2003; Theuerkauf et al., 2007; Theuerkauf, 2009; Kirilyuk et al., 2021), potentially associated with optimal hunting conditions. Such environmental factors called 'Zeitgeber' affect the activity of most animals, including wolves, entraining potential intrinsic rhythms (Aschoff, 1954; Heldmaier et al., 1989; Aronson et al., 1993; Grandin et al., 2006). For example, the diurnal and circannual variation of light in temperate zones is the major environmental cue for entraining individual activity and sleep–wake rhythms. In general, wolves tend to be more active during winter, as they are adapted to low temperatures and because of increased prey accessibility (Price, 1999). Wolf reproduction is timed accordingly: female wolves have a single annual oestrus period during the winter month (Scott & Fuller, 1965; Christie & Bell, 1971), which ensures that the pups are born in early spring at peak prey availability (Mech & Boitani, 2003). Variations in wolf circadian and circannual activity patterns may be induced by their need to avoid humans (Ciuccie et al., 1997; Vilà et al., 1995) or by temperature peaks during the day (Ciucci et al., 1997; Theuerkauf, 2009). Furthermore, as wolves tend to respond to prey densities, wolf behaviour and prey behaviour mutually affect each other (Theuerkauf, 2009). Therefore, seasonality (notably temperature), prey density and avoiding humans seem to be the main factors influencing the activity of wolves in the wild. Although the WSC wolves are captive, they should still adjust their behaviour to the season. Furthermore, as they interact daily with their trainers, who were also their hand-raisers, human presence should also affect their time budgets, but potentially to a lesser degree than in the dogs.

Dogs are much more diverse than wolves in their appearance, genetics (Parker et al., 2017) and lifestyle. Free-ranging dogs (i.e. dogs not under direct human control; Cafazzo et al., 2010) represent up to 80% of the world's 1 billion dogs (Lord et al., 2013; Hughes & Macdonald, 2013). The socioecology of these dogs differs from that of wolves. They live near humans and usually scavenge on refuse (Majumder et al., 2016; Vanak & Gompper, 2009). Unlike wolves, free-ranging dogs are 'facultatively social' (Majumder et al., 2014), living in relatively stable groups composed of several males and females (Bonanni & Cafazzo, 2014). Most females have two oestrus periods per year instead of one like wolves and are generally promiscuous, which could explain why males generally do not participate in raising the pups (Pal, 2005; Cafazzo et al., 2014). Humans are directly and indirectly responsible for 63% of the early deaths of pups and so can be a threat to free-ranging dogs (Paul et al., 2016). Conversely, humans can also provide food to dogs that beg (Bhadra & Bhadra, 2014; Majumder et al., 2014) and support pup-raising females. Therefore, humans may play important roles also for free-ranging dogs.

A minority of the world's dogs live in close companionship with human partners. Companion dogs depend on their humans in nearly every aspect of their life (Leonard et al., 2002; Scott & Fuller, 1965; Vanak et al., 2009; Wandeler et al., 1993; Kotrschal, 2018; Smith & Van Valkenburgh, 2021). Companion dogs tend to be active when the owner is present (Piccione et al., 2014), but rest more than shelter dogs (Hoffman et al., 2019), and their activity patterns vary more than those of wolves or free-ranging dogs (Griss et al., 2021), because the owners are the social Zeitgeber of their dogs (Leonhard & Randler, 2009) and, to a certain degree, also vice versa. In fact, pet dogs adjust their sleep–wake cycle to that of their owners (Randler et al., 2018), which includes conforming to their owners' 'social jetlag' (i.e. different sleep timing on workdays and free days). Despite not being companion dogs, the WSC dogs share close relationships with their hand-raisers, who also act as animal keepers and trainers. Hence, it is possible that these familiar humans play the role of owner-like social Zeitgeber for the WSC dogs.

Recently, we studied the resting patterns of the WSC wolves and dogs in search of domestication effects. We found considerable variation in the heart rates and heart rate variability of resting wolves and dogs, depending on the social context. For example, dogs and wolves were more relaxed when resting in their pack than when alone (Kortekaas & Kotrschal, 2019). Moreover, dogs, but not wolves, responded to the presence of familiar humans in a similarly relaxed way as their pack members (Jean-Joseph et al., 2019). When the animals were awake, wolves barely modulated their arousal due to humans' presence, whereas dogs were generally more alert around humans than when they were alone or with their pack mates. As a follow-up of Jean-Joseph et al. (2020), and by taking into account the major factors that could affect wolves and dogs in the wild (e.g. seasonality, biological cycle) and factors specific to the WSC (i.e. the presence of familiar and unfamiliar humans), we assessed the daylight time budgets and activities of the WSC's animals over a full year. We hypothesized that the behaviour of dogs as domesticated animals may be less motivated by energy efficiency than that of their wild form, the wolves, since humans provide them with food; hence, dogs would be less energy efficient in their behaviour than wolves, showing overall greater activity. Furthermore, according to the hypersociability hypothesis (von Holdt et al., 2017), selection during domestication has genetically predisposed dogs for hypersocial responses towards humans. Based on this hypothesis, we expected dogs to be more social towards humans and hence alter their behaviours more than wolves in the presence of humans. Finally, we expected that, due to their outdoor life and a generally similar physiology of dogs and wolves, both would be similarly affected by environmental factors, such as temperature and season.

METHODS

Ethical Note

This research was discussed and approved by the institutional ethics committee at the University of Veterinary Medicine, Vienna, in accordance with GSP guidelines and national legislation (ETK-12/11/2018). All the animals participating in the study were housed at the WSC, located in the Game Park Ernstbrunn in Austria (Licence No. AT00012014), and remained there after the study. Throughout the study, no animal was manipulated or exposed to stressful situations. The subjects were observed from outside their enclosure, a situation they are well used to and hence is not stressful to them.

Subjects

We observed seven wolf packs (16 individuals, 11 males and five females; Table 1) and four groups of dogs (11 individuals, five males and six females; Table 1). In 2018, when we started this study, subjects were between 2 and 10 years of age (wolves: mean ± SD = 7 + 3.1; dogs: mean ± SD = 6 ± 1.6). All animals were hand-raised from 10 days after birth in small groups of four to six in a 1000 m^2 outdoor enclosure with access to an indoor room where the hand-raisers spent the nights with them. At 5 months they were moved to other enclosures ranging from 2000 m^2 to 8000 m^2. They remained hormonally intact (i.e. not neutered or spayed), but male wolves and dogs were vasectomized to prevent unwanted

Table 1
List of the subjects

Individual	Species	Sex	Date of birth	Pack
Amarok	Wolf	♂	4 Apr 2012	1
Aragorn	Wolf	♂	4 May 2008	2
Chitto	Wolf	♂	7 Apr 2012	3
Etu	Wolf	♂	4 May 2016	4
Geronimo	Wolf	♂	2 May 2009	5
Kaspar	Wolf	♂	4 May 2008	2
Kenai	Wolf	♂	1 Apr 2010	1
Maikan	Wolf	♂	4 May 2016	4
Nanuk	Wolf	♂	28 Apr 2009	6
Shima†	Wolf	♀	4 May 2008	2
Taima	Wolf	♀	4 May 2016	7
Tala	Wolf	♀	4 Apr 2012	3
Tekoa	Wolf	♂	4 May 2016	7
Una	Wolf	♀	7 Apr 2012	6
Wamblee	Wolf	♂	22 Apr 2012	5
Yukon	Wolf	♀	2 May 2009	5
Asali	Dog	♂	19 Sep 2010	8
Bora	Dog	♀	2 Aug 2011	8
Enzi	Dog	♂	2 Apr 2014	9
Gombo	Dog	♂	21 Mar 2014	10
Haida[a]	Dog	♀	04 Jun 2007	10
Hiari	Dog	♂	21 Mar 2014	11
Imara	Dog	♀	21 Mar 2014	11
Layla	Dog	♀	2 Aug 2011	9
Meru[b]	Dog	♂	1 Oct 2010	11
Panya	Dog	♀	2 Apr 2014	9
Zuri	Dog	♀	24 May 2011	9/10[c]

[a] Subject excluded from the statistical analyses.
[b] Subject died during the observation period.
[c] Pack change on 13 June 2019.

reproduction. After the animals were integrated into conspecific packs at 5 months old, they had daily contact with their hand-raisers and trainers and, less regularly, with unfamiliar people (e.g. new scientific staff, visitor taking part in special visitor programmes). The wolves were fed carcasses of deer, pig, rabbit or chicken three to four times a week, while the dogs were fed The Good Stuff dry food daily regularly enriched with small pieces of deer, pig, rabbit or chicken to make wolf and dog feeding as similar as possible. Wolves and dogs also received veterinary and obedience training from puppyhood and participated in several behavioural tests on a daily to weekly basis. Water was available ad libitum for all wolves and dogs.

During the observation period, one wolf (Shima, 21 April 2019) and one dog (Meru, 12 August 2019) died of natural causes. Thus, the composition of some packs changed. One dog, Zuri, was moved from Pack 9 to Pack 10 on 13 June 2019 (see Table 1). Therefore, after 21 April 2019, only 15 wolves were observed and after 12 June 2019, only 10 dogs (see Table 1). One dog, Haida, joined the WSC on 10 October 2017, when she was already an adult, and thus she was excluded from analysis.

Data Collection

We conducted 29 h of preliminary observations to construct the ethogram for the main study (see Table 2, Appendix Table A1).

Data collection started on 1 December 2018 and ran until the end of November 2019. Three scientific interns (G.D., R.S., K.W.) collected the data (Appendix Table A1). Observations were conducted from dawn to dusk to take daylight hour variation in behaviours into account. As daylight varies with season, the number of observations per month for each individual/pack differed somewhat. However, averaged across the study, each part of the day was equally represented in the final sample for each individual/pack. Between seasons, the number of observations per individual/pack varied, as we had fewer observations in summer (June, July, August), mainly due to the transition in observers. Packs were only observed when all members were present. We also avoided conducting observations during particular events, such as guided tours, feeding or training demonstrations for visitors. We used the instantaneous scan sampling method (Bateson & Martin, 2021) to assess the behaviour of each member of the observed pack (see Table 2 for our ethogram). Each observation lasted 30 min divided into 30 intervals of 1 min. We conducted multiple observations per day but never observed the same pack twice in a row. We never

Table 2
Ethogram

Behaviour	Definition	Code
Resting	Not asleep or engaging in other behaviours, lying down, head down, eyes open	R
Sleeping	Lying down with head on the ground and eyes closed	S
Foraging	Searching with nose on the ground and sniffing or visual investigation (nose and eyes pointed to the ground to investigate an item)	F
Eating	Swallowing food provided, or animals they have caught, or grass in the enclosure	E
Drinking	Swallowing liquid, provided or e.g. puddles	Dr
Hunting	Chasing or stalking an animal that is not a conspecific	H
Vocalizing	Howling, barking, whining	V
Digging	Using paws to remove substrate	Di
Object manipulation	Playing, touching, moving, licking, biting an object, a form of enrichment or part of the enclosure	OM
Urinate	Releasing urine	U
Defecate	Releasing faeces	D
Stress behaviour	Yawning, body shaking, lip licking, scratching	StB
Social behaviour	All social behaviours, affiliative (e.g. play bow, greeting, etc.) or agonistic (e.g. jaw spar, fight, etc.)	SoB
Sexual behaviour	Mounting, mating	SeB
Maintenance behaviour	Autogrooming or scent rolling	MB
Locomotion		
Walking	Slow movement in one direction, at least one leg in contact with the ground; diagonal walk	W
Trotting	Medium pace; diagonal two-beat gait in which the left rear and right front legs move together and the left fore and right hind legs move together	T
Cantering	Fast movement in one direction, a three-beat gait with left hind leg starting, the right hind and left leg striking the ground together and the right foreleg landing and supporting the whole weight of the animal. There is a moment of suspension before the sequence is repeated and the sequence may be reversed	C
Immobile		
Sitting	Rear on the ground, with rear legs tucked in and the front legs extended	IS
Standing	All four feet are on the ground with torso off the ground	ISt
Lying	Torso on the ground; position of paws may vary, head up, eyes open	IL
Not visible	Animal cannot be seen	NV

observed the same pack twice during the same time slot across the same month. Upon arrival at the enclosure, the observer waited at least 2 min next to the fence and was visible to the animals to habituate them. A timer with an audible signal on every minute interval was used to ensure the observer's accuracy. At each sound signal, the observer noted the behaviour of each individual, always in the same order (i.e. min 1: ind1, ind2, ind3; min 2: ind1, ind2, ind3).

Additionally, the observer noted the presence or absence of visitors/staff and if dogs were visible to the study animals (unfamiliar visitor dogs, the trainers' dogs and other WSC packs' dogs that are familiar without being their pack's members) However, we chose not to analyse the data on dogs visible to the study animals as these data represented less than 1% of the data set (1142 data points) and were likely to be insufficient to draw conclusions on the effect of these dogs on our subjects and also because the dogs were always paired with a human. Visitors/staff and dogs were noted as 'present' if they were within 15 m of the enclosure's wire fences and not hidden by wooden fences or blinders. Several independent variables were coded: identity of the observer, date and time of the observation, which enclosure the observed pack was in (as enclosures have different size and vegetation coverage, which could lead to packs' preference for some enclosures over the others), temperature, weather (i.e. sunny, cloudy, rainy, snowy), proximity between the individual and the pack (alone, within one body length or within three body lengths) and, finally, whether there was a female in heat in the pack. The variable 'activity' was later derived from the observed behaviour. Activity was coded as 'no' (i.e. subject is not active) when the subject was observed sleeping, resting, lying, sitting or standing immobile or 'yes' (i.e. the subject is active) when the subject was performing any other behaviour.

We conducted a total of 1567 30 min observations. One observation was discarded because the subject observed went out of sight after 3 min and did not return. Therefore, our final sample size was 1566 observations (783 h) and 115 708 1 min data points. For all models (below), we excluded all scans where the subject was not visible. Consequently, final sample size for the activity model was 110 176 data points (24 434 active) and 110 176 data points (34 589 subject not alone) for the proximity model.

Statistical Analyses

We tested interobserver reliability (IOR) and found that the category 'proximity at three body lengths' scored low IOR (<70%); thus, it was not analysed. After exclusion of the unreliable category, IOR was 93.4%.

We compared the yearly daylight time budgets of wolves and dogs, performing first a Pearson chi-square test and, second, a pairwise post hoc chi-square. As a follow up, we divided the data set in two (human present and human absent) and then performed a Pearson chi-square test and pairwise post hoc chi-square on both data sets. For each test, we used the Bonferroni correction to adjust the P value for multiple testing to decrease the likelihood of potential type I error.

To test what factor could influence dogs' and wolves' activity, we used a generalized linear mixed model (GLMM, Baayen, 2008) with binomial error structure and logit link function. Temperature (in Celsius, chosen to represent the seasonal variation), start time of the observation (in hours, to represent the daily variation) as well as wolf or dog, the presence of humans (yes or no) and their interaction were included as fixed effects. Sex and age of the subject (in months) were added as fixed effect factors to control for their influence on wolves' and dogs' activity. Subject ID, pack, enclosure and observation ID were included as random effects. Furthermore, a combination of pack and enclosure was included as the last random effect to account for pack preference for particular enclosures. Additionally, we included all the identifiable random slopes (temperature within subject ID, age within pack, enclosure and observation ID and age, temperature, start time of the observation within enclosure/pack) to avoid inflated type I error rate (Schielzeth & Forstmeier, 2009; Barr et al., 2013). Correlations among random intercepts and slopes were unidentifiable (absolute correlation parameter mostly equal to 1) and therefore were excluded from the model (Matuschek et al., 2017). As a result, the model fit decreased moderately (model with correlation: $\text{logLik} = -48369.15$ ($df = 30$); model without correlation: $\text{logLik} = -48376.22$ ($df = 16$)).

To test the proximity of our subject to their pack members, we also used a GLMM with a binomial error structure and logit link structure with the same statistical approach as above; wolf or dog, the presence of humans (yes or no) and their interaction were included as fixed effects. Temperature, sex, age of the subject (in months) and the activity of the subject (active or not active) were added as fixed effect factors to control for their influence on wolves' and dogs' proximity to their pack mates. Subject ID, pack, enclosure, observation ID and the combination of pack and enclosure were included as random effects. Additionally, we included the only identifiable random slope, age within the combination of pack and enclosure. The final model fit was $\text{logLik} = -4179.81$ ($df = 15$).

For both models, age, temperature and start time of the observation were z-transformed (to a mean of zero and a standard deviation of one). Species, presence of humans, sex and activity were dummy coded (i.e. the categorical predictors were replaced by one or several dummy variables, consisting of 0 and 1, and then centred to a mean of zero before including them in the model.

To test the significance of our four fixed effects of interest, we used a likelihood ratio test (R function anova with argument test set to 'Chisq'; Dobson & Barnett, 2018) to compare our full models (Forstmeier & Schielzeth, 2011) to our null models. The significance of the individual effect was assessed with likelihood ratio tests comparing the full models with their respective reduced models.

For both models, stability was assessed by comparing the estimates of the full model to the estimates of reduced models, suppressing levels of random effect one at a time (Nieuwenhuis et al., 2012). We found no issues of stability in our models. We verified the absence of collinearity using the variance inflation factor (Field, 2013) for a standard linear model excluding all the random effects, which revealed no issues of collinearity in the two models. All statistical analyses were performed with R (version 4.0.5, R Core Team, 2021) using the function lmer of the R package lme4 (version 1.1–26; Bates et al., 2014) with the optimizer 'bobyqa'. Tests of the individual fixed effects were derived using likelihood ratio tests (Barr et al., 2013; R function drop1 with argument 'test' set to 'Chisq'). Pairwise post hoc chi-square analyses were made with the package chisq.posthoc.test (version 0.1.2).

RESULTS

Time Budgets

Overall, wolves' and dogs' diurnal time budgets were significantly different over the year (chi-square test: $\chi^2_{21} = 8720.8$, $P < 2.2e\text{-}16$; Fig. 1a and b). Dogs foraged and sat significantly more than wolves (see Table 3 for P values and details of the other behaviours). Wolves slept, lay on the ground, trotted, walked and vocalized more. Additionally, wolves and dogs differed in the frequency of behaviours they displayed in the presence of humans (chi-square test: $\chi^2_{21} = 4048.4$, $P < 2.2e\text{-}16$; Fig. 1c): dogs foraged, sat and vocalized more than wolves. On the other hand, when near humans, wolves trotted, walked, stood and lay on the ground more, as well as rested and slept more than the dogs. Wolves and dogs

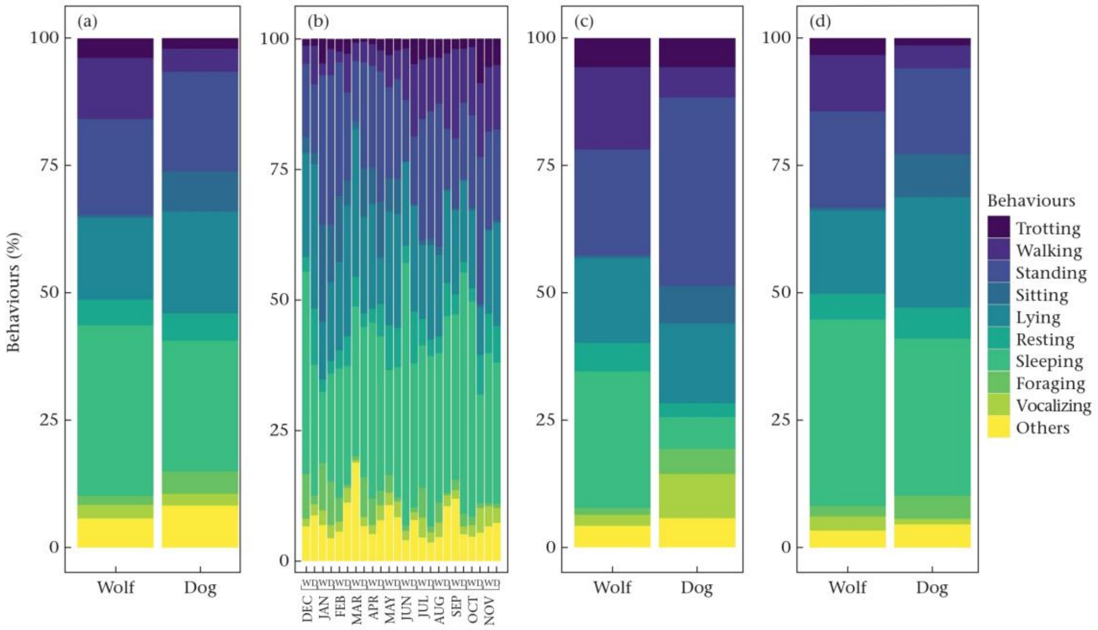

Figure 1. Bar plot of the differences in wolves' and dogs' behaviours. (a) Overall comparison; (b) over the months; (c) in the presence of humans; (d) in the absence of humans. Category 'Others' includes eating, drinking, defecating, urinating, hunting, object manipulation, social interaction and displays of stress behaviour.

also differed in the behaviours displayed in the absence of humans (chi-square test: $\chi^2_{20} = 6887.8$, $P < 2.2\text{e-}16$; Fig. 1d). Dogs were observed foraging and sitting more often than wolves which trotted, walked, stood, lay on the ground, rested and slept more than dogs. Finally, wolves vocalized more than dogs in the absence of humans (see Table 3).

Dog behaviours also differed between the absence and the presence of humans (chi-square test: $\chi^2_{18} = 5116.6$, $P < 2.2\text{e-}16$). In

Table 3
Pairwise post hoc comparison

Behaviours	nW	Overall	*P*	Human present[a]			Human absent[a]			W–W	D–D
		nD		nW	nD	*P*	nW	nD	*P*	*P*	*P*
Cantering	65	83	<0.001	39	72	1	26	11	<0.001	<0.001	<0.001
Defecating	16	6	1	2	0	1	14	6	1	1	1
Digging	11	131	<0.001	0	40	<0.001	11	91	1	1	0.001
Drinking	143	96	1	46	20	1	97	76	1	1	1
Eating	433	97	<0.001	115	42	<0.001	318	55	1	1	<0.001
Foraging	1289	1894	<0.001	216	342	<0.001	1073	1552	<0.001	<0.001	1
Hunting	6	6	1	2	0	1	4	6	1	1	1
Lying	11307	8490	<0.001	2782	1095	<0.001	8522	7395	<0.001	1	<0.001
Sitting	409	3389	<0.001	80	518	<0.001	329	2871	<0.001	1	0.127
Standing	13336	8364	0.082	3463	2601	<0.001	9873	5763	<0.001	<0.001	<0.001
Maintenance	873	698	<0.001	249	47	<0.001	624	651	<0.001	0.109	<0.001
Not visible	1772	1554	<0.001	2	0	1	1	0	1	1	–
Object manipulation	35	455	<0.001	8	73	<0.001	27	382	<0.001	1	1
Resting	3583	2254	1	930	187	<0.001	2653	2067	<0.001	0.449	<0.001
Sexual	52	0	<0.001	20	0	<0.001	32	0	<0.001	0.704	–
Sleeping	23635	10978	<0.001	4463	442	<0.001	19172	10536	<0.001	<0.001	<0.001
Social	740	379	0.4	241	127	0.037	499	252	<0.001	<0.001	<0.001
Stress	1	0	1	1	0	–	0	0	–	1	–
Trotting	2687	876	<0.001	948	398	<0.001	1739	478	<0.001	<0.001	<0.001
Urinating	32	25	1	5	3	1	27	22	1	1	1
Vocalizing	1857	989	0.06	367	612	<0.001	1490	377	<0.001	<0.001	<0.001
Walking	8520	1941	<0.001	2703	419	<0.001	5815	1522	<0.001	<0.001	<0.001
Total	70802	42705		16682	7038		52346	34113			

A dash indicates *P* values could not be calculated due to low sample size. nW: number of occurrences for the wolves; nD: number of occurrences for the dogs; W–W: comparison within the wolves, absence versus presence of humans; D–D: comparison within the dogs, absence versus presence of humans.

[a] The data do not include the observations where the presence or absence of humans was not available (3328 of 113 507 occasions).

Table 4
Results of the activity model

	Estimate	SE	χ^2	*df*	*P*[a]
Intercept	−1.959	0.153			
Species (0: wolf; 1: dog)	0.254	0.193			
Human (0: present; 1: absent)	1.102	0.046			
Time[b]	−0.090	0.038	5.149	1	**0.023**
Temperature[b]	−0.188	0.054	10.932	1	**0.001**
Age[b]	−0.102	0.100	1.011	1	0.315
Sex (0: M; 1: F)	−0.202	0.118	2.742	1	0.098
Wolf: human present	−0.503	0.058	74.186	1	**<0.001**

Bold type indicates a significant *P* value.

[a] Not indicated in cases where the *P* value had a limited interpretation.

[b] Predictors were z-transformed to a mean of zero and a standard deviation of one; original means (SD): time: 12.16 (2.78) h; temperature: 11.14 (8.76) °C; age: 85.3 (30.5) months.

the presence of humans, dogs cantered, trotted, walked and vocalized more than in the absence of humans. In the absence of humans, dogs were observed standing, lying on the ground, resting and sleeping more than when humans were present (see Table 3). Wolves' behaviour also differed between the presence and the absence of humans (chi-square test: $\chi^2_{21} = 1008.9$, $P < 2.2e-16$). In the presence of humans, wolves cantered more whereas in the absence of humans they foraged, trotted, walked, stood, slept and vocalized more and displayed more social behaviours (Table 3).

Activity

Overall, there was a significant effect of temperature, time of day and the interaction between wolf or dog and the presence or absence of humans on the activity of the subjects (full–null comparison likelihood ratio test: $\chi^2_2 = 866.903$, $P < 0.001$; Table 4). Activity decreased with increasing temperature (Table 4, Fig. 2a). It also decreased towards noon and then increased again (Table 4, Fig. 2b). Human presence had a different effect on wolves and dogs: dogs responded strongly to the presence of humans and were more active, whereas wolves were seemingly less responsive than dogs to the presence of humans (interaction between wolf/dog and human presence: Table 4, Fig. 3). We found no effect of sex and age of the individual.

Proximity

Overall, there was a significant effect of temperature, activity (active or not), the interaction between wolf/dog and the presence or absence of humans on the proximity of the subjects to their pack members (full–null comparison likelihood ratio test: $\chi^2_3 = 101.642$, $P < 0.001$; see Table 5). The likelihood of an individual being in proximity of a pack member increased with increasing temperature (Table 5). Not surprisingly, an increase in activity also decreased proximity (Table 5). In the presence of humans, dogs were in proximity of their pack members more than wolves (Table 5, Fig. 4). Sex and age of the individual had no effect (Table 5).

DISCUSSION

We found more subtle effects of domestication than expected. First, domestication has evidently not affected the impact of the

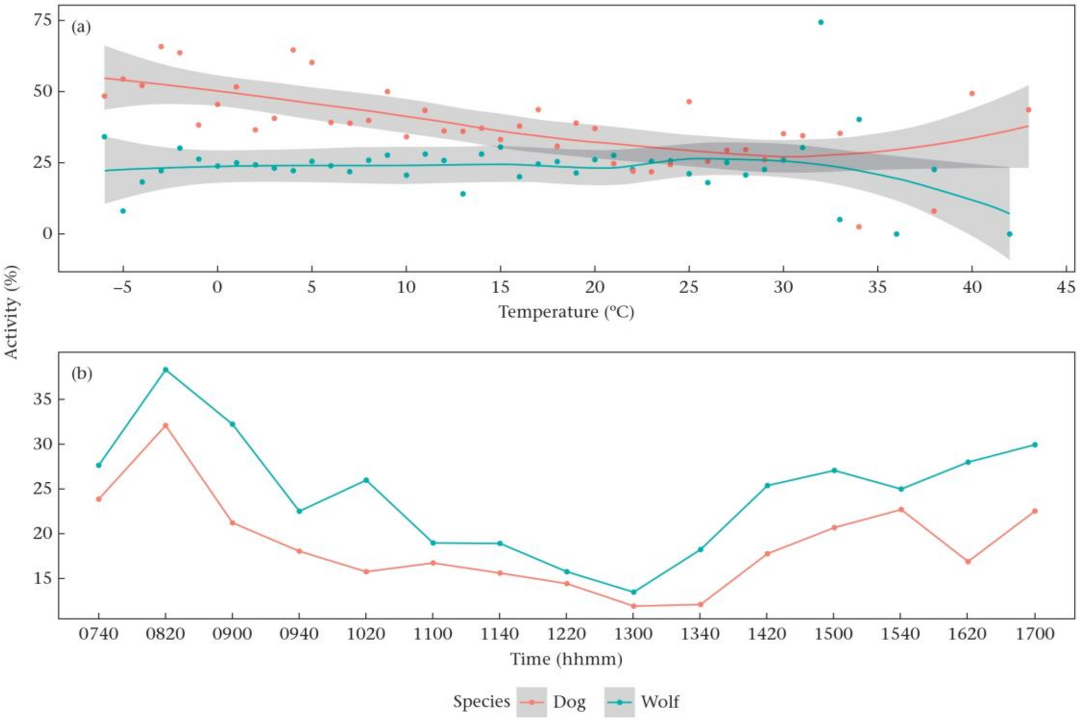

Figure 2. Levels of activity (percentage of behaviours per observation that were active) in wolves and dogs (a) with temperature and (b) over the day. All behaviours of the ethogram were considered as active except for sleeping, resting and immobile (lying, sitting and standing). The lines represent the model regression lines and the grey shaded area is the 95% confidence interval for the models.

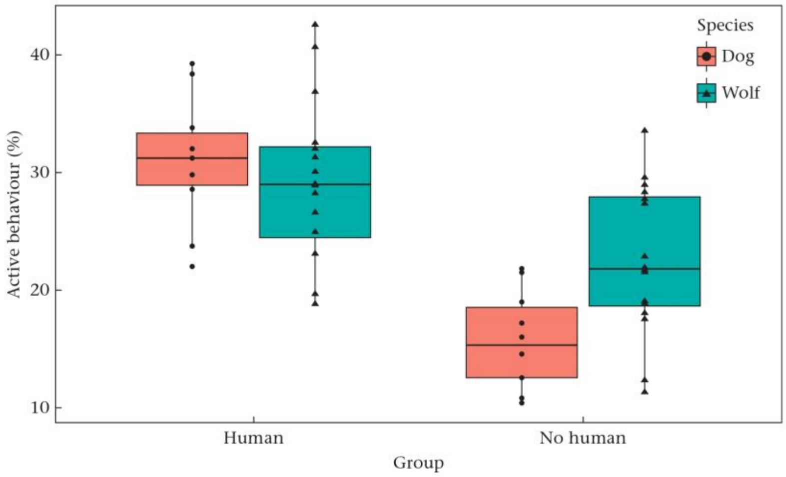

Figure 3. Wolves' and dogs' activity in relation to the presence or absence of humans around their enclosure. The graph is based on a selected range of temperature (10–25 °C) and time (1100–1300) to decrease the effect of temperature and time on the subjects' behaviours. However, statistical analyses were based on the full data set. The whiskers represent the minimum (bottom) and maximum (top) data points, the edges of the box represent the interquartile (Q3–Q1) and the bold line is the median. The dots represent the individual values of activity for dogs and wolves.

extrinsic Zeitgeber temperature and daily light regime, since our results have shown that level of activity in wolves and dogs varied in the same way. Both wolves and dogs showed the expected bimodal pattern of activity over the day, which suggests that the deviation from such patterns observed in companion dogs (Griss et al., 2021) is likely due to adjusting to certain humans rather than the result of domestication.

Second, we found no clear evidence for an overall decrease in behavioural efficiency (i.e. an intrinsically greater activity) in dogs. Dogs spent 78.5% of their overall time inactive and wolves 75% (see Appendix Table A2 for details). In the absence of humans, dogs were not more active than wolves, but they clearly were when humans were present. This would contradict the selection for tameness hypothesis predicting overall calmer, less agitated dogs than wolves, but is in line with the hypersociability hypothesis (Bentosela et al., 2016; von Holdt et al., 2017): dogs seem to be more interested in interacting with humans than wolves and are more excited about it. Moreover, this is in alignment with the generally higher cortisol level found in dogs compared to wolves (Vasconcellos et al., 2016; Wirobski et al., 2021a, 2021b). This may be related to a generally higher, 'ready-to-go' metabolism in dogs than wolves, which maintain high reactivity for swiftly responding to the often unpredictable challenges in a human-dominated environment.

Table 5
Results of the proximity model

	Estimate	SE	χ^2	*df*	*P*[a]
Intercept	0.380	0.391			
Species (0: wolf; 1: dog)	1.741	0.521			
Human (0: present; 1: absent)	-0.446	0.047			
Activity (0: not active; 1: active)	0.659	0.023	810.441	1	**<0.001**
Temperature[b]	0.251	0.087	7.586	1	**0.006**
Age[b]	-0.110	0.173	0.343	1	0.558
Sex (0: M; 1: F)	0.233	0.101	2.285	1	0.131
Wolf: Human present	0.556	0.064	74.140	1	**<0.001**

Bold type indicates a significant *P* value.

[a] Not indicated in cases where the *P* value had a limited interpretation.

[b] Predictors were z-transformed to a mean of zero and a standard deviation of one; original means (SD): temperature: 11.14 (8.76) °C; age 85.3 (30.5) months.

We expected distinct differences in the time budgets of wolves and dogs but found only minor variation between them in the time they devoted to different behaviours. However, the differences increased when compared between the presence and absence of humans. When humans were present, dogs were more active than in their absence (31.2% versus 16.1%; see Appendix Table A2 for details). Wolves' activity also increased around humans but less than in dogs (29.8% versus 22.5%). Differences in time spent with various behaviours in dogs and wolves increased in the presence of humans: dogs remarkably increased cantering, trotting, standing and vocalizing, whereas wolves moderately increased trotting, walking and standing (see Appendix Table A2 for details). These results support our prediction that domestication has shifted the dogs' focus towards responsiveness to humans and align with the previous findings (Jean-Joseph et al., 2020), which showed that dogs and wolves at rest reacted differently to the presence of humans: dogs were more relaxed (lower heart rate and higher heart variability) than wolves but when awake, dogs' and wolves' cardiac outputs were similar. Our results also line up with the study by Lazzaroni at al. (2020) showing that dogs (WSC, companion and free ranging) were more interested than wolves in interacting with humans. Hence, it seems than human presence influences both equally raised and kept dogs and wolves, but this effect is stronger and also qualitatively different in dogs, which seem more excited than wolves at the presence of humans.

Overall, our study agrees with previous work on the effects of visitors on canid welfare. The WSC wolves were out of sight during 2.5% of the observations (1772 occurrences versus 3.6% and 1554 occurrences for the dogs). This does not look like an important difference, but it is underscored by how this study was conducted: the observers actively tried to minimize occurrences of 'subject not visible' and when no subject was visible at all, the observation session was cancelled. This situation happened more often with wolves than with dogs, matching the result of a previous study on captive coyotes, *Canis latrans* (Schultz & Young, 2018): the captive wild canids tended to avoid open spaces and showed increased vigilance when visitors were present. However, these coyotes were not hand-raised and human-socialized the way the WSC wolves

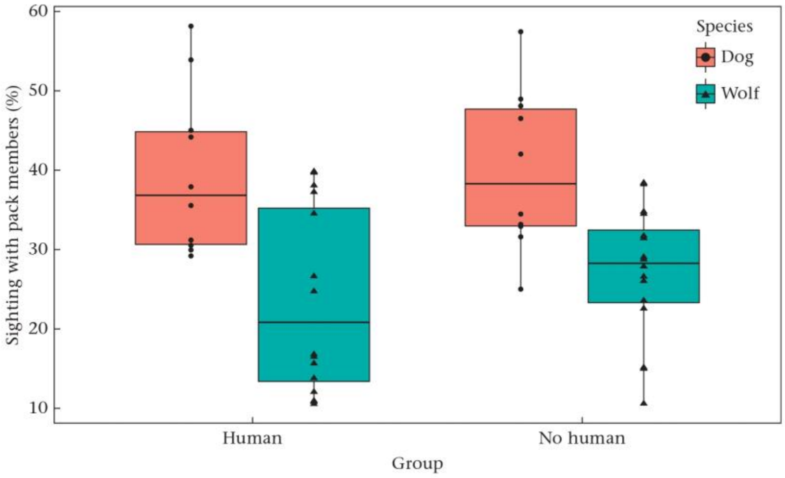

Figure 4. Wolves' and dogs' proximity to their pack in relation to the presence or absence of humans around their enclosure. The whiskers represent the minimum (bottom) and maximum (top) data points, the edges of the box represent the interquartile (Q3–Q1) and the bold line is the median. The dots represent the individual values of activity for dogs and wolves.

are. Still, visitors and the noise they produce may have affected our results, as these factors increased the vigilance behaviour in captive wolves (Boyle et al., 2020). In fact, the wolves in our study spent just slightly more time standing vigilant when humans were around (21% against 19%).

We are aware that the familiarity of the humans present near the enclosure to the animals could have affected our results, particularly when the trainers (i.e. the familiar humans) were sighted more around the dogs' enclosures than around those of the wolves, whereas the visitors (i.e. unfamiliar humans) were sighted more around the wolves' enclosures than those of the dogs (see Appendix Table A3). However, the design of our study could not accurately discriminate between familiar and unfamiliar humans. Indeed, most of the time a mix of both familiar and unfamiliar humans were present at the enclosures. A conclusive analysis regarding the behavioural effects of the familiarity of the humans would have required the presence of either familiar or unfamiliar humans and not both at the same time. Humans were observed near the enclosures for 23 718 of the 110 176 data points (21.5% of the total data set whereas no human was present for 78.5% of the times, 86 458 occurrences). Within these 23 718 occurrences, 4650 times we observed only familiar humans present (4.2%) and 11 662 times we observed only unfamiliar humans (10.6%). All other instances featured mixed groups of familiar and unfamiliar people (6.7%). Given the complexity of our models we considered the frequency of occurrence of either familiar or unfamiliar persons present insufficient for a conclusive analysis (see Appendix Table A4, Fig. A1).

We are aware of the lack of accuracy of the sampling method for some of the behaviours, but we chose to analyse and report them for the sake of completeness. For example, the observation of feeding behaviours may be underestimated because we chose not to observe them during feeding time due to differences in wolves' and dogs' feeding at the WSC. Dogs are fed dry food once or twice a day and tend to eat it all at once, whereas wolves were fed carcasses (whole chicken or rabbit or one portion of pig or deer) every 2 or 3 days. Therefore, wolves, but less so dogs, could have had access to some leftover food. Sexual behaviour, social interactions and stress-related behaviours are brief events that our observation method was not suited to record; ad libitum sampling would have been a more accurate method. However, we chose not to mix the two methods. Hence, our results for those behaviours are likely less accurate than the behaviours related to rest or locomotion, for example.

We were also unable to observe the animals' nocturnal behaviour; due to the size of the enclosures and the vegetation, the animals could not be observed accurately at night even with night gear, and artificial light may have affected their behaviour. To overcome these shortcomings, full 24 h behaviour budgets could be investigated by using GPS collars with accelerometers.

To conclude, our study indicates that domestication has not affected much the role of major environmental factors, such as temperature and time of day, as Zeitgeber for dogs. We did not find marked overall changes in behaviour and activity between wolf and dog, as could have been predicted by selection for tameness as the major domestication mechanism. Rather, we found that wolf–dog differences were context dependent, with humans evidently being more important for the dogs than for equally socialized wolves.

Author Contributions

H.J.J.: Conceptualization, Methodology, Validation, Formal analysis, Writing: Original Draft, Visualization. G.D.: Methodology, Investigation, Data Curation, Writing: Review & Editing. K.K: Conceptualization, Writing: Review & Editing, Supervision, Funding acquisition. All authors have contributed to, seen and approved the manuscript.

Data Availability

The corresponding author will provide the data on request.

Declaration of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationship that could be construed as a potential conflict of interest.

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References

Agnvall, B., Katajamaa, R., Altimiras, J., & Jensen, P. (2015). Is domestication driven by reduced fear of humans? Boldness, metabolism and serotonin levels in divergently selected red junglefowl (*Gallus gallus*). *Biology Letters, 11*(9), 20150509. https://doi.org/10.1098/rsbl.2015.0509

Aronson, B. D., Bell-Pedersen, D., Block, G. D., Bos, N. P. A., Dunlap, J. C., Eskin, A., Garceau, N. Y., Geusz, M. E., Johnson, K. A., Khalsa, S. B. S., Koster-Van Hoffen, G. C., Koumenis, C., Lee, T. M., LeSauter, J., Lindgren, K. M., Liu, Q., Loros, J. J., Michel, S. H., Mirmiran, M., … Zucker, I. (1993). Circadian rhythms. *Brain Research Reviews, 18*(3), 315–333. https://doi.org/10.1016/0165-0173(93)90015-R

Aschoff, J. (1954). Zeitgeber der tierischen Tagesperiodik. *Naturwissenschaften, 41*(3), 49–56. https://doi.org/10.1007/BF00634164

Baayen, R. H. (2008). *Analyzing linguistic data: A practical introduction to statistics using R*. Cambridge University Press.

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language, 68*(3), 255–278. https://doi.org/10.1016/j.jml.2012.11.001

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). *Fitting linear mixed-effects models using lme4*. ArXiv, 1406.5823 [Stat] http://arxiv.org/abs/1406.5823.

Bateson, M., & Martin, P. (2021). *Measuring behaviour: An introductory guide*. Cambridge University Press.

Belyaev, D. K. (1979). Destabilizing selection as a factor in domestication. *Journal of Heredity, 70*(5), 301–308. https://doi.org/10.1093/oxfordjournals.jhered.a109263

Bentosela, M., Wynne, C. D. L., D'Orazio, M., Elgier, A., & Udell, M. A. R. (2016). Sociability and gazing toward humans in dogs and wolves: Simple behaviors with broad implications. *Journal of the Experimental Analysis of Behavior, 105*(1), 68–75. https://doi.org/10.1002/jeab.191

Bhadra, A., & Bhadra, A. (2014). Preference for meat is not innate in dogs. *Journal of Ethology, 32*(1), 15–22. https://doi.org/10.1007/s10164-013-0388-7

Bonanni, R., & Cafazzo, S. (2014). Chapter 3—the social organisation of a population of free-ranging dogs in a suburban area of Rome: A reassessment of the effects of domestication on dogs' behaviour. In J. Kaminski, & S. Marshall-Pescini (Eds.), *The social dog* (pp. 65–104). Academic Press. https://doi.org/10.1016/B978-0-12-407818-5.00003-6.

Botigué, L. R., Song, S., Scheu, A., Gopalan, S., Pendleton, A. L., Oetjens, M., Taravella, A. M., Seregély, T., Zeeb-Lanz, A., Arbogast, R.-M., Bobo, D., Daly, K., Unterländer, M., Burger, J., Kidd, J. M., & Veeramah, K. R. (2017). Ancient European dog genomes reveal continuity since the Early Neolithic. *Nature Communications, 8*, 16082. https://doi.org/10.1038/ncomms16082

Boyle, S. A., Berry, N., Cayton, J., Ferguson, S., Gilgan, A., Khan, A., Lam, H., Leavelle, S., Mulder, I., Myers, R., Owens, A., Park, J., Siddiq, I., Slevin, M., Weidow, T., Yu, A. J., & Reichling, S. (2020). Widespread behavioral responses by mammals and fish to zoo visitors highlight differences between individual animals. *Animals, 10*(11), 2108. https://doi.org/10.3390/ani10112108

Cafazzo, S., Bonanni, R., Valsecchi, P., & Natoli, E. (2014). Social variables affecting mate preferences, copulation and reproductive outcome in a pack of free-ranging dogs. *PLoS One, 9*(6), Article e98594. https://doi.org/10.1371/journal.pone.0098594

Cafazzo, S., Marshall-Pescini, S., Lazzaroni, M., Virányi, Z., & Range, F. (2018). The effect of domestication on post-conflict management: Wolves reconcile while dogs avoid each other. *Royal Society Open Science, 5*(7), 171553. https://doi.org/10.1098/rsos.171553

Cafazzo, S., Valsecchi, P., Bonanni, R., & Natoli, E. (2010). Dominance in relation to age, sex, and competitive contexts in a group of free-ranging domestic dogs. *Behavioral Ecology, 21*(3), 443–455. https://doi.org/10.1093/beheco/arq001

Christie, D. W., & Bell, E. T. (1971). Some observations on the seasonal incidence and frequency of oestrus in breeding bitches in Britain. *Journal of Small Animal Practice, 12*(3), 159–167. https://doi.org/10.1111/j.1748-5827.1971.tb06213.x

Ciucci, P., Boitani, L., Francisci, F., & Andreoli, G. (1997). Home range, activity and movements of a wolf pack in central Italy. *Journal of Zoology, 243*(4), 803–819. https://doi.org/10.1111/j.1469-7998.1997.tb01977.x

Darwin, C. R. (1859). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. J. Murray.

Dobson, A. J., & Barnett, A. G. (2018). *An introduction to generalized linear models* (4th ed.). Chapman & Hall/CRC. https://doi.org/10.1201/9781315182780

Fam, B. S. O., Paré, P., Felkl, A. B., Vargas-Pinilla, P., Paixão-Côrtes, V. R., Viscardi, L. H., & Bortolini, M. C. (2018). Oxytocin and arginine vasopressin systems in the domestication process. *Genetics and Molecular Biology, 41*, 235–242. https://doi.org/10.1590/1678-4685-GMB-2017-0069

Field, A. (2013). *Discovering statistics using IBM SPSS statistics*. Sage.

Forstmeier, W., & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: Overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology, 65*(1), 47–55. https://doi.org/10.1007/s00265-010-1038-5

Frank, H. (1987). *Man and wolf: Advances, issues, and problems in captive wolf research*. W. Junk.

Frank, H., & Frank, M. G. (1982). Comparison of problem-solving performance in six-week-old wolves and dogs. *Animal Behaviour, 30*(1), 95–98.

Frank, H., & Frank, M. G. (1985). Comparative manipulation-test performance in ten-week-old wolves (*Canis lupus*) and Alaskan malamutes (*Canis familiaris*): A Piagetian interpretation. *Journal of Comparative Psychology, 99*(3), 266–274.

Gácsi, M., Gyoöri, B., Virányi, Z., Kubinyi, E., Range, F., Belényi, B., & Miklósi, Á. (2009). Explaining dog wolf differences in utilizing human pointing gestures: Selection for synergistic shifts in the development of some social skills. *PLoS One, 4*(8), Article e6584. https://doi.org/10.1371/journal.pone.0006584

Grandin, L. D., Alloy, L. B., & Abramson, L. Y. (2006). The social zeitgeber theory, circadian rhythms, and mood disorders: Review and evaluation. *Clinical Psychology Review, 26*(6), 679–694. https://doi.org/10.1016/j.cpr.2006.07.001

Griss, S., Riemer, S., Warembourg, C., Sousa, F. M., Wera, E., Berger-Gonzalez, M., Alvarez, D., Bulu, P. M., Hernández, A. L., Roquel, P., & Dürr, S. (2021). If they could choose: How would dogs spend their days? Activity patterns in four populations of domestic dogs. *Applied Animal Behaviour Science, 243*, 105449. https://doi.org/10.1016/j.applanim.2021.105449

Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Sciences, 9*(9), 439–444. https://doi.org/10.1016/j.tics.2005.07.003

Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour, 83*(3), 573–585. https://doi.org/10.1016/j.anbehav.2011.12.007

Hecht, E. E., Kukekova, A. V., Gutman, D. A., Acland, G. M., Preuss, T. M., & Trut, L. N. (2021). Neuromorphological changes following selection for tameness and aggression in the Russian farm-fox experiment. *Journal of Neuroscience, 41*(28), 6144–6156. https://doi.org/10.1523/JNEUROSCI.3114-20.2021

Heldmaier, G., Steinlechner, S., Ruf, T., Wiesinger, H., & Klingenspor, M. (1989). Photoperiod and thermoregulation in vertebrates: Body temperature rhythms and thermogenic acclimation. *Journal of Biological Rhythms, 4*(2), 139–153. https://doi.org/10.1177/074873048900400211

Hoffman, C. L., Ladha, C., & Wilcox, S. (2019). An actigraphy-based comparison of shelter dog and owned dog activity patterns. *Journal of Veterinary Behavior, 34*, 30–36. https://doi.org/10.1016/j.jveb.2019.08.001

von Holdt, B. M., Shuldiner, E., Koch, I. J., Kartzinel, R. Y., Hogan, A., Brubaker, L., Wanser, S., Stahler, D., Wynne, C. D. L., Ostrander, E. A., Sinsheimer, J. S., & Udell, M. A. R. (2017). Structural variants in genes associated with human Williams-Beuren syndrome underlie stereotypical hypersociability in domestic dogs. *Science Advances, 3*(7), Article e1700398. https://doi.org/10.1126/sciadv.1700398

Hughes, J., & Macdonald, D. W. (2013). A review of the interactions between free-roaming domestic dogs and wildlife. *Biological Conservation, 157*, 341–351. https://doi.org/10.1016/j.biocon.2012.07.005

Jean-Joseph, H., Kortekaas, K., Range, F., & Kotrschal, K. (2020). Context-specific arousal during resting in wolves and dogs: effects of domestication? *Frontiers in Psychology, 11*, Article 568199. https://doi.org/10.3389/fpsyg.2020.568199

Kaminski, J., Waller, B. M., Diogo, R., Adam Hartstone-Rose, A., & Burrows, A. M. (2019). Evolution of facial muscle anatomy in dogs. *Proceedings of the National Academy of Sciences, 116*(29), 14677–14681.

Kirilyuk, A. V., Kirilyuk, V. E., & Minaev, A. N. (2021). Daily activity patterns of wolves in open habitats in the Dauria ecoregion, Russia. *Nature Conservation Research, 6*(4), 95–109. https://doi.org/10.24189/ncr.2021.049

Klinghammer, E., & Goodman, P. A. (1987). Socialization and management of wolves in captivity. In H. Frank (Ed.), *Man and wolf: Advances, issues, and problems in captive wolf research* (pp. 281–304). W. Junk.

Kortekaas, K., & Kotrschal, K. (2019). Does socio-ecology drive differences in alertness between wolves and dogs when resting? *Behavioural Processes, 166*, 103877. https://doi.org/10.1016/j.beproc.2019.05.024

Kotrschal, K. (2018). How wolves turned into dogs and how dogs are valuable in meeting human social needs. *People and Animals: The International Journal of Research and Practice, 1*(1), 6. https://docs.lib.purdue.edu/paij/vol1/iss1/6.

Kubinyi, E., Viranyi, Z., & Miklósi, Á. (2007). Comparative social cognition: From wolf and dog to humans. *Comparative Cognition & Behavior Reviews, 2*, 26–46. http://cogs.indiana.edu/spackled/2008readings/comparat_cognition_Miklosi_2007.pdf.

Künzl, C., & Sachser, N. (1999). The behavioral endocrinology of domestication: A comparison between the domestic Guinea pig (*Cavia aperea f. porcellus*) and its wild ancestor, the Cavy (*Cavia aperea*). *Hormones and Behavior, 35*(1), 28–37. https://doi.org/10.1006/hbeh.1998.1493

Lazzaroni, M., Range, F., Backes, J., Portele, K., Scheck, K., & Marshall-Pescini, S. (2020). The effect of domestication and experience on the social interaction of dogs and wolves with a human companion. *Frontiers in Psychology, 11*, 785. https://doi.org/10.3389/fpsyg.2020.00785

Leonard, J. A., Wayne, R. K., Wheeler, J., Valadez, R., Guillén, S., & Vilà, C. (2002). Ancient DNA evidence for old world origin of new world dogs. *Science, 298*(5598), 1613–1616. https://doi.org/10.1126/science.1076980

Leonhard, C., & Randler, C. (2009). Sync with the family: Children and partners influence the sleep-wake circadian rhythm and social habits of women. *Chronobiology International, 26*(3), 510–525. https://doi.org/10.1080/07420520902821101

Lord, K., Feinstein, M., Smith, B., & Coppinger, R. (2013). Variation in reproductive traits of members of the genus *Canis* with special attention to the domestic dog (*Canis familiaris*). *Behavioural Processes, 92*, 131–142. https://doi.org/10.1016/j.beproc.2012.10.009

Majumder, S. S., Bhadra, A., Ghosh, A., Mitra, S., Bhattacharjee, D., Chatterjee, J., Nandi, A. K., & Bhadra, A. (2014). To be or not to be social: Foraging associations of free-ranging dogs in an urban ecosystem. *Acta Ethologica, 17*(1), 1–8. https://doi.org/10.1007/s10211-013-0158-0

Majumder, S., Paul, M., Sau, S., & Bhadra, A. (2016). Denning habits of free-ranging dogs reveal preference for human proximity. *Scientific Reports, 6*(1), 32014. https://doi.org/10.1038/srep32014

Marshall-Pescini, S., Cafazzo, S., Virányi, Z., & Range, F. (2017). Integrating social ecology in explanations of wolf–dog behavioral differences. *Current Opinion in Behavioral Sciences, 16*, 80–86. https://doi.org/10.1016/j.cobeha.2017.05.002

Matuschek, H., Kliegl, R., Vasishth, S., Baayen, H., & Bates, D. (2017). Balancing type I error and power in linear mixed models. *Journal of Memory and Language, 94*, 305–315. https://doi.org/10.1016/j.jml.2017.01.001

Mech, L. D., & Boitani, L. (2003). *Wolves: Behavior, ecology, and conservation*. University of Chicago Press.

Mech, L. D., & Peterson, R. O. (2003). Wolf-prey relations. In L. David Mech, & L. Boitani (Eds.), *Wolves: Behavior, ecology, and conservation* (pp. 131–160). University of Chicago Press.

Merrill, S. B., & Mech, L. D. (2003). The usefulness of GPS telemetry to study wolf circadian and social activity. *Wildlife Society Bulletin, 31*(4), 947–960.

Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., & Csányi, V. (2003). A simple reason for a big difference: Wolves do not look back at humans, but dogs do. *Current Biology, 13*(9), 763–766.

Nieuwenhuis, R., Grotenhuis, H. F. te, & Pelzer, B. J. (2012). *influence.ME: Tools for detecting influential data in mixed effects models*. https://journal.r-project.org/archive/2012/RJ-2012-011/index.html.

Packard, J. M. (2003). Wolf behavior: Reproductive, social, and intelligent. In L. David Mech, & L. Boitani (Eds.), *Wolves: Behavior, ecology, and conservation* (pp. 35–65). University of Chicago Press.

Pal, S. K. (2005). Parental care in free-ranging dogs, *Canis familiaris*. *Applied Animal Behaviour Science, 90*(1), 31–47. https://doi.org/10.1016/j.applanim.2004.08.002

Parker, H. G., Dreger, D. L., Rimbault, M., Davis, B. W., Mullen, A. B., Carpintero-Ramirez, G., & Ostrander, E. A. (2017). Genomic analyses reveal the influence of geographic origin, migration, and hybridization on modern dog breed development. *Cell Reports, 19*(4), 697–708. https://doi.org/10.1016/j.celrep.2017.03.079

Paul, M., Sen Majumder, S., Sau, S., Nandi, A. K., & Bhadra, A. (2016). High early life mortality in free-ranging dogs is largely influenced by humans. *Scientific Reports, 6*(1), 19641. https://doi.org/10.1038/srep19641

Piccione, G., Marafioti, S., Giannetto, C., Di Pietro, S., Quartuccio, M., & Fazio, F. (2014). Comparison of daily distribution of rest/activity in companion cats and dogs. *Biological Rhythm Research, 45*(4), 615–623. https://doi.org/10.1080/09291016.2014.884303

Price, E. O. (1999). Behavioral development in animals undergoing domestication. *Applied Animal Behaviour Science, 65*(3), 245–271. https://doi.org/10.1016/S0168-1591(99)00087-8

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/.

Randler, C., Díaz-Morales, J. F., & Jankowski, K. S. (2018). Synchrony in chronotype and social jetlag between dogs and humans across Europe. *Time & Society, 27*(2), 223–238. https://doi.org/10.1177/0961463X15596705

Range, F., Kassis, A., Taborsky, M., Boada, M., & Marshall-Pescini, S. (2019a). Wolves and dogs recruit human partners in the cooperative string-pulling task. *Scientific Reports, 9*(1), 1–10. https://doi.org/10.1038/s41598-019-53632-1

Range, F., Marshall-Pescini, S., Kratz, C., & Virányi, Z. (2019b). Wolves lead and dogs follow, but they both cooperate with humans. *Scientific Reports, 9*(1), 3796. https://doi.org/10.1038/s41598-019-40468-y

Range, F., Ritter, C., & Virányi, Z. (2015). Testing the myth: Tolerant dogs and aggressive wolves. *Proceedings of the Royal Society B: Biological Sciences, 282*(1807), 20150220. https://doi.org/10.1098/rspb.2015.0220

Range, F., & Virányi, Z. (2015). Tracking the evolutionary origins of dog-human cooperation: the "canine cooperation hypothesis. *Frontiers in Psychology, 5*, 1582. https://doi.org/10.3389/fpsyg.2014.01582

Range, F., & Virányi, Z. (2014). Wolves are better imitators of conspecifics than dogs. *PLoS One, 9*(1), Article e86559. https://doi.org/10.1371/journal.pone.0086559

Robert, S., Dancosse, J., & Dallaire, A. (1987). Some observations on the role of environment and genetics in behaviour of wild and domestic forms of *Sus scrofa* (European wild boars and domestic pigs). *Applied Animal Behaviour Science, 17*(3), 253–262. https://doi.org/10.1016/0168-1591(87)90150-X

Schielzeth, H., & Forstmeier, W. (2009). Conclusions beyond support: Overconfident estimates in mixed models. *Behavioral Ecology, 20*(2), 416–420. https://doi.org/10.1093/beheco/arn145

Schultz, J. T., & Young, J. K. (2018). Behavioral and spatial responses of captive coyotes to human activity. *Applied Animal Behaviour Science, 205*, 83–88. https://doi.org/10.1016/j.applanim.2018.05.021

Scott, J. P., & Fuller, J. L. (1965). *Genetics and the social behavior of the dog*. University of Chicago Press.

Smith, T. D., & Van Valkenburgh, B. (2021). The dog–human connection. *Anatomical Record, 304*(1), 10–18. https://doi.org/10.1002/ar.24534

Thalmann, O., Shapiro, B., Cui, P., Schuenemann, V. J., Sawyer, S. K., Greenfield, D. L., Germonpré, M. B., Sablin, M. V., López-Giráldez, F., Domingo-Roura, X., Napierala, H., Uerpmann, H.-P., Loponte, D. M., Acosta, A. A., Giemsch, L., Schmitz, R. W., Worthington, B., Buikstra, J. E., Druzhkova, A., … Wayne, R. K. (2013). Complete mitochondrial genomes of Ancient canids suggest a European origin of domestic dogs. *Science, 342*(6160), 871–874. https://doi.org/10.1126/science.1243650

Theuerkauf, J. (2009). What drives wolves: Fear or hunger? Humans, diet, climate and wolf activity patterns. *Ethology, 115*(7), 649–657. https://doi.org/10.1111/j.1439-0310.2009.01653.x

Theuerkauf, J., Gula, R., Pirga, B., Tsunoda, H., Eggermann, J., Brzezowska, B., Rouys, S., & Radler, S. (2007). Human impact on wolf activity in the Bieszczady Mountains, SE Poland. *Annales Zoologici Fennici, 44*(3), 225–231.

Troxell-Smith, S. M., Tutka, M. J., Albergo, J. M., Balu, D., Brown, J. S., & Leonard, J. P. (2016). Foraging decisions in wild versus domestic *Mus musculus*: What does life in the lab select for? *Behavioural Processes, 122*, 43–50. https://doi.org/10.1016/j.beproc.2015.10.020

Trut, L. N., Plyusnina, I. Z., & Oskina, I. N. (2004). An experiment on fox domestication and debatable issues of evolution of the dog. *Russian Journal of Genetics, 40*, 644–655. https://doi.org/10.1023/B:RUGE.0000033312.92773.c1

Trut, L. N., Oskina, I., & Kharlamova, A. (2009). Animal evolution during domestication: the domesticated fox as a model. *Bioessays, 31*(3), 349–360. https://doi.org/10.1016/j.cpnec.2021.100100

Vanak, A. T., & Gompper, M. E. (2009). Dogs *Canis familiaris* as carnivores: Their role and function in intraguild competition. *Mammal Review, 39*(4), 265–283. https://doi.org/10.1111/j.1365-2907.2009.00148.x

Vasconcellos, A. da S., Virányi, Z., Range, F., Ades, C., Scheidegger, J. K., Möstl, E., & Kotrschal, K. (2016). Training reduces stress in human-socialised wolves to the same degree as in dogs. *PLoS One, 11*(9), Article e0162389. https://doi.org/10.1371/journal.pone.0162389

Vilà, C., Urios, V., & Castroviejo, J. (1995). Observations on the daily activity patterns in the Iberian wolf. In L. N. Carbyn, S. H. Fritts, & D. R. Seip (Eds.), *Ecology and conservation of wolves in a changing world* (pp. 335–340). Canadian Circumpolar Institute.

Wandeler, A. I., Matter, H. C., Kappeler, A., & Budde, A. (1993). The ecology of dogs and canine rabies: A selective review. *Revue Scientifique et Technique (International Office of Epizootics), 12*(1), 51–71. https://doi.org/10.20506/rst.12.1.663

Wilkins, A. S., Wrangham, R. W., & Fitch, W. T. (2014). The 'domestication syndrome' in mammals: A unified explanation based on neural crest cell behavior and genetics. *Genetics, 197*(3), 795–808. https://doi.org/10.1534/genetics.114.165423

Wirobski, G., Range, F., Schaebs, F. S., Palme, R., Deschner, T., & Marshall-Pescini, S. (2021a). Endocrine changes related to dog domestication: Comparing urinary cortisol and oxytocin in hand-raised, pack-living dogs and wolves. *Hormones and Behavior, 128*, 104901. https://doi.org/10.1016/j.yhbeh.2020.104901

Wirobski, G., Range, F., Schaebs, F. S., Palme, R., Deschner, T., & Marshall-Pescini, S. (2021b). Life experience rather than domestication accounts for dogs' increased oxytocin release during social contact with humans. *Scientific Reports, 11*(1), 14423. https://doi.org/10.1038/s41598-021-93922-1

Chapter 3|

Equally raised and kept wolves and dogs show similar risk-proneness – no matter whether alone or with a familiar human

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Equally raised and kept wolves and dogs show similar risk-proneness – no matter whether alone or with a familiar human

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Abstract

Due to domestication, dogs and wolves differ in a mosaic of mental and behavioural parameters. A basic mechanism of domestication is the selection for fearlessness and acceptance of humans as social partners, which may affect risk-taking behavior and the ability to use humans as social supporters both at the behavioural and physiological levels. We combined behavioural observations with heart rate parameters (i.e., HR; and heart rate variability, HRV) to assess the activity of the autonomic nervous system (ANS) in equally raised and kept wolves and dogs when offered food in the vicinity of a potential stressor (an unknown spinning object), with and without social support by a familiar human. Based on previous studies on neophobia in wolves and dogs, we expected dogs to be less scared of the object than wolves, approach more quickly, show less ambivalent behaviour, lower HR, and higher HRV, especially in situations when the human partner was present. However, we found that age, rather than species or the presence of a familiar human, affected the behaviour and HR rate parameters in our subjects: Older wolves or dogs were generally bolder and faster to approach the food. Wolves and dogs showed particularly high HRs at the beginning and end of the test sessions. We conclude that, according to our paradigm, wolves' and dogs' risk-proneness differed according to age, rather than species and neither dogs nor our human-socialized wolves seemed to respond behaviourally and physiologically to the presence of a familiar human.

Keywords

Dog; dog-human relationship; domestication; heart rate; heart rate variability; risk-taking; wolves.

Introduction

Engaging in potentially dangerous activities may raise fear and stress, affecting behavior and physiology by activating the autonomic nervous system and the hypothalamo-pituary-adrenal axis (Koolhaas et al., 1999), triggering “flight”, “fight”, “freeze” or “flirt” behaviors (Riemer et al., 2013; Walker et al., 1997). Physiological parameters affected include cardiac rhythmicity (Kreibig, 2010; Porges, 1995, 2001, 2003, 2009; Rajendra Acharya et al., 2006), such as heart rate (HR) and heart rate variability (HRV). They are relevant indicators of both the physiological (ANS) and affective states of a subject (Luque-Casado et al., 2013; Maros et al., 2008; Visser et al., 2002; von Borell et al., 2007). In fact, previous studies have used HR as a measure of the response of dogs to different types of stimuli, including scary ones (Beerda et al., 1998; King et al., 2003). Risk-taking behaviour, defined as any controlled behaviour with a perceived uncertainty about its outcomes (Trimpop, 1994), can trigger such physiological responses. By presenting food in a situation that is potentially considered scary, risk-taking behaviours and (potentially) associated physiological responses can be observed, with risk-proneness being the propensity to be attracted to, or the willingness to tolerate, options that entail a potentially high risk of loss (according to the APA Dictionary of psychology).

Dogs, particularly in comparison to wolves, are a relevant species to study how domestication has affected risk-taking behaviours and risk-proneness (Frantz et al., 2016; Olsen, 1985). Reduced fear and stress responsiveness are common components of the domestication syndrome present in most, if not all, domesticated animals (Darwin, 1868; Pörtl & Jung, 2019; Wilkins, 2017). As dogs are the domesticated form of wolves, they should be less neophobic, i.e., less reactive to novel situations and stimuli (Barnett, 1958). Hence, more risk-prone than wolves with the same experiences. In fact, in a number of experiments, dogs have been found to be less neophobic than wolves (Kaulfuß & Mills, 2008; Moretti et al., 2015), which were more explorative and persistent in interacting with novel objects than dogs (Marshall-Pescini, Virányi, et al., 2017; Udell, 2015). In a very different approach to the one employed in the current study, the risk was defined as the uncertainty to receive a preferred reward and in that context; wolves turned out to be more risk-prone than dogs (Marshall-Pescini et al., 2016).

Different feeding ecologies could explain such differences in risk-proneness (Marshall-Pescini, Cafazzo, et al., 2017): Whereas wolves are mainly cooperative hunters (Mech & Boitani, 2003; Stahler et al., 2006), free-ranging dogs tend to scavenge on human waste (Butler et al., 2018; Paul et al., 2016). In fact, dogs are adapted to an agriculturalist human diet as they are better at digesting starch than wolves (Axelsson et al., 2013). Accordingly, wolves, due to their hunting lifestyle, should be more neophobic than dogs but also more persistent and risk-prone. These predictions are in line with studies showing that species or populations dealing with unreliable food sources are more risk-prone than those living on a relatively stable food supply (tits: Kawamori & Matsushima, 2012; parrots: Mettke-Hofmann et al., 2002; blackbirds: Mettke-Hofmann et al., 2013; apes: Heilbronner et al., 2008; Rosati & Hare, 2013).

Personality is another factor that might influence risk-taking behaviours at the individual level. Indeed, the bold-shy personality dimension has been found in various species, from invertebrates (Wilson et al., 2010) to mammals (Dammhahn, 2012; Réale et al., 2009), including dogs (Svartberg, 2005; Svartberg & Forkman, 2002) and wolves (Fox, 1972). Boldness includes a relatively high readiness to approach uncertainty and take risks (Dammhahn & Almeling, 2012; Réale et al., 2007). As such, bold individuals are more risk-prone than shy ones. Boldness may vary with age as, for example, older female seals (Bubac et al., 2018) or female eiders (Mohring et al., 2022) are bolder than younger ones. In contrast, boldness in dogs seems to decrease with increasing age (Chapagain et al., 2020; Kubinyi et al., 2009; Starling et al., 2013); older and more experienced wolves seem to be bolder (Barry et al., 2020; Cassidy et al., 2017).

Finally, individual risk-proneness may also be affected by social environment (Rault, 2012; van Oers et al., 2005). In fact, both dogs and wolves were more risk-prone when approaching novel objects in the presence of their pack mates (Moretti et al., 2015). Dogs may be a special case, as the *hypersociability hypothesis* suggests that due to domestication dogs not only seek more often social interactions with conspecifics, but also with humans than socialized wolves (vonHoldt et al., 2017). In fact, dogs benefit from the presence of their caretakers in stressful situations (Gácsi et al., 2009, 2013; Mariti et al., 2013; Prato-Previde et al., 2003; Topál et al., 1998; Valsecchi et al., 2010) and use them as a safe base (Gácsi et al., 2013; Palmer & Custance, 2008; Solomon et al., 2019). Furthermore, it has been proposed that the selection against fear and aggression led to higher cognitive skills in dogs compared to wolves, enabling them to use human communicative cues (*Emotional reactivity hypothesis*, Hare et al., 2005). Whether being able to benefit from humans as social support and motivators in risky or stressful situations is indeed due to domestication or rather an effect of experience with humans is still unclear. Due to their social organization, wolves rely on their group members (Mech & Boitani, 2003). Their cooperative social system may enable them to accept humans as social partners and supporters, if properly socialized with humans. In line with this, wolves were shown to have all the necessary skills to successfully cooperate with humans, notably high social tolerance and attentiveness (Range & Marshall-Pescini, 2022c; Range & Virányi, 2011, 2013, 2014). Similar to dogs, they can form attachment-like relationships with humans (Hall et al., 2015; Lenkei et al., 2020; Ujfalussy et al., 2017) and cooperative training sessions with people decreased salivary cortisol in both dogs and equally raised and kept wolves (Vasconcellos et al., 2016). On that basis, the *Canine Cooperation Hypothesis* suggests that dogs' basic abilities to cooperate and pay attention to humans were not newly acquired during domestication but are derived from the wolves' capacity to cooperate with their conspecifics (Range & Virányi, 2015).

Relatedly, the *Two Stage Hypothesis* (Dorey et al., 2010; Udell et al., 2010) proposes that dogs are highly cooperative with humans because they 1) accept humans as social companions, which is acquired early in life through socialization and 2) learn from humans to follow their gestures and actions through conditioning, whereas wolves do not typically live with humans and thus do not learn to pay attention to humans. Accordingly, if highly socialized with humans and exposed to many instances where they can learn to pay attention to humans and their actions, the two hypotheses predict that both wolves and dogs would be able to benefit from the presence of a human in a stressful situation and pay attention to human motivating gestures and actions.

In the current study, we presented equally socialized and kept dogs and wolves with a risk-taking paradigm in a foraging context. We used cardiac parameters and behaviours to test whether domestication affected risk-proneness in dogs as compared to wolves, and we assessed to what extent wolves and dogs would use a familiar person as a social support and motivator during the challenge. According to selection for reduced fearfulness as the basic mechanism of domestication, we predicted that dogs would show relatively moderate responses to the apparatus and show less fear-related behaviour and a reduced physiological reaction than wolves. Therefore, we predicted that dogs should be more risk-prone, showing shorter latencies to reach the food and spending more time in its proximity than the wolves. Furthermore, in line with the *hypersociability hypothesis* (vonHoldt et al., 2017) and the *emotional reactivity hypothesis*, we predicted that social support by a familiar human and their communicative actions to engage the subjects with the apparatus would affect dogs more than human-socialized wolves, as observed in our previous studies (Jean-Joseph et al., 2020, 2022)

In contrast, based on the *Canine Cooperation Hypothesis* (Range & Virányi, 2015) and the *Two Stage Hypothesis* (Udell et al., 2010), we predicted there would be no differences between equally raised and kept dogs and wolves due to similar positive exposure to humans during their early development, thus allowing them to regard humans as social partners and pay attention to motivating gestures of the humans. Dogs and wolves could be equally spread on a scale ranging from fearful to not fearful, risk-prone to risk-avoidant, which would indicate that the main factors affecting the animals during this test would be life history parameters such as age and/or personality, rather than domestication.

Methods and Materials

Subjects

Our subjects were wolves, *Canis lupus occidentalis* (N=13) and dog mongrels, *Canis lupus familiaris* (N=15) raised and housed in the same way at the Wolf Science Center (WSC) in Ernstbrunn, Austria (see Table 1). All wolves and dogs were born in captivity and hand-raised by humans in a standard way from 10 days of age before being integrated into already existing packs at five months of age (Range & Marshall-Pescini, 2022a; Range & Virányi, 2014). All animals are kept year-round in outside enclosures ranging from 2000 to 8000 m^2; all enclosures contain bushes, trees, rocks, shelters, and water points providing water *ad libitum* to the animals. The subjects were between 2 and 9 years of age when tested (wolves: median (range) = 6 (2–9); dogs: median (range) = 7 (4–8)) and weighed between 17 and 52 kg (wolves: median (range) = 40 (28–52); dogs: median (range) = 25 (17–34), see Table 1 for details). The wolves were fed carcasses of deer, rabbit, or chicken three to four times a week while the dogs were fed commercial dog food daily. In addition, dogs were regularly provided with small pieces of deer, rabbit, or chicken to make wolf and dog feeding as similar as possible.

Table 1: List of the subjects

Individual	Species	Sex	Date of birth	Weight*	1^{st} condition
Amarok	Wolf	♂	4.04.2012	40.25	NS
Aragorn	Wolf	♂	4.05.2008	49.20	NS
Chitto	Wolf	♂	7.04.2012	44.57	S
Etu	Wolf	♂	4.05.2016	50.07	S
Geronimo	Wolf	♂	2.05.2009	40.25	S
Nanuk	Wolf	♂	28.04.2009	44.10	NS
Shima	Wolf	♀	4.05.2008	39.70	NS
Taima	Wolf	♀	4.05.2016	27.85	NS
Tala	Wolf	♀	4.04.2012	37.45	S
Tekoa	Wolf	♂	4.05.2016	34.05	NS
Una	Wolf	♀	7.04.2012	32.95	NS
Wamblee	Wolf	♂	22.04.2012	37.25	S
Yukon	Wolf	♀	2.05.2009	38.21	S
Asali	Dog	♂	19.09.2010	34.01	S
Banzai	Dog	♂	2.04.2014	23.00	NS
Binti	Dog	♀	13.09.2010	25.00	S
Bora	Dog	♀	2.08.2011	20.57	NS
Enzi	Dog	♂	2.04.2014	29.01	S
Gombo	Dog	♂	21.03.2014	28.45	NS
Hiari	Dog	♂	21.03.2014	24.87	S
Imara	Dog	♀	21.03.2014	21.25	NS

Layla	Dog	♀	2.08.2011	21.45	S
Maisha	Dog	♂	18.12.2009	21.00	NS
Meru	Dog	♂	1.10.2010	34.30	S
Nia	Dog	♀	21.07.2011	17.00	NS
Panya	Dog	♀	2.04.2014	25.20	S
Sahibu	Dog	♂	21.03.2014	26.00	NS
Zuri	Dog	♀	24.05.2011	20.08	S

* Weights displayed are the mean of the weight measured during the two tests

NS: non-social condition; S: social condition

Experimental apparatus and setting

The experimental apparatus was composed of three parts: (1) an ornated disc (i.e., ribbons with wooden marbles or ropes with plastic glasses), (2) a two-meter metal axis, and (3) a drill fixed on an 80 cm pole (see Fig.1). The drill was fixed outside the fence, then the metal axis was attached to the drill in order to go through the fence into the enclosure and the disk was attached to the other end of the axis. The drill acted as the motor of the apparatus. When turned on, the drill rotated the metal axis and the disc. The food was one piece of meat (≈ 100g) - a highly attractive reward for both wolves and dogs (Rao et al., 2018) - and was placed 1 m in front of the spinning disc in a red bowl well known by all the animals. Thus, the apparatus provided visual and acoustic stimulation via the gentle noise of the drill and the ornaments.

Every subject was confronted with the apparatus once in each of two conditions: alone (non-social condition) or with a familiar human (social condition). The familiar human was defined as the trainer with the best relationship with the subject according to the judgment of the trainers themselves, which has been shown to be reliable (Burkhard et al., 2023). Subjects received conditions in a counterbalanced order with at least one-month intervals between conditions. In addition, the size, pattern, and ornaments of the rotating disc differed between the two conditions to prevent habituation. The discs, sex, and age of the subjects were counterbalanced across conditions.

Figure 1: The apparatus we used. A) Close-up of the apparatus. B) Apparatus. C) The differently patterned discs used

<u>Procedure</u>

Each individual was tested in its home enclosure in the absence of its pack members. All the animals are shifted between enclosures of the Wolf Science Center on a regular basis and are used to this procedure; packs are rotated between enclosures every few weeks so that each pack is familiar with each of the enclosures. Here we define home enclosure as the one where a pack had spent at least one night prior to the test. Before the beginning of each test session, the experimenters installed blinds on the fence of the home enclosure to ensure that neither the animal tested nor its pack members could see the installation of the apparatus or the actual testing. After these were installed, the entire pack was shifted out of the home enclosure. The subject was isolated from its pack and remained in the shifting system (i.e., a system of corridor-like enclosures used to move the animals between enclosures without direct contact with the trainer), whereas the rest of the pack was moved into the enclosure adjacent to the home enclosure. Once the subject was isolated from the pack, the trainers equipped the subject with a polar belt measuring cardiac outputs, a routine procedure for the animals. We used the Polar® RS800CX system (Polar Electro Oy, 2010) designed for human use (Jean-Joseph et al., 2020; Kortekaas & Kotrschal, 2019, 2020). It consists of three parts: a chest belt with electrodes, a clip-on to send measurements, and a watch-like data logger. First, an animal trainer wetted the belt with ethanol (70%) to improve conductivity, then the clip-on was fixed on the belt and the belt secured to the animal's chest with the clip-on over the heart of the animal. Second, the trainer fastened the belt on the animal's chest behind the shoulders and applied ethanol (70%) between the belt and the animal's fur, again to enhance conductivity. The watch-like data logger was started and the quality of the signal between the clip-on and logger was checked. If the signal was suboptimal, the trainer adjusted the belt and the position of the clip-on or added more ethanol to the fur of the animal. Once the signal was satisfactory, the data logger was attached to an additional collar around the animal's neck. After a two-minute waiting period (for the subject to calm down), the subject was released into its enclosure, the apparatus was turned on (i.e., the disc started to spin), and the test started. The test lasted until the animal ate all the food available or after a cutoff time of eight minutes in cases when the animal did not approach the food bowl. At the end of the test, the individual was shifted out of the enclosure again and after a two-minute waiting period (for the subject to calm down after the test), the HR device was taken off by a trainer. Afterward, the experimenter removed the apparatus from the enclosure and the respective pack was shifted back to their home enclosure.

During the social condition, the familiar human entered the enclosure before the subject (i.e., while the subject was fitted with the belt and HR device) and stood roughly five body lengths away from the apparatus; five m for dogs and eight m away for wolves to account for the differences in body size. The familiar human did not give food to the subject during the experiment. Additionally, during the test the familiar human was instructed to act in a specific way, as described in Table 2. The familiar human left the enclosure after the animal was shifted out of the enclosure at the end of the test. The trainer shifting and fastening the HR device was not the same person as the trainer acting as the familiar human in the social condition.

Table 2: Instructions for the human during the test

Time (min)	Allowed Behaviours	Position
0 to 2	No interaction with the subject unless the subject initiates it[1] No looking at the apparatus No gaze alternation between apparatus and subject	Stands immobile
2 to 4	Pointing at the food Gaze alternation between the subject and the food	Takes one step toward the apparatus
4 to 6	Pointing at the food Gaze alternation between the subject and the food	Crosses half the distance towards the food
6 to 8	Call the subject's name Gaze alternation (with clear head movement toward the food) Praising the subject in a cheerful voice Petting the subject if it seeks physical contact	Crouches down by the food

[1] if the animal established eye contact, the experimenter would look back and if approached, the

person could talk to the animal in a cheerful but calm voice. If the animal touched the experimenter, she would crouch down and shortly pet the animal.

Behavioural analysis

Each session was recorded with two cameras to capture the entire area surrounding the apparatus. The frequency, latency, and duration of several behaviours were coded with the Behavioral Observation Research Interactive Software (BORIS©; http://www.boris.unito.it/, Friard & Gamba, 2016; see Table 3 for details). In addition, we coded what or whom (i.e., object, food, familiar human) the wolves and the dogs chose to approach first. A choice was defined as coming within one body length of the object, food, or familiar human while having the head and eyes fixed on either the object, food, or familiar human.

Table 3: List of recorded behaviours (adapted from Marshall-Pescini et al., 2017)

Behaviours	Definition	Target	Type of coding
Fear related behaviours			
Avoidance	Being at the back of the enclosure, out of sight of the camera.		Duration
Close to entry/exit	Standing within one body length of the door/exit of the enclosure.		Duration, frequency
Jumping back	Brief movement backward, staring at the source of fear.		Frequency
Freeze	To stop moving and staring at the source of the fear.		Frequency
Vocalizations	To whine, whimper, growl, bark, or howl.		Frequency
Stress-related behaviours			
Circling/Pacing	Walking or trotting back and forth.		Duration, frequency

Mouth liking	Tongue moved over the lips.		Frequency
Panting	To gasp for breath. The tongue is visibly moving inside and outside the mouth.		Frequency
Scratching	To nibble or scratch different body parts with front or hind paws.		Frequency
Shaking	To wiggle the whole body, starting with the head and finishing with the hind part of the body.		Frequency
Yawning	To open the mouth widely, slightly close the eyes and backward the ears.		Frequency
Approach	Moving forward within less than one body length.	Apparatus, familiar human, food	Frequency
Proximity	Staying within one body length of	Apparatus, familiar human, food	Duration, frequency

Heart rate parameters analysis

We selected three sequences of HR for each individual, the first 30s after the subject entered the enclosure (begin), the last 30s before the subject took the food (end), and 30s in between these two periods toward the middle of the HR recording (middle, the position of the middle period varied relatively to the time an individual took to reach the meat). The rationale for choosing these three sequences was that the beginning might reflect the first reaction to the apparatus whereas the middle could be reflective of the decision-making process, i.e, approaching or not approaching the apparatus, and the end would reflect the reaction of the animal when taking the food, or in the case they did not their physiological state at the arbitrary end of the test (i.e., 8 minutes). The individuals with less than 30s of recording were excluded from the analyses (four individuals for both conditions and six individuals for only one condition, each time these individuals approached and ate the food in less than 30s). Individuals with recordings between 30s and 1min had only two HR sequences (begin and end) to avoid using identical data points in the different HR sequences. To sum up, all animals were recorded twice, once in the social condition and once in the non-social condition. Those recording range from 15s to 8 minutes. Recording shorter than 30s were excluded from analyses and depending on the total duration of the test, we extracted two to three 30s HR sequences from the whole HR recording. As the Polar system may produce artifacts (Essner et al., 2013, 2015; Jonckheer-Sheehy et al., 2012), the resulting strings of raw data need to be edited and corrected, in this case using the algorithm-supported visual error correction (AVEC) of HR measurements(Schöberl et al., 2015). Sequences with more than 5% of errors were excluded from analyses. As a result, three individuals were completely excluded from the HR parameter analyses. The corrected data strings were then used to calculate one mean HR and one RMSSD (a proxy for the HRV) per 30s strings with the software Kubios ©.

Statistical Analyses

We fitted the models in R (version 4.2.1; R Core Team, 2021) using the package lme4 (1.1-29; Bates et al., 2014) with the function lmer for the linear mixed model (LME, Baayen, 2008) and function glmer for the generalized linear mixed model (GLMM; Baayen, 2008). The package DHARMa (0.4.5; Hartig, 2018) was used to test for overdispersion and zero-inflation, and the packages survival (3.2-10; Therneau & Grambsch, 2000) and coxme (2.2-16; Therneau, 2015) for the survival model used to analyzed latencies.

Latency to take the food model

To understand whether latency to take the food differed depending on “species” (wolf or dog) and conditions (social or non-social) of the test, we fitted a survival model comprising the fixed factors “species”, conditions, and their interaction. Furthermore, sex and age of the individual, as well as the order of the conditions, were included as control factors. Identity of the animal was added as a random factor to control for pseudo-replication. Then we compared this model, designated as the full model, to a null model (comprising only sex, age, order of the condition, and the random factor animal identity).

First Choice models

Finally, we used Pearson chi-square tests, to assess what or who dogs and wolves chose to approach first in each condition (social or non-social). The samples for the Pearson chi-square tests were 23 data points for the social condition and 17 data points for the non-social condition. One dog and three wolves in the social condition as well as seven dogs and four wolves in the non-social condition refused to choose and therefore were excluded from the analyses.

Behaviours models

Furthermore, we analyzed relevant behavioural responses. The continuous response variables such as proximity to the human, proximity to the food, time spend circling, time spent avoiding the apparatus, and time spent in the entry were analyzed using the same methods as the cardiac outputs. Each variable was fitted in a linear mixed model comprising of “species” (wolf or dog), condition (social or non-social), and their interaction as fixed factors. Sex, age of the individual, as well as the order of the conditions, were included as control factors, and identity of the animal was added as a random factor to control for pseudo-replication. Those full models were then compared to their respective null models comprising only sex, age, order of the conditions, and the random factor animal identity. The models for the proximity to the familiar human and to the apparatus did not converge and therefore were excluded from further analyses.

The count response variables, i.e., number of approaches toward the food, the familiar human, the apparatus, and the number of stress and fear behaviours were fitted using generalized linear mixed models using a poisson error structure. Each variable was fitted in a model comprising "species" (wolf or dog), conditions (social or non-social), and their interaction as fixed factors. Sex and age of the individual as well as the order of the conditions were included as control factors, and identity of the animal was added as a random factor to control for pseudo-replication. These models were tested for overdispersion and zero-inflation with the package DHARMa. The model for the total number of stress and fear responses was heavily overdispersed (parameter dispersion: 3.44) and thus corrected using a negative binomial structure (package lme4, function glmer.nb). Full models were then compared to their respective null models comprising only sex, age, order of the condition, and the random factor animal identity. Despite correction for overdispersion, the model for the number of approaches toward the apparatus and toward the humans did not converge and were therefore excluded from further analyses.

The sample for the other variables was 55 data points collected on 28 animals tested twice each (one data point, Layla in the social condition, is missing due to an issue with the camera during the test).

Cardiac outputs models

To test whether cardiac output would differ between species depending on the conditions of the test the response variables "mean" HR and RMSSD (a proxi of the heart rate variability, HRV) were both analyzed in two separate linear mixed effect models (LME, Baayen, 2008)."Species" (wolf or dog), condition of the test (social or non-social), order of the condition, and stage of the test (beginning, middle, or end) were included as fixed effects factors. We also included in the model the interaction between species and conditions to understand how wolves' and dogs' cardiac parameters were affected by the social environment. To control for the effects of temperature, body mass, age, sex, and success (i.e., the subject did take the food yes or no) these factors were also included as fixed effects. Subject identity was included as a random intercept to account for individual differences and to avoid pseudo-replication, as all subjects were tested in each condition. None of the random slopes and their correlations were identifiable; hence, we chose to not include them (Barr et al., 2013; Matuschek et al., 2017; Schielzeth & Forstmeier, 2009). Visual inspection of the qqplot and the residuals plotted against the fitted values indicated no obvious deviation from the normality and homogeneity assumptions. We checked for model stability by excluding subjects one at a time from the data and comparing the model estimates derived for these subsets of the data with those derived for the full data set. We inspected Variance Inflation Factors (VIF, Field, 2009) which we derived using the function VIF of the R-package car (Fox & Weisberg, 2018), applied to a standard linear model excluding the random effects and interactions. This revealed that species and body mass were collinear with a VIF of 8.12 and 9.80, respectively. However, there was also a considerable variation of body mass within both wolves and dogs; hence, the results obtained for these two predictors should not be distorted by collinearity among them. To avoid cryptic multiple testing and to keep type I error rate at the nominal level of 0.05 (Forstmeier & Schielzeth, 2011), we tested the significance of the full model as compared to the null model (comprising only age, body mass, sex, temperature, and the random effects) by means of a likelihood ratio test (R function anova with argument test set to “Chisq”; Dobson & Barnett, 2018). To allow for a likelihood ratio test, we fitted the models using maximum likelihood (rather than Restricted Maximum Likelihood; Bolker et al., 2009). P-values for the individual effects were based on likelihood ratio tests comparing the full of the respective reduced models (Barr et al., 2013; R function drop1).

The sample for the cardiac outputs’ models consisted of 75 data points after corrections of the HR strands collected on 21 individuals.

Results

Latency to take the food

Fourteen out of 15 dogs took the food in the social condition whereas only seven out of 13 wolves did. In the non-social condition, seven out of 15 dogs took the food, whereas 8 out of 13 wolves did. Overall, only one dog and five wolves never took the food in any of the conditions; seven dogs and seven wolves always took the food.

Overall, our full model (species * conditions + sex + age + order + animal ID) was statistically significant (likelihood ratio test: χ2 = 18.446, df = 6, P =0.005) compared to our null model (animal ID). However, we found no effect of species, conditions, or their interaction on the latency to take the food. Age of the subject was the main factor affecting this latency (z =3.42, P< 0.001; Fig.2, Table 4). The older the animals, the faster they were in taking the food.

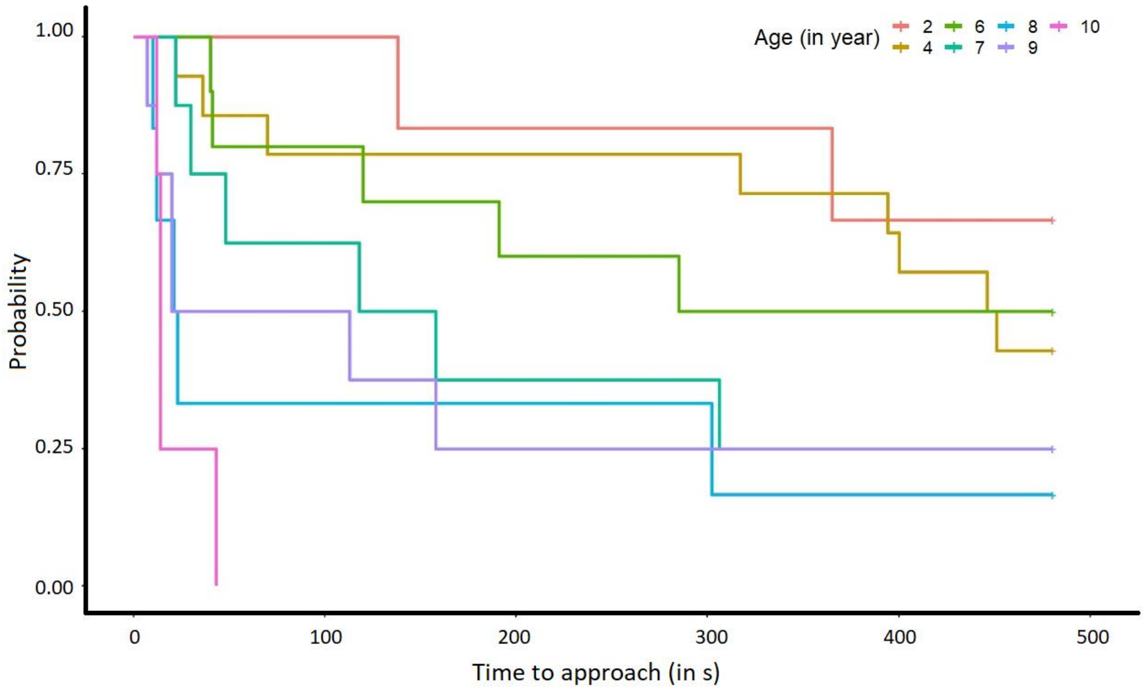

Figure 2: Latency to take the food in function of the age of the subjects. W=Wolves, D=Dog; Effective per age group: 2 years old 3 W - 0 D; 4 years old 0 W - 7 D; 6 years old 5 W - 0 D; 7 years old 0 W - 4 D; 8 years old 0 W - 3 D; 9 years old 3 W – 1 D; 10 years old 2 W – 0 D.

Table 4: Results of the survival model for the latency to eat the food

	Estimate	SE	z	P
Species	-0.411	0.888	-0.46	0.640
Conditions	0.945	0.550	1.72	0.086
Sex	0.595	0.755	0.79	0.430
Age	0.594	0.173	3.42	<0.001
Order	0.677	0.404	1.67	0.094
Species:Conditions	-0.930	0.815	-1.14	0.250

First Choice

Of the animals that approached the experimental set-up during the non-social condition, no clear choice for the apparatus nor the food was apparent ($\chi^2=1.98^{-31}$, df=1, $P>0.05$, Fig.3A).

Of the animals that approached the experimental set-up during the social condition, no clear preference for the apparatus, the food nor the familiar human was apparent ($\chi^2=1.34$, df=2, $P>0.05$; see Fig.3B).

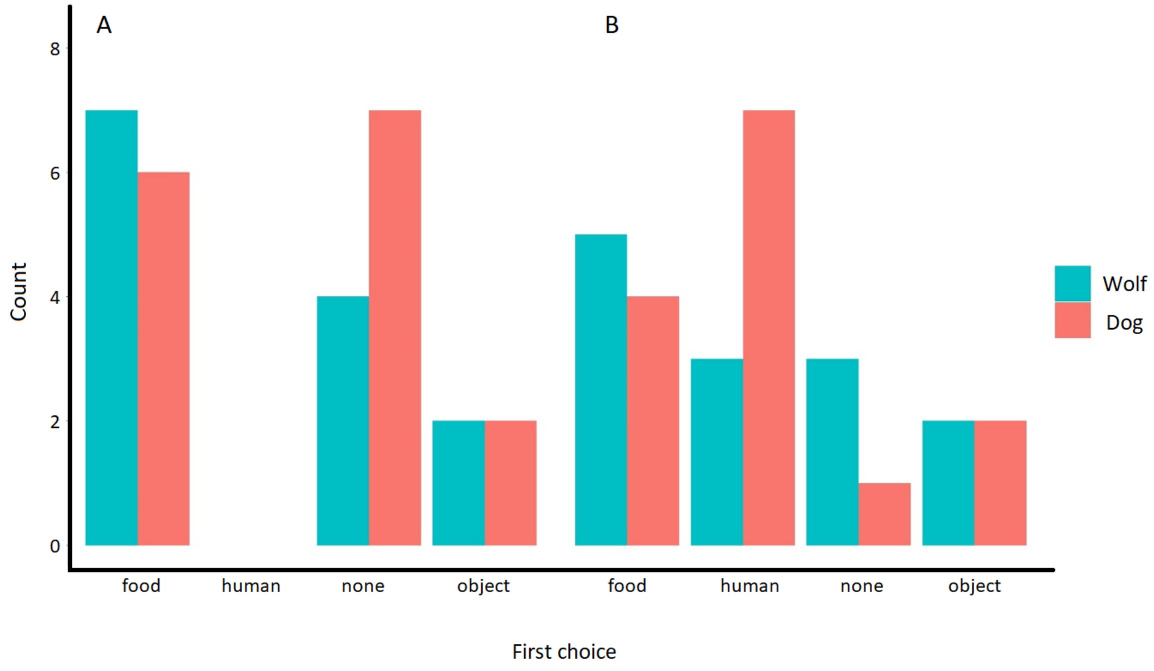

Figure 3: Histogram of the first choice the wolves and dogs made after starting the test in A. Non-social condition; B. Social condition. Choice was defined as approaching within one body length (head toward, eyes fixed on) of either the object, the food, or the human.

<u>Behaviours</u>

Overall, three wolves and one dog never approached the food, and 9 wolves and 11 dogs never approached the apparatus no matter the condition. 9 dogs and three wolves approached the familiar human at least once (for more detail see Table S1).

We found no statistically significant difference in our wolves' and dogs' behaviours, be it the time spent in proximity of the food ($\chi2$ = 4.54, df=3, P=0.2), in the number of approaches towards the food ($\chi2$ = 7.49, df=4, P=0.11), nor the number of stress-related and fear-related behaviours ($\chi2$ = 9.70, df=6, P=0.13).

Cardiac output Models

Our full HR model (species*conditions + temperature + order + sex + age + weight + test stage + success + animal ID) was statistically different from our null HR model (age + weight + temperature + sex + success + animal ID) meaning that at least one of the factors of our full model affected our results (likelihood ratio test: $\chi2 = 18.56$, df= 6, $P< 0.005$). Indeed, the stage of the test had an effect on the mean HR of the animals: HR was higher at the beginning of the test when the animal first entered the enclosure. It then decreased during the test before increasing slightly at the end of the test, i.e., when most of the animals faced the apparatus to take the food ($\chi2=15.65$, $P<0.001$, Fig.4a, b, Table 5 and Table S2).

The comparison of our full HRV model against the null HVR model was not significant meaning that none of our factors of interest, i.e., species, condition, test stage, and their interaction influenced the RMSSD (likelihood test ratio: $\chi2=7.55$, df=6, $P>0.05$, Fig.4c, d).

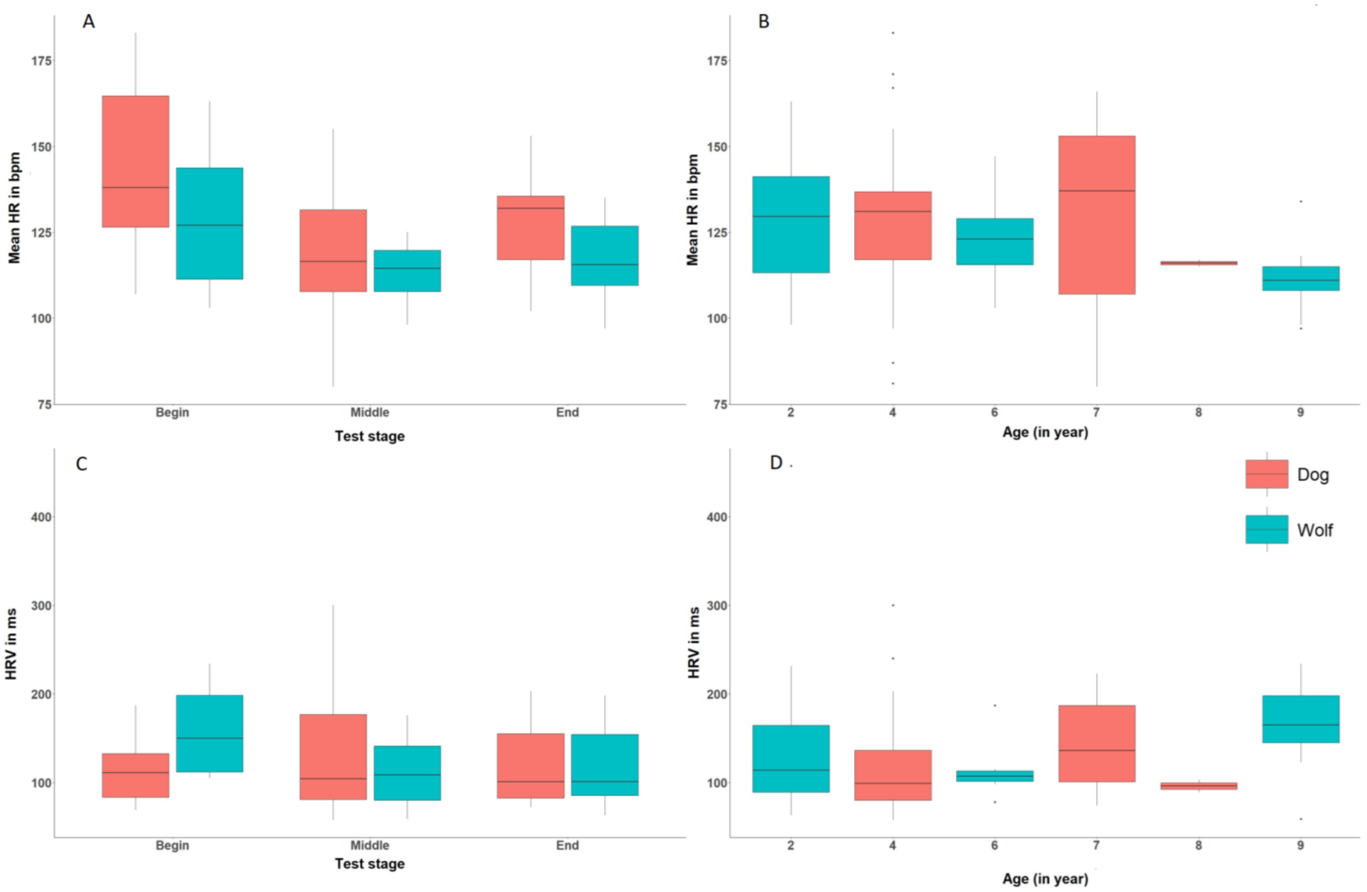

Figure 4: Boxplot of the cardiac output of the wolves and dogs. A) Mean HR in function of test stage. B) Mean HR in function of age. C) HRV as related to test stage. D) HRV as related to age. The whiskers represent the minimum (bottom) and maximum (top) data points, the edges of the box represent the interquartile (Q3–Q1) and the bold line is the median.

Table 5: Results of the heart rate model

	Estimate	SE	X^2	df	P
(Intercept)	163.114	21.406			
Species (Wolf; Dog)	-10.21	13.621			
Conditions (S; NS)	-1.185	6.325			
Temperature	-0.145	0.553	0.066	1	0.797
Order (1; 2)	-6.655	6.049	1.192	1	0.275
Age	-1.89	1.138	2.612	1	0.106
Sex (M; F)	-3.193	7.816	0.162	1	0.687
Weight	-0.209	0.803	0.067	1	0.796
Success (Yes; No)	2.325	6.68	0.120	1	0.729
HR Stage	-22.622	5.621	15.650	2	<0.001
	-14.495	4.751			
Species x Conditions	10.536	10.223	1.054	1	0.304

Discussion

In our risk-taking paradigm, the behaviours of equally raised and kept wolves and dogs did not differ significantly, rather, age was the main factor affecting the time to take the food close to the spinning wheel. The main factor affecting cardiac parameters was the stage of the test, start or end.

As we found little to no differences between equally raised and kept socialised wolves and dogs, our results support the canine cooperation hypothesis as dogs and wolves demonstrated similar behaviour toward a familiar human in a risk-taking paradigm. Additionally, as they seem to react similarly to human communicative gestures, our results also support the two-stage hypothesis. However, our result contrast with classic selection for tameness hypothesis (Belyaev, 1979; Darwin, 1868; Price, 1999; Trut et al., 2004) and *emotional reactivity hypothesi*s (Hare et al., 2005, 2012) as dogs were not less reactive than wolves. Those results also contrast with previous findings in dogs' and wolves' risk-proneness and neophobia. The animals kept at the WSC were tested for risk-proneness in a two-choice foraging paradigm where wolves behaved more risk-prone than dogs (Marshall-Pescini et al., 2016). In a novel object paradigm, wolves were found to be more neophobic than dogs but also more persistent (Moretti et al., 2015). The differences between the studies could be due to the paradigms used. The study by Marshall-Pescini et al. (2016) involved food but in a highly cognitive task that the dogs might have had difficulties understanding. The study comparing neophobia in wolves and dogs by Moretti et al., (2015) presented a novel object to the subjects in their home enclosure but did not involve food; dogs seemed less interested than wolves, as half of them never even approached the objects. The present study used a combination of a foraging context with a novel object. However, the novel object was probably not sufficiently scary for every individual since the animals had already a lot of experience with novel objects and moving apparatuses. Only one dog out of 15 did not approach the food in both conditions, social or non-social, whereas three out of 13 wolves did not approach the food in any condition and two of those were the youngest ones. As our main result was that age affected the behavioural responses of the animals most, this could also be the reason for the differences in the three studies, as the animals in our study were older than in the two previous ones (in our study mean age for the wolves was 6.4 and 5.9 for the dogs whereas in the Marshall et al. study it was respectively 4.7 and 3.2. We could not find this information for the Moretti et al. study). Hence, age and similar experiences in a rich environment (i.e., the animals at the WSC all frequently participate in different trainings and experiments) could have leveled out potential differences in the behavioural and physiological responses of wolves and dogs.

Age also seems to affect risk-proneness in other species (Dammhahn, 2012; Fisher et al., 2015; Hall et al., 2015; Seltmann et al., 2012; Sinn et al., 2008) and our results fit the life history framework, which holds that individuals balance their risk proneness with remaining lifetime reproductive odds. Hence, older individuals generally tend to be more risk-prone than younger ones (Dammhahn, 2012). In fact, in wild wolves, older animals engaged more in conflicts with other packs in defense of their kin than younger ones (Cassidy et al., 2017).

Another outcome of our study was that cardiac output was more affected by the stage of the test, with the highest HR values at the beginning when the animals first entered the enclosure. This could be caused by expectancy arousal as generally, our animals are eager to participate in experiments. This was also found by Vasconcellos et al. (2016) in salivary cortisol of wolves and dogs ahead of a training situation. Alternatively, individuals may have noticed the potential danger related to getting the desired food item, which could explain the second HR peak at the end of the test when the animals get close to the potential danger to reach the food.

Vasconcellos et al. (2016) found that in an experimental one-to-one positive reinforcement training situation with wolves and dogs, while salivary cortisol decreased after a training session, wolves´ salivary cortisol was lower than that of dogs before the training even started. The results may reflect high inherent readiness for action in dogs in human-related tasks dogs as compared to wolves, but may also indicate that dogs gear up their physiology in preparation for action more than wolves.

The presence of the humans did not make any difference for the dogs in our experiment, which were raised and kept the same way as the wolves. This contrasts with previous studies where dogs did benefit from the social support of familiar people in potentially stressful situations (Palmer & Custance, 2008; Solomon et al., 2019; Topál et al., 1998) including a study at the WSC where, when separated from their pack, the WSC dogs displayed lower HR and higher HRV if they were resting near a familiar human, whereas wolves did not. Hence, there was a greater calming effect due to the presence of a familiar human in dogs than the wolves (Jean-Joseph et al., 2020).

As body mass and age (Ferasin et al., 2010; Hezzell et al., 2013; Mosier, 1989; Strasser et al., 1997) may affect cardiac output, we controlled for both parameters by adding them into the statistical models but found no influence of these parameters on HR and HRV in the full data set. Although in mammals, HR is generally negatively correlated with body mass (Brody, 1945), there is no clear evidence for this in dogs (Kirkwood, 1985; Sutter et al., 2007). In fact, some previous studies failed to show such a relationship (Ferasin et al., 2010; Lamb et al., 2010; Nganvongpanit et al., 2011; Rishniw et al., 2012). Moreover, studies that indicated a correlation between body mass and HR in dogs disagreed on its direction and the strength of this effect (Cruz Aleixo et al., 2017; Hamlin et al., 1967; Hezzell et al., 2013).

To conclude, according to our paradigm, wolves' and dogs' risk-proneness differs according to age rather than species and neither dogs nor our human-socialized socialized wolves seem to respond behaviourally and physiologically to the presence of a familiar human. This suggests that in this case, domestication effects might be overshadowed by other factors such as age, life experience, and/or motivation. Furthermore, our results support previous suggestions that domestication should be investigated in a range of relevant contexts (Jean-Joseph et al., 2020) rather than assuming selection for tameness as the basic mechanism of domestication would produce robust predictions for all possible mechanisms, domains, and contexts. It seems that domestication does not uniformly affect all environmental responses and behaviours in dogs as compared to wolves but has rather produced a mosaic of context-dependent modifications (Range & Marshall-Pescini, 2022c, 2022b).

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References

Axelsson, E., Ratnakumar, A., Arendt, M.-L., Maqbool, K., Webster, M. T., Perloski, M., Liberg, O., Arnemo, J. M., Hedhammar, Å., & Lindblad-Toh, K. (2013). The genomic signature of dog domestication reveals adaptation to a starch-rich diet. *Nature*, *495*(7441), Article 7441. https://doi.org/10.1038/nature11837

Baayen, R. H. (2008). *Analyzing Linguistic Data: A Practical Introduction to Statistics using R* (1st ed.). Cambridge University Press. https://doi.org/10.1017/CBO9780511801686

Barnett, S. A. (1958). Experiments on 'Neophobia' in Wild and Laboratory Rats. *British Journal of Psychology*, *49*(3), 195–201. https://doi.org/10.1111/j.2044-8295.1958.tb00657.x

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, *68*(3), Article 3. https://doi.org/10.1016/j.jml.2012.11.001

Barry, T., Gurarie, E., Cheraghi, F., Kojola, I., & Fagan, W. F. (2020). Does dispersal make the heart grow bolder? Avoidance of anthropogenic habitat elements across wolf life history. *Animal Behaviour*, *166*, 219–231. https://doi.org/10.1016/j.anbehav.2020.06.015

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting Linear Mixed-Effects Models using lme4. *ArXiv:1406.5823 [Stat]*. http://arxiv.org/abs/1406.5823

Beerda, B., Schilder, M. B. H., van Hooff, J. A. R. A. M., de Vries, H. W., & Mol, J. A. (1998). Behavioural, saliva cortisol and heart rate responses to different types of stimuli in dogs. *Applied Animal Behaviour Science*, *58*(3–4), Article 3–4. https://doi.org/10.1016/S0168-1591(97)00145-7

Belyaev, D. K. (1979). Destabilizing selection as a factor in domestication. *Journal of Heredity*, *70*(5), Article 5. https://doi.org/10.1093/oxfordjournals.jhered.a109263

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), Article 3. https://doi.org/10.1016/j.tree.2008.10.008

Brody, S. (1945). *Bioenergetics and growth New York: Reinhold Publ*. Corp.

Bubac, C. M., Coltman, D. W., Don Bowen, W., Lidgard, D. C., Lang, S. L. C., & den Heyer, C. E. (2018). Repeatability and reproductive consequences of boldness in female gray seals. *Behavioral Ecology and Sociobiology*, *72*(6), 100. https://doi.org/10.1007/s00265-018-2515-5

Burkhard, M. E., Range, F., Ward, S. J., & Robinson, L. M. (2023). Bonded by nature: Humans form equally strong and reciprocated bonds with similar raised dogs and wolves. *Frontiers in Psychology*, *13*. https://www.frontiersin.org/articles/10.3389/fpsyg.2022.1044940

Butler, J. R. A., Brown, W. Y., & Du Toit, J. T. (2018). Anthropogenic Food Subsidy to a Commensal Carnivore: The Value and Supply of Human Faeces in the Diet of Free-Ranging Dogs. *Animals*, *8*(5), Article 5. https://doi.org/10.3390/ani8050067

Cassidy, K. A., Mech, L. D., MacNulty, D. R., Stahler, D. R., & Smith, D. W. (2017). Sexually dimorphic aggression indicates male gray wolves specialize in pack defense against conspecific groups. *Behavioural Processes*, *136*, 64–72. https://doi.org/10.1016/j.beproc.2017.01.011

Chapagain, D., Wallis, L. J., Range, F., Affenzeller, N., Serra, J., & Virányi, Z. (2020). Behavioural and cognitive changes in aged pet dogs: No effects of an enriched diet and lifelong training. *PLOS ONE*, *15*(9), e0238517. https://doi.org/10.1371/journal.pone.0238517

Cruz Aleixo, A. S., Alfonso, A., Oba, E., Ferreira de Souza, F., Salgueiro Cruz, R. K., Fillippi, M. G., Chiacchio, S. B., Tsunemi, M., & Gomes Lourenço, M. L. (2017). Scaling Relationships Among Heart Rate, Electrocardiography Parameters, and Body Weight. *Topics in Companion Animal Medicine*, *32*(2), Article 2. https://doi.org/10.1053/j.tcam.2017.06.002

Dammhahn, M. (2012). Are personality differences in a small iteroparous mammal maintained by a life-history trade-off? *Proceedings of the Royal Society B: Biological Sciences*, *279*(1738), Article 1738. https://doi.org/10.1098/rspb.2012.0212

Dammhahn, M., & Almeling, L. (2012). Is risk taking during foraging a personality trait? A field test for cross-context consistency in boldness. *Animal Behaviour*, *84*(5), 1131–1139. https://doi.org/10.1016/j.anbehav.2012.08.014

Darwin, C. (1868). *The Variation of Animals and Plants Under Domestication*. O. Judd.

Dobson, A. J., & Barnett, A. G. (2018). *An Introduction to Generalized Linear Models*. CRC Press.

Dorey, N. R., Udell, M. A. R., & Wynne, C. D. L. (2010). When do domestic dogs, Canis familiaris, start to understand human pointing? The role of ontogeny in the development of interspecies communication. *Animal Behaviour*, *79*(1), Article 1. https://doi.org/10.1016/j.anbehav.2009.09.032

Essner, A., Sjöström, R., Ahlgren, E., Gustås, P., Edge-Hughes, L., Zetterberg, L., & Hellström, K. (2015). Comparison of Polar® RS800CX heart rate monitor and electrocardiogram for measuring inter-beat intervals in healthy dogs. *Physiology & Behavior*, *138*, 247–253. https://doi.org/10.1016/j.physbeh.2014.10.034

Essner, A., Sjöström, R., Ahlgren, E., & Lindmark, B. (2013). Validity and reliability of Polar® RS800CX heart rate monitor, measuring heart rate in dogs during standing position and at trot on a treadmill. *Physiology & Behavior*, *114*(Supplement C), Article Supplement C. https://doi.org/10.1016/j.physbeh.2013.03.002

Ferasin, L., Ferasin, H., & Little, C. J. L. (2010). Lack of correlation between canine heart rate and body size in veterinary clinical practice. *Journal of Small Animal Practice*, *51*(8), Article 8. https://doi.org/10.1111/j.1748-5827.2010.00954.x

Field, A. P. (2009). *Discovering statistics using SPSS: And sex, drugs and rock "n" roll* (3rd ed). SAGE Publications.

Fisher, D. N., David, M., Tregenza, T., & Rodríguez-Muñoz, R. (2015). Dynamics of among-individual behavioral variation over adult lifespan in a wild insect. *Behavioral Ecology*, *26*(4), 975–985. https://doi.org/10.1093/beheco/arv048

Forstmeier, W., & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: Overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology*, *65*(1), Article 1. https://doi.org/10.1007/s00265-010-1038-5

Fox, J., & Weisberg, S. (2018). *An R Companion to Applied Regression*. SAGE Publications.

Fox, M. W. (1972). Socio-Ecological Implications of Individual Differences in Wolf Litters: A Developmental and Evolutionary Perspective. *Behaviour*, *41*(3–4), 298–313. https://doi.org/10.1163/156853972X00077

Frantz, L. A. F., Mullin, V. E., Pionnier-Capitan, M., Lebrasseur, O., Ollivier, M., Perri, A., Linderholm, A., Mattiangeli, V., Teasdale, M. D., Dimopoulos, E. A., Tresset, A., Duffraisse, M., McCormick, F., Bartosiewicz, L., Gál, E., Nyerges, É. A., Sablin, M. V., Bréhard, S., Mashkour, M., … Larson, G. (2016). Genomic and archaeological evidence suggest a dual origin of domestic dogs. *Science*, *352*(6290), Article 6290. https://doi.org/10.1126/science.aaf3161

Friard, O., & Gamba, M. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, *7*(11), Article 11. https://doi.org/10.1111/2041-210X.12584

Gácsi, M., Kara, E., Belényi, B., Topál, J., & Miklósi, Á. (2009). The effect of development and individual differences in pointing comprehension of dogs. *Animal Cognition*, *12*(3), Article 3. https://doi.org/10.1007/s10071-008-0208-6

Gácsi, M., Maros, K., Sernkvist, S., Faragó, T., & Miklósi, Á. (2013). Human Analogue Safe Haven Effect of the Owner: Behavioural and Heart Rate Response to Stressful Social Stimuli in Dogs. *PLOS ONE*, *8*(3), Article 3. https://doi.org/10.1371/journal.pone.0058475

Hall, N. J., Lord, K., Arnold, A.-M. K., Wynne, C. D. L., & Udell, M. A. R. (2015). Assessment of attachment behaviour to human caregivers in wolf pups (Canis lupus lupus). *Behavioural Processes*, *110*(Supplement C), Article Supplement C. https://doi.org/10.1016/j.beproc.2014.11.005

Hamlin, R. L., Olsen, I., Smith, C. R., & Boggs, S. (1967). Clinical relevancy of heart rate in the dog. *Journal of the American Veterinary Medical Association*, *151*(1), Article 1.

Hare, B., Plyusnina, I., Ignacio, N., Schepina, O., Stepika, A., Wrangham, R., & Trut, L. (2005). Social Cognitive Evolution in Captive Foxes Is a Correlated By-Product of Experimental Domestication. *Current Biology*, *15*(3), Article 3. https://doi.org/10.1016/j.cub.2005.01.040

Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour*, *83*(3), Article 3. https://doi.org/10.1016/j.anbehav.2011.12.007

Hartig, F. (2018). DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R package v. 0.2. 0. *Regensbg. Univ. Regensbg*.

Heilbronner, S. R., Rosati, A. G., Stevens, J. R., Hare, B., & Hauser, M. D. (2008). A fruit in the hand or two in the bush? Divergent risk preferences in chimpanzees and bonobos. *Biology Letters*, *4*(3), 246–249. https://doi.org/10.1098/rsbl.2008.0081

Hezzell, M. J., Humm, K., Dennis, S. G., Agee, L., & Boswood, A. (2013). Relationships between heart rate and age, bodyweight and breed in 10,849 dogs. *Journal of Small Animal Practice*, *54*(6), Article 6. https://doi.org/10.1111/jsap.12079

Jean-Joseph, H., Dooey, G., & Kotrschal, K. (2022). Diurnal activity patterns of equally socialized and kept wolves, Canis lupus, and dogs, Canis lupus familiaris. *Animal Behaviour*, *190*, 41–52. https://doi.org/10.1016/j.anbehav.2022.05.009

Jean-Joseph, H., Kortekaas, K., Range, F., & Kotrschal, K. (2020). Context-Specific Arousal During Resting in Wolves and Dogs: Effects of Domestication? *Frontiers in Psychology*, *11*. https://www.frontiersin.org/articles/10.3389/fpsyg.2020.568199

Jonckheer-Sheehy, V. S. M., Vinke, C. M., & Ortolani, A. (2012). Validation of a Polar® human heart rate monitor for measuring heart rate and heart rate variability in adult dogs under stationary conditions. *Journal of Veterinary Behavior: Clinical Applications and Research*, *7*(4), Article 4. https://doi.org/10.1016/j.jveb.2011.10.006

Kaulfuß, P., & Mills, D. S. (2008). Neophilia in domestic dogs (Canis familiaris) and its implication for studies of dog cognition. *Animal Cognition*, *11*(3), Article 3. https://doi.org/10.1007/s10071-007-0128-x

Kawamori, A., & Matsushima, T. (2012). Sympatric divergence of risk sensitivity and diet menus in three species of tit. *Animal Behaviour*, *84*(4), Article 4. https://doi.org/10.1016/j.anbehav.2012.07.026

King, T., Hemsworth, P. H., & Coleman, G. J. (2003). Fear of novel and startling stimuli in domestic dogs. *Applied Animal Behaviour Science*, *82*(1), Article 1. https://doi.org/10.1016/S0168-1591(03)00040-6

Kirkwood, J. K. (1985). The influence of size on the biology of the dog. *Journal of Small Animal Practice*, *26*(2), Article 2. https://doi.org/10.1111/j.1748-5827.1985.tb02090.x

Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. W., & Blokhuis, H. J. (1999). Coping styles in animals: Current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews*, *23*(7), Article 7. https://doi.org/10.1016/S0149-7634(99)00026-3

Kortekaas, K., & Kotrschal, K. (2019). Does socio-ecology drive differences in alertness between wolves and dogs when resting? *Behavioural Processes*, *166*, 103877. https://doi.org/10.1016/j.beproc.2019.05.024

Kortekaas, K., & Kotrschal, K. (2020). Social Context Influences Resting Physiology in Dogs. *Animals*, *10*(12), Article 12. https://doi.org/10.3390/ani10122214

Kreibig, S. D. (2010). Autonomic nervous system activity in emotion: A review. *Biological Psychology*, *84*(3), Article 3. https://doi.org/10.1016/j.biopsycho.2010.03.010

Kubinyi, E., Pongrácz, P., & Miklósi, Á. (2009). Dog as a model for studying conspecific and heterospecific social learning. *Journal of Veterinary Behavior: Clinical Applications and Research*, *4*(1), Article 1. https://doi.org/10.1016/j.jveb.2008.08.009

Lamb, A. P., Meurs, K. M., & Hamlin, R. L. (2010). Correlation of heart rate to body weight in apparently normal dogs. *Journal of Veterinary Cardiology*, *12*(2), Article 2. https://doi.org/10.1016/j.jvc.2010.04.001

Lenkei, R., Újváry, D., Bakos, V., & Faragó, T. (2020). Adult, intensively socialized wolves show features of attachment behaviour to their handler. *Scientific Reports*, *10*(1), Article 1. https://doi.org/10.1038/s41598-020-74325-0

Luque-Casado, A., Zabala, M., Morales, E., Mateo-March, M., & Sanabria, D. (2013). Cognitive Performance and Heart Rate Variability: The Influence of Fitness Level. *PLoS ONE*, *8*(2), Article 2. https://doi.org/10.1371/journal.pone.0056935

Mariti, C., Ricci, E., Carlone, B., Moore, J. L., Sighieri, C., & Gazzano, A. (2013). Dog attachment to man: A comparison between pet and working dogs. *Journal of Veterinary Behavior*, *8*(3), 135–145. https://doi.org/10.1016/j.jveb.2012.05.006

Maros, K., Dóka, A., & Miklósi, Á. (2008). Behavioural correlation of heart rate changes in family dogs. *Applied Animal Behaviour Science*, *109*(2–4), Article 2–4. https://doi.org/10.1016/j.applanim.2007.03.005

Marshall-Pescini, S., Besserdich, I., Kratz, C., & Range, F. (2016). Exploring Differences in Dogs' and Wolves' Preference for Risk in a Foraging Task. *Frontiers in Psychology*, *7*. https://doi.org/10.3389/fpsyg.2016.01241

Marshall-Pescini, S., Cafazzo, S., Virányi, Z., & Range, F. (2017). Integrating social ecology in explanations of wolf–dog behavioral differences. *Current Opinion in Behavioral Sciences*, *16*, 80–86. https://doi.org/10.1016/j.cobeha.2017.05.002

Marshall-Pescini, S., Virányi, Z., Kubinyi, E., & Range, F. (2017). Motivational Factors Underlying Problem Solving: Comparing Wolf and Dog Puppies' Explorative and Neophobic Behaviors at 5, 6, and 8 Weeks of Age. *Frontiers in Psychology*, *8*. https://doi.org/10.3389/fpsyg.2017.00180

Matuschek, H., Kliegl, R., Vasishth, S., Baayen, H., & Bates, D. (2017). Balancing Type I Error and Power in Linear Mixed Models. *Journal of Memory and Language*, *94*, 305–315. https://doi.org/10.1016/j.jml.2017.01.001

Mech, L. D., & Boitani, L. (2003). *Wolves: Behavior, Ecology, and Conservation*. University of Chicago Press.

Mettke-Hofmann, C., Winkler, H., Hamel, P. B., & Greenberg, R. (2013). Migratory New World Blackbirds (Icterids) Are More Neophobic than Closely Related Resident Icterids. *PLOS ONE*, *8*(2), Article 2. https://doi.org/10.1371/journal.pone.0057565

Mettke-Hofmann, C., Winkler, H., & Leisler, B. (2002). The Significance of Ecological Factors for Exploration and Neophobia in Parrots. *Ethology*, *108*(3), Article 3. https://doi.org/10.1046/j.1439-0310.2002.00773.x

Mohring, B., Angelier, F., Jaatinen, K., Steele, B., Lönnberg, E., & Öst, M. (2022). Drivers of within- and among-individual variation in risk-taking behaviour during reproduction in a long-lived bird. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1983), 20221338. https://doi.org/10.1098/rspb.2022.1338

Moretti, L., Hentrup, M., Kotrschal, K., & Range, F. (2015). The influence of relationships on neophobia and exploration in wolves and dogs. *Animal Behaviour*, *107*(Supplement C), Article Supplement C. https://doi.org/10.1016/j.anbehav.2015.06.008

Mosier, J. E. (1989). Effect of Aging on Body Systems of the Dog. *Veterinary Clinics of North America: Small Animal Practice*, *19*(1), Article 1. https://doi.org/10.1016/S0195-5616(89)50001-9

Nganvongpanit, K., Kongsawasdi, S., Chuatrakoon, B., & Yano, T. (2011). Heart rate change during aquatic exercise in small, medium and large healthy dogs. *Thai Journal of Veterinary Medicine*, *41*, 455–461.

Olsen, S. J. (1985). *Origins of the domestic dog: The fossil record*. University of Arizona Press.

Palmer, R., & Custance, D. (2008). A counterbalanced version of Ainsworth's Strange Situation Procedure reveals secure-base effects in dog–human relationships. *Applied Animal Behaviour Science*, *109*(2), Article 2. https://doi.org/10.1016/j.applanim.2007.04.002

Paul, M., Sen Majumder, S., Sau, S., Nandi, A. K., & Bhadra, A. (2016). High early life mortality in free-ranging dogs is largely influenced by humans. *Scientific Reports*, *6*(1), 19641. https://doi.org/10.1038/srep19641

Porges, S. W. (1995). Orienting in a defensive world: Mammalian modifications of our evolutionary heritage. A Polyvagal Theory. *Psychophysiology*, *32*(4), Article 4. https://doi.org/10.1111/j.1469-8986.1995.tb01213.x

Porges, S. W. (2001). The polyvagal theory: Phylogenetic substrates of a social nervous system. *International Journal of Psychophysiology*, *42*(2), Article 2. https://doi.org/10.1016/S0167-8760(01)00162-3

Porges, S. W. (2003). The Polyvagal Theory: Phylogenetic contributions to social behavior. *Physiology & Behavior*, *79*(3), Article 3. https://doi.org/10.1016/S0031-9384(03)00156-2

Porges, S. W. (2009). The polyvagal theory: New insights into adaptive reactions of the autonomic nervous system. *Cleveland Clinic Journal of Medicine*, *76*(Suppl 2), Article Suppl 2. https://doi.org/10.3949/ccjm.76.s2.17

Pörtl, D., & Jung, C. (2019). Physiological pathways to rapid prosocial evolution. *Biologia Futura*, *70*(2), Article 2. https://doi.org/10.1556/019.70.2019.12

Prato-Previde, E., Spiezio, C., Sabatini, F., & Custance, D. M. (2003). Is the dog-human relationship an attachment bond? An observational study using Ainsworth's strange situation. *Behaviour*, *140*(2), Article 2. https://doi.org/10.1163/156853903321671514

Price, E. O. (1999). Behavioral development in animals undergoing domestication. *Applied Animal Behaviour Science*, *65*(3), Article 3. https://doi.org/10.1016/S0168-1591(99)00087-8

Rajendra Acharya, U., Paul Joseph, K., Kannathal, N., Lim, C. M., & Suri, J. S. (2006). Heart rate variability: A review. *Medical & Biological Engineering & Computing*, *44*(12), Article 12. https://doi.org/10.1007/s11517-006-0119-0

Range, F., & Marshall-Pescini, S. (2022a). Comparing the Behaviour and Cognition of Wolves and Dogs. In F. Range & S. Marshall-Pescini (Eds.), *Wolves and Dogs: Between Myth and Science* (pp. 19–46). Springer International Publishing. https://doi.org/10.1007/978-3-030-98411-3_2

Range, F., & Marshall-Pescini, S. (2022b). Taking confounding factors and life experience seriously. *Trends in Cognitive Sciences*, *26*(9), 730–731. https://doi.org/10.1016/j.tics.2022.06.007

Range, F., & Marshall-Pescini, S. (2022c). *Wolves and Dogs: Between Myth and Science*. Springer International Publishing. https://doi.org/10.1007/978-3-030-98411-3

Range, F., & Virányi, Z. (2011). Development of Gaze Following Abilities in Wolves (Canis Lupus). *PLOS ONE*, *6*(2), Article 2. https://doi.org/10.1371/journal.pone.0016888

Range, F., & Virányi, Z. (2013). Social learning from humans or conspecifics: Differences and similarities between wolves and dogs. *Frontiers in Psychology*, *4*. https://doi.org/10.3389/fpsyg.2013.00868

Range, F., & Virányi, Z. (2014). Wolves Are Better Imitators of Conspecifics than Dogs. *PLOS ONE*, *9*(1), Article 1. https://doi.org/10.1371/journal.pone.0086559

Range, F., & Virányi, Z. (2015). Tracking the evolutionary origins of dog-human cooperation: The "Canine Cooperation Hypothesis." *Frontiers in Psychology*, *5*. https://doi.org/doi.org/10.3389/fpsyg.2014.01582

Rao, A., Range, F., Kadletz, K., Kotrschal, K., & Marshall-Pescini, S. (2018). Food preferences of similarly raised and kept captive dogs and wolves. *PLOS ONE*, *13*(9), Article 9. https://doi.org/10.1371/journal.pone.0203165

Rault, J.-L. (2012). Friends with benefits: Social support and its relevance for farm animal welfare. *Applied Animal Behaviour Science*, *136*(1), Article 1. https://doi.org/10.1016/j.applanim.2011.10.002

Réale, D., Martin, J., Coltman, D. W., Poissant, J., & Festa-Bianchet, M. (2009). Male personality, life-history strategies and reproductive success in a promiscuous mammal. *Journal of Evolutionary Biology*, *22*(8), 1599–1607. https://doi.org/10.1111/j.1420-9101.2009.01781.x

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, *82*(2), Article 2. https://doi.org/10.1111/j.1469-185X.2007.00010.x

Riemer, S., Müller, C., Virányi, Z., Huber, L., & Range, F. (2013). Choice of conflict resolution strategy is linked to sociability in dog puppies. *Applied Animal Behaviour Science*, *149*(1), Article 1. https://doi.org/10.1016/j.applanim.2013.09.006

Rishniw, M., Ljungvall, I., Porciello, F., Häggström, J., & Ohad, D. G. (2012). Sleeping respiratory rates in apparently healthy adult dogs. *Research in Veterinary Science*, *93*(2), Article 2. https://doi.org/10.1016/j.rvsc.2011.12.014

Rosati, A. G., & Hare, B. (2013). Chimpanzees and Bonobos Exhibit Emotional Responses to Decision Outcomes. *PLOS ONE*, *8*(5), e63058. https://doi.org/10.1371/journal.pone.0063058

Schielzeth, H., & Forstmeier, W. (2009). Conclusions beyond support: Overconfident estimates in mixed models. *Behavioral Ecology*, *20*(2), Article 2. https://doi.org/10.1093/beheco/arn145

Schöberl, I., Kortekaas, K., Schöberl, F. F., & Kotrschal, K. (2015). Algorithm-supported visual error correction (AVEC) of heart rate measurements in dogs, Canis lupus familiaris. *Behavior Research Methods*, *47*(4), Article 4. https://doi.org/10.3758/s13428-014-0546-z

Seltmann, M. W., Öst, M., Jaatinen, K., Atkinson, S., Mashburn, K., & Hollmén, T. (2012). Stress responsiveness, age and body condition interactively affect flight initiation distance in breeding female eiders. *Animal Behaviour*, *84*(4), 889–896. https://doi.org/10.1016/j.anbehav.2012.07.012

Sinn, D. L., Gosling, S. D., & Moltschaniwskyj, N. A. (2008). Development of shy/bold behaviour in squid: Context-specific phenotypes associated with developmental plasticity. *Animal Behaviour*, *75*(2), 433–442. https://doi.org/10.1016/j.anbehav.2007.05.008

Solomon, J., Beetz, A., Schöberl, I., Gee, N., & Kotrschal, K. (2019). Attachment security in companion dogs: Adaptation of Ainsworth's strange situation and classification procedures to dogs and their human caregivers. *Attachment & Human Development*, *21*(4), Article 4. https://doi.org/10.1080/14616734.2018.1517812

Stahler, D. R., Smith, D. W., & Guernsey, D. S. (2006). Foraging and Feeding Ecology of the Gray Wolf (Canis lupus): Lessons from Yellowstone National Park, Wyoming, USA. *The Journal of Nutrition*, *136*(7), Article 7. https://doi.org/10.1093/jn/136.7.1923S

Starling, M. J., Branson, N., Thomson, P. C., & McGreevy, P. D. (2013). "Boldness" in the domestic dog differs among breeds and breed groups. *Behavioural Processes*, *97*, 53–62. https://doi.org/10.1016/j.beproc.2013.04.008

Strasser, A., Simunek, M., Seiser, M., & Hofecker, G. (1997). Age-dependent Changes in Cardiovascular and Metabolic Responses to Exercise in Beagle Dogs. *Journal of Veterinary Medicine Series A*, *44*(1–10), Article 1–10. https://doi.org/10.1111/j.1439-0442.1997.tb01130.x

Sutter, N. B., Bustamante, C. D., Chase, K., Gray, M. M., Zhao, K., Zhu, L., Padhukasahasram, B., Karlins, E., Davis, S., Jones, P. G., Quignon, P., Johnson, G. S., Parker, H. G., Fretwell, N., Mosher, D. S., Lawler, D. F., Satyaraj, E., Nordborg, M., Lark, K. G., … Ostrander, E. A. (2007). A Single IGF1 Allele Is a Major Determinant of Small Size in Dogs. *Science*, *316*(5821), Article 5821. https://doi.org/10.1126/science.1137045

Svartberg, K. (2005). A comparison of behaviour in test and in everyday life: Evidence of three consistent boldness-related personality traits in dogs. *Applied Animal Behaviour Science*, *91*(1), 103–128. https://doi.org/10.1016/j.applanim.2004.08.030

Svartberg, K., & Forkman, B. (2002). Personality traits in the domestic dog (Canis familiaris). *Applied Animal Behaviour Science*, *79*(2), Article 2. https://doi.org/10.1016/S0168-1591(02)00121-1

Therneau, T. M. (2015). *Mixed Effects Cox Models*. R package version, 2(3). https://cran.hafro.is/web/packages/coxme/coxme.pdf

Therneau, T. M., & Grambsch, P. M. (2000). The Cox Model. In T. M. Therneau & P. M. Grambsch (Eds.), *Modeling Survival Data: Extending the Cox Model* (pp. 39–77). Springer. https://doi.org/10.1007/978-1-4757-3294-8_3

Topál, J., Miklósi, Á., Csányi, V., & Dóka, A. (1998). Attachment behavior in dogs (Canis familiaris): A new application of Ainsworth's (1969) Strange Situation Test. *Journal of Comparative Psychology*, *112*(3), Article 3. https://doi.org/10.1037/0735-7036.112.3.219

Trimpop, R. M. (1994). *The Psychology of Risk Taking Behavior*. Elsevier.

Trut, L. N., Plyusnina, I. Z., & Oskina, I. N. (2004). An Experiment on Fox Domestication and Debatable Issues of Evolution of the Dog. *Russian Journal of Genetics*, *40*(6), Article 6. https://doi.org/10.1023/B:RUGE.0000033312.92773.c1

Udell, M. A. R. (2015). When dogs look back: Inhibition of independent problem-solving behaviour in domestic dogs (Canis lupus familiaris) compared with wolves (Canis lupus). *Biology Letters*, *11*(9), 20150489. https://doi.org/10.1098/rsbl.2015.0489

Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2010). What did domestication do to dogs? A new account of dogs' sensitivity to human actions. *Biological Reviews*, *85*(2), 327–345. https://doi.org/10.1111/j.1469-185X.2009.00104.x

Ujfalussy, D. J., Kurys, A., Kubinyi, E., Gácsi, M., & Virányi, Z. (2017). Differences in greeting behaviour towards humans with varying levels of familiarity in hand-reared wolves (Canis lupus). *Royal Society Open Science*, *4*(6), Article 6. https://doi.org/10.1098/rsos.160956

Valsecchi, P., Previde, E. P., Accorsi, P. A., & Fallani, G. (2010). Development of the attachment bond in guide dogs. *Applied Animal Behaviour Science*, *123*(1), Article 1. https://doi.org/10.1016/j.applanim.2009.12.012

van Oers, K., Klunder, M., & Drent, P. J. (2005). Context dependence of personalities: Risk-taking behavior in a social and a nonsocial situation. *Behavioral Ecology*, *16*(4), Article 4. https://doi.org/10.1093/beheco/ari045

Vasconcellos, A. da S., Virányi, Z., Range, F., Ades, C., Scheidegger, J. K., Möstl, E., & Kotrschal, K. (2016). Training Reduces Stress in Human-Socialised Wolves to the Same Degree as in Dogs. *PLOS ONE*, *11*(9), Article 9. https://doi.org/10.1371/journal.pone.0162389

Visser, E. K., van Reenen, C. G., van der Werf, J. T. N., Schilder, M. B. H., Knaap, J. H., Barneveld, A., & Blokhuis, H. J. (2002). Heart rate and heart rate variability during a novel object test and a handling test in young horses. *Physiology & Behavior*, *76*(2), Article 2. https://doi.org/10.1016/S0031-9384(02)00698-4

von Borell, E., Langbein, J., Després, G., Hansen, S., Leterrier, C., Marchant-Forde, J., Marchant-Forde, R., Minero, M., Mohr, E., Prunier, A., Valance, D., & Veissier, I. (2007). Heart rate variability as a measure of autonomic regulation of cardiac activity for assessing stress and welfare in farm animals—A review. *Physiology & Behavior*, *92*(3), Article 3. https://doi.org/10.1016/j.physbeh.2007.01.007

vonHoldt, B. M., Shuldiner, E., Koch, I. J., Kartzinel, R. Y., Hogan, A., Brubaker, L., Wanser, S., Stahler, D., Wynne, C. D. L., Ostrander, E. A., Sinsheimer, J. S., & Udell, M. A. R. (2017). Structural variants in genes associated with human Williams-Beuren syndrome underlie stereotypical hypersociability in domestic dogs. *Science Advances*, *3*(7), Article 7. https://doi.org/10.1126/sciadv.1700398

Walker, R., Fisher, J., & Neville, P. (1997). The treatment of phobias in the dog. *Applied Animal Behaviour Science*, *52*(3), Article 3. https://doi.org/10.1016/S0168-1591(96)01128-8

Wilkins, A. S. (2017). Revisiting two hypotheses on the "domestication syndrome" in light of genomic data. *Vavilov Journal of Genetics and Breeding*, *21*(4), Article 4. https://doi.org/10.18699/VJ17.262

Wilson, A. D. M., Whattam, E. M., Bennett, R., Visanuvimol, L., Lauzon, C., & Bertram, S. M. (2010). Behavioral correlations across activity, mating, exploration, aggression, and antipredator contexts in the European house cricket, Acheta domesticus. *Behavioral Ecology and Sociobiology*, *64*(5), 703–715. https://doi.org/10.1007/s00265-009-0888-1

Chapter 4|

Domestication and social environment modulate fear responses in young chickens

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HJJ, KKot, and PJ designed the experiments. HJJ collected the data and ran the statistical analyses. GJ coded the data. HJJ and GJ wrote the article. KKot and PJ revised the article.

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Domestication and social environment modulate fear responses in young chickens

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ABSTRACT

Domesticated species differ from their wild ancestors in a mosaic of traits. Classical domestication theories agree that reactivity to fear and stress is one of the main traits affected. Domesticated species are expected to be less fear and stress prone to than their wild counterparts. To test this hypothesis, we compared the behavioural responses of White Leghorn (WL) chicks to their wild counterparts, Red Junglefowl (RJF) chicks in risk-taking situations. In order to obtain food, the chicks faced an unknown and potentially harmful object at the presence or absence of a social partner. We found that according to our predictions, RJF were more stressed and fearful of the object than the WL. Still, RJF were more explorative than WL. Additionally, the presence of a social partner reduced the fear response in both, but had a stronger effect on RJF. Finally, WL were more food orientated than the RJF. Our results confirmed classical domestication hypotheses of downregulation of the stress system and importance of the social partner in domesticated farm chicken.

1. Introduction

Any behaviour with a perceived uncertainty about its outcomes, its possible benefit or cost is defined as risk-taking behaviour (Trimpop, 1994). Situations subjectively perceived as risky could trigger various responses such as fear and stress and the behavioural expressions thereof. However, the response itself could vary between subjects depending on a certain number of factors. Indeed, responses to stressors depend on the stressor's perceived severity, as well as the individuals' resilience to stress and ability to quickly recover after a stressor (Ross et al., 2020). Individual resilience is subject to several components such as genetics and ontogeny as well as external effects such as social context and support (Biggio et al., 2019). It seems that feeding ecology also plays a role in how risk-prone a species is (Kawamori and Matsushima, 2012; Marshall-Pescini et al., 2017; Mettke-Hofmann et al., 2002). In addition, personality traits like boldness have been shown to influence risk-taking in different species (mice: (Błaszczyk et al., 2000); cichlid fishes: (Brick and Jakobsson, 2002)), as well as social environment (Cimarelli et al., 2021; van Oers et al., 2005).

In fact, in numerous social species, being among other conspecifics helps individuals to cope with stressful situations (Rault, 2012). This phenomenon is known as (emotional) social support. As a response to environmental challenges, sociality is crucial in these species (Wilson, 2000). Studies have shown that farm animals, in response to stress, will seek out social interaction (Epley, 1974; Armario et al., 1983; Geverink et al., 1998; Marin et al., 2001; Ishiwata et al., 2007; Rault, 2012), a phenomenon also observed in wild populations (Koolhaas et al., 1999). However, domesticated animals do not appear to be as easily agitated by potential stressors as their wild relatives. Such, domestication could also be a factor impacting response to stressors and risk-taking behaviours.

Indeed, domestication has altered various animal characteristics, including behavioural responses to various stimuli, and it is shown that even varying degrees of selection pressures linked to domestication, results in equivalent effects in hen laying behaviour (Darwin, 1859; Dudde et al., 2018; Wilkins et al., 2014). Domestic animals must tolerate human handling and be able to reproduce in captivity, which is an important step in the early stages of domestication, (Price, 2002). They must cope with the environment humans provide, hence, reduced sensitivity and increased adaptability to environmental changes would be some of the most important behavioural changes during

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domestication (Price, 2002). Indeed, reduced stress susceptibility as a trait seems to be recurring in the so-called domesticated phenotype (Künzl and Sachser, 1999; Dwyer, 2004; Lindqvist and Jensen, 2009; Douxfils et al., 2011; Solberg et al., 2020). Domesticated animals often display a reduced stress response when compared to wild conspecifics and possibly this could be attributed to artificial selection on reduced fearfulness (Künzl and Sachser, 1999; Trut et al., 2009; Moretti et al., 2015). Additionally, domestication may have altered the stress buffering effects of social support as humans have selected for tameness and low fear animals. So, the ability to handle and recover from stressful situations might depend less on social support and social buffer in domesticated animals (Wirén et al., 2013).

However, it is not necessarily so, since experimental comparisons between equally raised and kept wolves and dogs revealed that, contrary to popular belief, dogs were less relaxed during resting and sleeping (Kortekaas and Kotrschal, 2019), that they did not differ much in their diurnal time budgets (Jean-Joseph et al., 2022) suggesting that wolves were not really more responsive to environmental stimuli than dogs.

The chicken is a good model to investigate domestication, being the most numerous (i.e., higher number of individuals) domestic species worldwide today (Wang et al., 2020; Lawler, 2016). Their wild ancestor is the Red Junglefowl (RJF), a bird native to south and south-east Asia (Abdulwahid and Zhao, 2022). RJF are shy in the wild and hide in shrubs and thickets, only venturing out in small clearings to forage, avoiding humans. As social birds, RJF lives either in small families or in larger mixed groups (Schütz et al., 2001; Siegel et al., 1992). Domestic chickens are also social; however, the environment humans provide them differs from the RJF natural environment both socially and physically. Any disturbance in their social environment can cause damaging stress in chickens and may affect their cognition as well as health and productivity (Duncan et al., 1986; Jones and Harvey, 1987; Mills and Faure, 1990; Mendl, 1999). For example, when a chick is put in an open and novel area, its two main goals would be to reinstate contact with conspecifics and to avoid detection by potential predators (Bryan Jones and Merry, 1988). The White Leghorns (WL), a common breed selected for eggs production, have not lost these behaviours, but have become less fearful than their wild relatives through the selection on increased production. Indeed, in poultry breeding and husbandry, anti-predator behaviours have not been a major selection factor as the predation pressure has been reduced, and the energy saved in this domain is channelled into reproduction (Lindqvist and Jensen, 2009; Schütz et al., 2001).

Response to stress is an important parameter, determining how adaptive a species is and how well it will cope with its environment. In domesticated chickens like WL, the meaning of, and the responsiveness to, stressors was modified by selection for production. In the present study, we compared wild chickens (i.e., RJF) and domestic ones (i.e., WL) with respect to their response to a stressor and how the social environment would modulate this response. We first determined the risk-taking behaviour of young chicks facing a potentially frightening object when obtaining food. Secondly, we compared RJF chicks to domesticated WL chicks to assess how domestication has changed risk-taking behaviour. In agreement with current domestication hypotheses, we expected the domesticated chicks to be less fearful and less stressed, as well as being generally more food-orientated under these conditions than wild chicks. Finally, we assessed how environment - non-social or social - impact risk-taking behaviours in both types of chickens. We predict that the presence of a social partner would affect both wild and domesticated chicks but that the effect would be less in domesticated chicks as domestication would have relaxed the need for a partner to overcome stress and fear.

2. Material and methods

2.1. Ethical note

The experiments were carried out under the ethical licence from Linköping Animal Ethics Committee, licence no. 14916–2018. All procedures were carried out according to the protocol.

2.2. Subjects

We tested young (16 days old) unsexed chicks from two different breeding line: the Red Junglefowls (RJF; *Gallus gallus*), the ancestor of domestic chicken and a domestic breed of chicken, the White Leghorn (WL; *Gallus gallus domesticus*) originally selected and bred for egg production. The RJF (n = 20) were hatched at Linköping University, Sweden, from a captive pedigree-bred population. This population is kept at the facility for ongoing research (see details in Campler et al., 2009). The WL (n = 20) from the Lohmann LSL strain (Lohmann Tierzucht, Germany) were also hatched at Linköping University. The parental lines of the RJF were kept at the breeding facility of Linköping University, while the WL chicks came from commercial lines. After egg collection, the eggs from each of the two breeds were kept in the same type of incubator with the setting 37.8 °C and 5% relative humidity. The eggs were transferred separately on incubation day 18 to a hatcher (Masalles Type 25 HS), which was set to 37.5 °C and 65% relative humidity. The hatching happened in darkness, in groups. After hatching, the chicks were taken out of the incubator, weighed, wing-tagged and vaccinated. Throughout the entire experiment, RFJ and WL were kept separated in identical pens equipped with wood chips, food and water and a heat lamp. From hatching they were kept in a pen (70 cm × 70 cm x 160 cm) in the hatching facility. The room had a 12-hour light/dark schedule and temperature of 20°C. Three days before the test the chicks were moved to the test room and placed in in two identical pens (0,7 m x 0,68 m x 0,57 m, daylight from 07:00 AM to 07:00 PM, temperature: 21°C). The birds were kept on wood chips and given *ad libitum* access to food and water, as well as heating lamps, throughout the experiment.

2.3. Test arena

The test arena was a circular pen (diameter 1 m) made of cardboard, with a cardboard wall (25 cm long x 20 cm high, see Fig. 1, D) providing a possible hiding place in the middle of the arena. The novel object was a desk fan (diameter 10 cm, see Fig. 1, A) with five three cm long pieces of red ribbon attached to it. The fan could be turned on remotely, which would make the ribbons move in an unpredictable fashion and blow air toward the subject. It was placed against the edge of the arena facing the

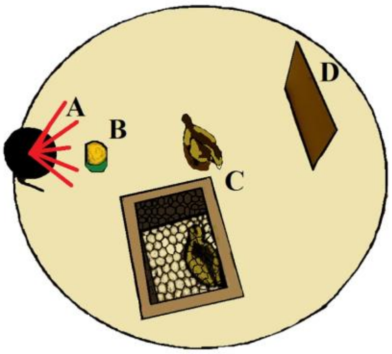

Fig. 1. Drawing of the test arena. A: the fan and ribbons, B: the feeder, C: the social box, D: the wall.

Table 1
Ethogram of behaviours recorded during the social and non-social test in chicks of Red Junglefowl and White Leghorn.

Behaviours	Description
Agitated	Standing or walking, with eyes opened and A) neck stretched with, even doing rapid heads-flicks from side to side with focus on the source of agitation. B) Escape-attempt, the bird tries to escape from the test arena by jumping or making fly attempts towards the roof
Alert	Stands (legs erect) or walks 3 or more steps, with open eyes, attending to the surrounding or Sits (legs bent, body touches ground) with open eyes, attending to the surroundings
Feeding	Eating from food container + Distinct pecks at supplied feed
Freeze	Stiff posture, stand, sit or lie motionless, vigilant, open eyes
Object investigation	Head close to the object of interest, eyes focusing on the object. Being at least one body length away from the object, the subject can peck at object of interest, including fittings in environment and use its beak to lift, move or otherwise manipulate object
Ground Investigation/foraging	Walking or standing with head close to ground (below back), eyes focusing on ground items. Subject can also scratch and peck at the ground. Subject's eyes focusing on feed or other edible objects in case of foraging
Relaxed	Standing (legs erect) with reduced attention, eyes may be partly closed, neck short, no alert head movements or Sitting (legs bent) with reduced attention, eyes may be partly closed, neck short, no alert head movements, performing grooming (used beek to trim and arrange feathers, used feet to scratch, clean and preen feathers)
Locomotion	Two or more steps in any direction, including walking and running.
Latency to peck at the food	Time until the subject pecks at the food for the first time
Latency to move	Time until the subject takes a first step in any direction from the moment light turns on
Latency to approach object	Time until the subject approach the scary object
Latency to approach conspecific	Only during the social condition. Time until the subject approach the social partner in the box, e.g., go in front of the open side of the box with maximum of one body length away from the wire mesh.
Proximity to food	Time spent in proximity (10 cm or less) of the food
Proximity to conspecific	Time spent in proximity of the conspecific

inner part of it. A feeder filled with corn was put between the inner wall and the novel object at a distance of 10 cm. A cage that could contain a social partner (20 cm × 17 cm x 15 cm, see Fig. 1, C) was made out of cardboard on three sides and of fence on the top and the back side. Hence, the social partner could not see the novel object but could still see and interact with the tested subject on one side of the box. For an overview of the arena, see Fig. 1.

2.4. *Test protocol*

One week before the first test, all the subjects were fed once a day with corn in addition to their usual food to habituate them to the food reward to be used during the test. Two days before the test, all the subjects were put into the empty arena (without food or novel object) in a group of 10 individuals for 15 min to get habituated to the arena. The day before the test all subjects were individually put in the empty arena for 5 min to get habituated to being alone in the arena. During testing, the chick was either on its own in the arena, or together with a companion from the same group that was placed in the cage in the arena.

For testing, one chick was randomly taken out of its pen. The bird was identified by its wing-tag and weighed, then the lights of the test room were turned off and the chick was placed in the middle of the arena while in darkness. After two minutes the lights were turned on, and the test started and lasted five minutes. After one minute of the light period, the novel object (i.e., the fan with ribbons) was turned on for 30 seconds then turned off again for the remaining period of the test (i.e., three minutes and 30 seconds). At the end of the test the chick was removed and placed back in its pen with the other already tested birds. All chicks were tested twice, once in the social condition and once in the non-social condition. The order of the conditions was counterbalanced between the birds, so half of them started with the social condition and the other half started with the non-social one. It is crucial to note that even with counterbalanced conditions between the birds, each animal encountered the novel object twice, with true novelty presented only during the initial trial. The tests were recorded with a camera (GoPro Hero5) placed on the top of the arena. From the videos, we coded the duration of the behaviours outlined in Table 1, as well as the latency to move, to approach the object, and to feed. Moreover, we measured the time the chicks spent in proximity to the food. In the social condition, we also measured the latency to approach the social partner and the time spent in its proximity.

2.5. *Statistical analyses*

We fitted the models in R (version 4.0.5; R Core Team, 2021) using the package lme4 (Bates et al., 2014), function lmer for the linear mixed model (LME, (Baayen, 2008)) and the packages survival (3.2–10) and coxme (2.2–16) for the survival model used to analyse latencies. Species (RJF or WL), condition of the test (social or non-social) and their interaction were included as fixed factors. We added order of the condition (social first vs non-social first) as a control factor. Moreover, we added the body mass of the birds as a control factor since it is one of the most visible differences between the RJF and WL chicks. Furthermore, subject identity was included as a random factor to account for individual differences and subjects being tested twice. Body mass was z-transformed (to a mean of zero and a standard deviation of one) to facilitate model computation.

For each model, we visually inspected qqplots and the residuals plotted against fitted values. Both indicated no violation of the normal distribution and homogeneity assumptions. We checked for model stability by excluding subjects one at a time from the data and comparing the model estimates derived for these subsets of the data with those derived for the full data set. We inspected Variance Inflation Factors (VIF, (Field, 2005) using the function VIF of the R-package car (Fox and Weisberg, 2018), applied to a standard linear model excluding the random effects and interactions. This revealed that species and body mass were collinear with a VIF of 42.77 and 48.16, respectively. However, there was considerable variation of body mass within both species and, hence, the results obtained for these two predictors should not be distorted by collinearity among them.

To reduce the risk of cryptic multiple testing and keep type I error rate at the nominal level of 0.05 (Forstmeier and Schielzeth, 2011) we tested the significance of the full model as compared to the null model (comprising only body mass, order of the condition and the random effect) by means of a likelihood ratio test (R function anova with argument test set to "Chisq"; (Dobson and Barnett, 2018). To allow for a likelihood ratio test we fitted the models using maximum likelihood (rather than Restricted Maximum Likelihood; (Bolker et al., 2009). *P*-values for the individual effects were based on likelihood ratio tests comparing the full with the respective reduced models (Barr et al., 2013); R function drop1).

Moreover, we tested whether the time spent in proximity of a social partner differed between RJF and WL. To this end, we followed the procedure described above and we fitted a model comprising species as a fixed effect factor, body mass and order of the condition as control factor

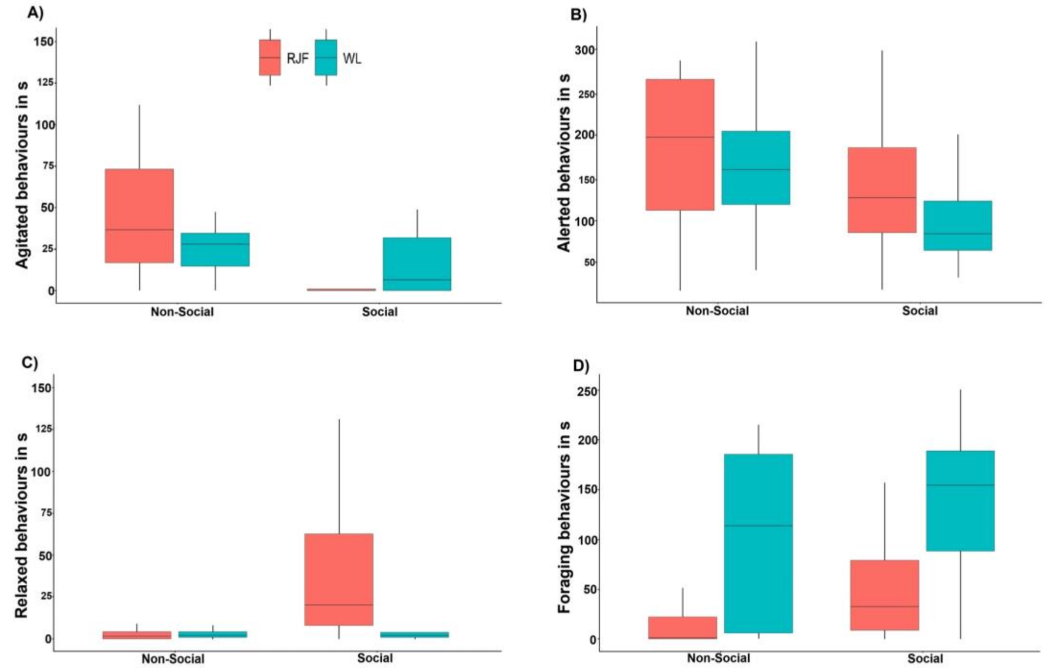

Fig. 2. Duration in seconds of the different behaviours of Red Junglefowl (RJF) and White Leghorn (WL) according to the condition of the 5 min test, the boxplots show median values ± one quartile and the maximum and minimum range. The condition was either non-social, or social. A) Agitated Behaviour. B) Alert Behaviour. C) Relaxed Behaviour. D) Foraging behaviour.

and the identity of the social partner as a random factor.

Furthermore, we tested whether the latency to approach the scary object, the latency to peck the corn and the latency to first move at the beginning of the test, were affected by species (RJF or WL) and condition of the test (social, non-social). These three response variables (latency to approach object, latency to move, latency to peck) were analysed in separate mixed cox regression models. For each response variable, we included the two-way interaction with species and condition. To control for the effect of treatment order, we included the order in which the subject passed the tests as a fixed effect. The body mass of the chicks on the days of the test was also included as a control factor. Moreover, subject identity was included as a random factor to account for individual differences. Additionally, we tested whether species of the subject affected their response to the social condition. We fitted a mixed cox regression model with latency to approach conspecific as responses variable. Species, order of treatment and weight were included as fixed factors. Identity of the subject was included as a random factor.

The sample size for most of these models was 79 observations made on 40 individuals (20 RJF, 20 WL). One data point was missing due to a technical issue during recording (one WL in social condition). The models concerning the proximity to the social partner and the latency to approach the social partner had a sample size of 39 data points.

3. Results

All tested chicks but two (one RJF and one WL) contacted the companion during the social test. The different behaviours according to the condition of the test is given in Fig. 2.

3.1. *Agitated behaviours*

In the non-social condition the RJF were more agitated than the WL, however in the social condition it was the reverse, RJF were less agitated than WL (Fig. 1A). Overall, the full model was significant compared to the null model (likelihood ratio test: $\chi2 = 27.22$, df = 3, $P < 0.001$), i.e., species, conditions, or their interaction, body mass and order of the condition affected how agitated the chicks behaved. More specifically, the interaction between species and conditions was significant indicating that both species and conditions had an effect on how agitated the chicks were ($\chi2 = 7.02$, df = 2, $P = 0.008$; Table S1; Fig. 1A).

3.2. *Alert behaviours*

RJF showed more alert behaviour than WL in both the social and non-social condition, and both breeds showed less alert behaviour in the social condition (Fig. 2B). Overall, the full model was significant compared to the null model (likelihood ratio test: $\chi2 = 15.28$, df = 3, $P < 0.001$), i.e., species, conditions, or their interaction, body mass and order of the condition had an effect on the alertness of the chicks. However, since the interaction between species and condition was not significant (likelihood ratio test: $\chi2 = 0.31$, df = 1, $P = 0.5$), we removed it from the model to explore the significance of the factors species (WL or RJF) and conditions (social or non-social) separately. Conditions was significant ($\chi2 = 14.52$, df = 1, $P < 0.001$; Table S2; Fig. 2B).

3.3. *Relaxed behaviours*

WL and RJF showed the same number of relaxed behaviours in the non-social condition. However, in the presence of a partner, RJF showed

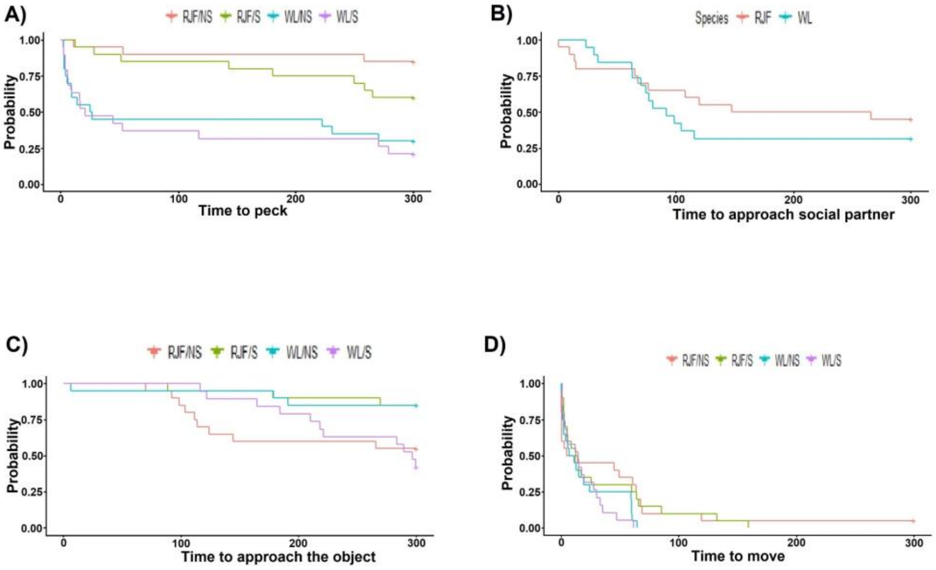

Fig. 3. The latency to A) to peck at the food, B) to approach the social partner, C) to approach the object and D) to move, during the 5 min test. Both species, Red Junglefowl (RJF) and White Leghorn (WL) got tested once with each condition non-social (RJF = RJF/NS, WL = WL/NS) and social (RJF = RJF/S, WL = WL/S).

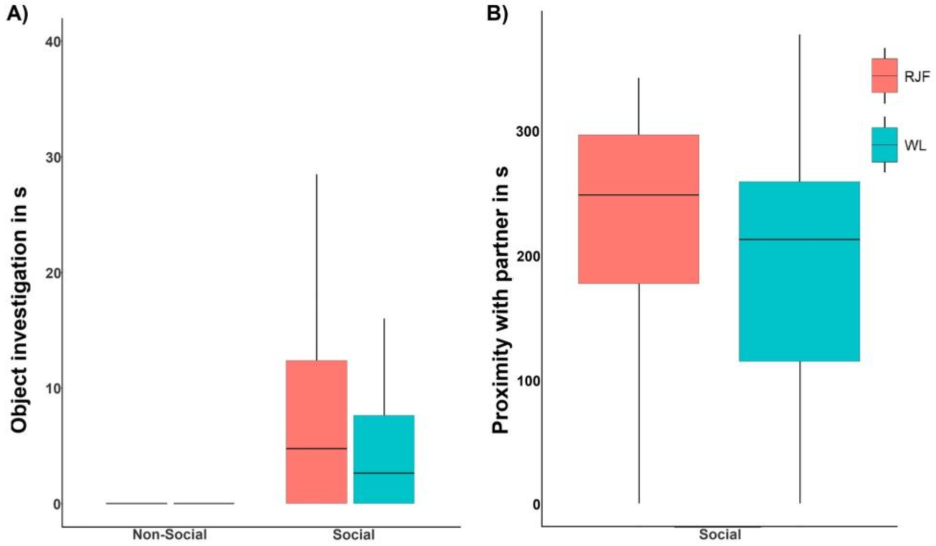

Fig. 4. Duration in seconds of different behaviours displayed by White Leghorn (WL) and Red Junglefowl (RJF), during the 5 min test. The boxplots show median values ± one quartile and the min – max range. A) Object investigation according to the conditions of the test. B) Proximity with the social partner during the social condition.

an increase of relaxed behaviours whereas WL did not (Fig. 2C). Overall, the full model was significant compared to the null model (likelihood ratio test: $\chi2 = 17.20$, df = 3, $P < 0.001$), i.e., species, conditions, or their interaction, body mass and order of the condition had an effect on the relaxation of the chicks. More specifically, the interaction between species and conditions was significant ($\chi2 = 6.92$, df = 1, $P = 0.008$; Table S3; Fig. 2C).

3.4. Foraging, proximity and latency to the food

Overall, WL reached the food earlier than RJF. Additionally, the social condition had a similar effect on both RJF and WL, both were faster to feed when a partner was present. Furthermore, WL spent more time foraging than RJF in both the social and the non-social condition, and both breeds spent more time foraging in the social than the non-social condition (Fig. 2D). However, there was no significant difference in the time the RJF and WL spent in proximity to the food (likelihood ratio test:$\chi2 = 4.95$, df = 0, $P > 0.1$). Overall, the full model was significant compared to the null model (likelihood ratio test: $\chi2 = 10.47$, df = 3, $P < 0.05$), i.e., species, conditions, or their interaction, body mass and order of the condition had an effect on the foraging behaviours of the chicks. However, since the interaction between species and condition was not significant (likelihood ratio test: $\chi2 = 0.30$, df = 1, $P = 0.5$), we removed it from the model to explore the significance of the factors species and conditions separately. Conditions was significant ($\chi2 = 6.79$, df = 1, $P < 0.01$; Table S4, Fig. 2D), as well as body mass ($\chi2 = 20.68$, df = 1, $P < 0.001$) and order of the conditions ($\chi2 = 4.20$ b, df = 1, $P < 0.05$). The delay to reach the food was also different (likelihood ratio test: $\chi2 = 24.95$, df = 3, $P < 0.001$). More specifically, there was an effect of species ($z = 3.88$, $P < 0.001$), conditions ($z = 2.13$, $P < 0.05$) and order of the conditions ($z = 3.52$, $P < 0.001$; Table S5; Fig. 3A) on the delay to reach the food.

3.5. *Object investigation & latency to approach it*

In the social condition, WL and RJF behaved in a similar way and spend more time investigating the object than in the non-social condition (Fig. 4A). However, condition had an opposite effect on the latencies to approach the object. Indeed, in the social condition RJF approached the object later than in the non-social condition whereas in the social condition WL approached the object sooner than in the non-social condition. Additionally, more WL choose to investigate the object: more than 50% choose to do so whereas less than 50% of the RJF investigated the object (Fig. 3C). Overall, the full model was significant compared to the null model (likelihood ratio test: $\chi2 = 9.28$, df = 3, $P < 0.05$), i.e., species, conditions, or their interaction, body mass and order of the condition had an effect on the agitation of the chicks. However, since the interaction between species and condition was not significant (likelihood ratio test: $\chi2 = 1.125$, df = 1, $P > 0.5$), we removed it from the model to explore the significance of the factors species and conditions separately. Condition was significant ($\chi2 = 7.282$, df = 1, $P = 0.007$; Table S6; Fig. 4A), and moreover, latencies to approach the object differed between the breeds (likelihood ratio test: $\chi2 = 12.50$, df = 3, $P < 0.005$), indeed the interaction between species and condition was significant ($z = 3.27$, $P < 0.001$, Table S7; Fig. 3C).

3.6. *Proximity to and latency to approach the social partner*

RJF spent more time in proximity of their partner than WL. However, there was no significant difference in the latency to approach the social partner (likelihood ratio test: $\chi2 = 1.17$, df = 3, $P > 0.05$; Fig. 3B). Overall, the full model was significant compared to the null model (likelihood ratio test: $\chi2 = 4.68$, df = 1, $P < 0.05$), i.e., species, body mass and order of the conditions had an effect on the time the chicks spent in proximity of their social partner. More specifically, species ($\chi2 = 4.68$, df = 1, $P < 0.05$) and body mass ($\chi2 = 4.07$, df = 1, $P < 0.05$; Table S8; Fig. 4B) were significant.

3.7. *Locomotion and latency to first move*

There was no significant difference between RJF and WL with respect to overall locomotion (likelihood ratio test: $\chi2 = 3.24$, df = 3, $P > 0.05$) or with respect to latency to take the first step at the beginning of the test ($\chi2 = 0.89$, df = 4, $P > 0.05$; Fig. 3D).

4. Discussion

We found evidence supporting the domestication hypothesis, since the domesticated White Leghorn (WL) chicks showed less agitated and less alerted behaviours than their wild-type counterparts, the Red Junglefowl (RJF). Additionally, WL were faster to reach the food than RJF and spent more time foraging. But the wild chicks were more investigative than domesticated chicks, they approached the novel object sooner and spent more time in its proximity and also seemed more socially interested than WL as they spent more time near their partner and displayed more relaxed behaviours than WL in the social condition. The WL chicks foraged more and spent more time in close proximity to food. RJF, on the other hand, spent more time near their conspecific under the social condition, and they also started earlier to groom and groomed more. Grooming was one behaviour categorized as a relaxed behaviour in our study, therefore RJF appeared to be more relaxed than WL in our analysis. However, this could be deceptive, as we do not know the actual experience and emotional state (stressed versus relaxed) of the WL chicks while they were feeding versus the RJF while they were grooming.

These results are in agreement with our prediction and consistent with previous observations in RJF (Schütz et al., 2002; Schütz et al., 2001). Selection for traits such as egg production, sexual maturity, growth and food intake, has shown to be genetically linked to fear-related behaviour (Schütz et al., 2004). Moreover, our results align with previous findings within other species. Indeed, other studies on domesticated versus their wild ancestor has shown that stress susceptibility has changed through the domestication. For example, dogs were less neophobic than wolves in a novel object test (Moretti et al., 2015). Additionally, consistent with what we observed in our experiment, wolves were more investigative than dogs (Marshall-Pescini et al., 2017). In addition, rather than finding clear differences between wolves and dog's alertness at rest, Jean-Joseph and colleagues found differences based on the social context during rest (Jean-Joseph et al., 2020).

More in line with our results, Künzl and Sachser (1999) found that domestic guinea pigs were generally less alert than wild cavies. They concluded that lower responsiveness and stress levels are physiological mechanisms permitting domesticated animals to adapt to man-made environment. This decrease in vigilance and receptivity to environmental change is one of the phenotypic traits shared by most, if not all domesticated animals (Price, 1984). Rats selected for high and low anxiety-related behaviour showed significant differences in response to stressors such as emotional defeat and navigating an unfamiliar maze (Liebsch et al., 1998). Domestication might also interfere with animals' personality traits, such as boldness (Agnvall et al., 2015); in sticklebacks (*Gasterosteus aculeatus*), for example, bolder individuals were shown to display greater initiative and be to be less responsive to their social partners (Harcourt et al., 2009). In quail, a behavioural experiment on two selection lines for high or low stress responses (Satterlee et al., 2000) showed that this resulted in significant differences in their responsiveness to long-term social and physical environmental stress. In quail, a comparison between two selection lines for either low or high stress showed that the high stress line expressed more fear and had greater adrenocortical responsiveness to an immobility test, as well as exposure to a novel environment (Jones et al., 1992).

In agreement with our prediction, RJF seemed to be more socially motivated than WL. RFJ individuals indeed, tended to spend more time with their conspecific, when provided with one, which is in accordance with previous results (Väisänen and Jensen, 2003). The potential social support by a companion bird appeared particularly important for the wild-type birds, since the RJF chicks in our study showed a more than five-fold increase of observed Relaxed behaviour with a conspecific as compared to when they were alone, while WL only increased their Relaxed behaviour by just slightly more than 50%. Very likely, domestication is the main reason for this difference. It is possible that the WL breeds' features such as growth, feed intake and reduced fear of humans, increases their propensity to prioritize food above seeking safety. This is in line with previous studies, where RJF bred for low fear of humans (increased tameness as a proxy for early domestication), indeed, showed higher frequency of separating themselves from their group, compared to RJF selected for high fear of humans (Gjøen and Jensen, 2021).

Interbreed genetic variability in social responses has been found to exist already in four-day-old domestic chicks of genetically isolated breeds (Versace et al., 2021). In other social species also, a social companion reduces behavioural and physiological responses during a stressful event or facilitates faster recovery. In wolves and dogs, for example, the presence of a social partner or the entire pack increased investigation of a novel object (Moretti et al., 2015). Additionally, wolves and dogs rested more and were more relaxed in presence of their pack members (Jean-Joseph et al., 2020; Kortekaas and Kotrschal, 2020). Additionally, dogs were also more responsive to the presence of familiar humans than wolves during rest and their day-to-day life (Jean-Joseph et al., 2020, 2022). In horses, the effect of a social buffer depended on the stimulus delivered, but not on the familiarity status of the partner (Ricci-Bonot et al., 2021). Horses which are highly social domesticated animals, seemed to prefer any conspecifics, familiar or not to loneliness.

Also, in line with previous literature, WL fed more and more readily in our experiments than RJF, which is consistent with their heavier body mass and faster growth rate (Väisänen and Jensen, 2003; Schütz and Jensen, 2001). Regardless of condition, social or non-social, WL significantly displayed more feeding behaviour than RJF. Although this was not statistically significant, WL chicks did increase their feeding behaviour by almost 20% in the social condition, whilst it more than doubled in RJF. The RJF spent more time in contact with their social partner while WL spent more time feeding than RJF regardless of their social environment. Most likely these results are explained by a century of selection for production traits in domestic chickens, since increased egg production and growth demand more energy. A previous study on chicks of RJF and WL has also shown that these two breeds differ in social reinstatement behaviour (Väisänen and Jensen, 2004). The lower effect of social support in WL could also reflect altered social behaviour. A study on social preference in laying hens demonstrated that laying hens rapidly adapted to unknown chickens despite first preferring familiar hens (Bradshaw, 1992). Although our test animals were hatched together with the stimulus animal used in the experiment, they were separated before the testing started and housed separately. Given the reduced fear response and the increased exploratory behaviour, domestic chicks may be more likely to decide not to seek social support unlike the more fearful RJF which are less discriminatory when it comes to social reinstatement and the need to feel safety in numbers.

Domesticated animals may use less time habituating with, and getting familiar to, a stimulus (Katajamaa and Jensen, 2020) than the wild-type animals. The more familiar a situation is, the more time the chicks are likely to spend time with feeding (Jones, 1977). In our study, we did not find such an effect, most likely because two expositions to the stimulus were not sufficient to build habituation.

Our study gathered results from young, unsexed chicks prior to sexual maturation. Social motivation determines young chicks adopted strategy during stressful events as well as increases social affiliation (Bryan Jones and Merry, 1988; Marin et al., 2001). While using animals of a different age could have yielded different results, previous findings have shown that high fearfulness in chicks at six weeks of age is associated with greater plasma-corticosterone levels at 33 weeks of age. Additionally, fearfulness in a group can influence individual stress response, with even one high fearful bird increasing overall fearfulness significantly and having long-term effects on stress in laying hens (De Haas et al., 2012). However, the effect of social buffering could be different after sexual maturity due to changes related to establishing hierarchy and mating behaviour (Rushen, 1982a; Rushen, 1982b). Previous research has also shown that early sexual maturation can provide developmental advantages in establishing dominance within groups of pullets (Craig et al., 1965). As our study did not include hormonal effects related to sexual maturity and emergence of more aggressive behaviour and social dominance, the age of our subjects was important.

To conclude, our study has shown that domestication including the selection for high production rendered chickens less fearful and susceptible to stress while at the same time reducing their exploratory behaviours and greatly increased the motivation and need to feed. In addition, domesticated chickens were less dependent on conspecific social support for coping with the stressful procedures in the experiment than individuals from the wild-type breeding strain.

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CRediT authorship contribution statement

All authors have contributed to, seen, and approved the manuscript. HJJ: Conceptualization, Methodology, Statistical analysis, Writing-Original Draft, Data visualization. JG: Data curation, Data coding, figure drawing, Writing-Original Draft. KKot: Conceptualization, Writing-Review & Editing, Supervision, Funding acquisition. PJ: Conceptualization, Material acquisition, Subject acquisition, Writing-Review & Editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationship that could be construed as a potential conflict of interest.

Data Availability

Data were provided in the Supplementary material.

Acknowledgements

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Ethical note

The experiments were carried out under the ethical licence from Linköping Animal Ethics Committee, licence no. 14916–2018. All procedures were carried out according to the protocol.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2023.104906.

References

Abdulwahid, A.M., Zhao, J.B., 2022. China as a center of origin and domestication of chicken: a review. Agric. Rev. 43, 170–177. https://doi.org/10.18805/ag.R-206.

Agnvall, B., Katajamaa, R., Altimiras, J., Jensen, P., 2015. Is domestication driven by reduced fear of humans? Boldness, metabolism and serotonin levels in divergently selected red junglefowl (Gallus gallus). Biol. Lett. 11, 20150509.

Armario, A., Luna, G., Balasch, J., 1983. The effect of conspecifics on corticoadrenal response of rats to a novel environment. Behav. Neural Biol. 37, 332–337.

Baayen, R.H., 2008. Analyzing linguistic data: A practical introduction to statistics using R. Cambridge University Press.

Barr, D.J., Levy, R., Scheepers, C., Tily, H.J., 2013. Random effects structure for confirmatory hypothesis testing: Keep it maximal. Journal of Memory and Language 68, 255–278. https://doi.org/10.1016/j.jml.2012.11.001.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2014. Fitting Linear Mixed-Effects Models using lme4. arXiv:1406.5823.

Biggio, F., Mostallino, M.C., Talani, G., Locci, V., Mostallino, R., Calandra, G., Sanna, E., Biggio, G., 2019. Social enrichment reverses the isolation-induced deficits of neuronal plasticity in the hippocampus of male rats. Neuropharmacology 151, 45–54.

Błaszczyk, J.W., Tajchert, K., Łapo, I., Sadowski, B., 2000. Acoustic startle and open-field behavior in mice bred for magnitude of swim analgesia. Physiology & Behavior 70 (5), 471–476. https://doi.org/10.1016/S0031-9384(00)00289-4.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.-S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24, 127–135. https://doi.org/10.1016/j.tree.2008.10.008.

Bradshaw, R., 1992. Conspecific discrimination and social preference in the laying hen. Appl. Anim. Behav. Sci. 33, 69–75.

Brick, O., Jakobsson, S., 2002. Individual variation in risk taking: the effect of a predatory threat on fighting behavior in Nannacara anomala. Behavioral Ecology 13, 439–442. https://doi.org/10.1093/beheco/13.4.439.

Bryan Jones, R., Merry, B.J., 1988. Individual or paired exposure of domestic chicks to an open field: Some behavioural and adrenocortical consequences. Behav. Process. 16, 75–86.

Cimarelli, G., Marshall-Pescini, S., Range, F., Berghänel, A., Virányi, Z., 2021. Relationship quality affects social stress buffering in dogs and wolves. Anim. Behav. 178, 127–140.

Craig, J.V., Ortman, L.L., Guhl, A.M., 1965. Genetic selection for social dominance ability in chickens. Anim. Behav. 13, 114–131.

Darwin, C.L., Kebler, 1859. On the origin of species by means of natural selection, or, The preservation of favoured races in the struggle for life. J.Murray,, London.

De Haas, E.N., Kops, M.S., Bolhuis, J.E., Groothuis, T.G., Ellen, E.D., Rodenburg, T.B., 2012. The relation between fearfulness in young and stress-response in adult laying hens, on individual and group level. Physiol. Behav. 107, 433–439.

Dobson, A.J., Barnett, A.G., 2018. An Introduction to Generalized Linear Models. CRC Press.

Douxfils, J., Mathieu, C., Mandiki, S.N.M., Milla, S., Henrotte, E., Wang, N., Vandecan, M., Dieu, M., Dauchot, N., Pigneur, L.M., Li, X., Rougeot, C., Mélard, C., Silvestre, F., Van Doninck, K., Raes, M., Kestemont, P., 2011. Physiological and proteomic evidences that domestication process differentially modulates the immune status of juvenile Eurasian perch (Perca fluviatilis) under chronic confinement stress. Fish. Shellfish Immunol. 31, 1113–1121.

Dudde, A., Schrader, L., Weigend, S., Matthews, L.R., Krause, E.T., 2018. More eggs but less social and more fearful? Differences in behavioral traits in relation to the phylogenetic background and productivity level in laying hens. Appl. Anim. Behav. Sci. 209, 65–70.

Duncan, I., Slee, G.S., Kettlewell, P., Berry, P., Carlisle, A.J., 1986. Comparison of the stressfulness of harvesting broiler chickens by machine and by hand. Br. Poult. Sci. 27, 109–114.

Dwyer, C.M., 2004. How has the risk of predation shaped the behavioural responses of sheep to fear and distress? Anim. Welf. 13, 269–281.

Epley, S.W., 1974. Reduction of the behavioral effects of aversive stimulation by the presence of companions. Psychol. Bull. 81, 271.

Field, A., 2005. Discovering Statistics Using SPSS. Sage Publications, London.

Forstmeier, W., Schielzeth, H., 2011. Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. Behav Ecol Sociobiol 65, 47–55. https://doi.org/10.1007/s00265-010-1038-5.

Fox, J., Weisberg, S., 2018. An R Companion to Applied Regression. SAGE Publications.

Geverink, N.A., Bühnemann, A., Van De Burgwal, J.A., Lambooij, E., Blokhuis, H.J., Wiegant, V.M., 1998. Responses of slaughter pigs to transport and lairage sounds. Physiol. Behav. 63, 667–673.

Gjøen, J., Jensen, P., 2021. Selection for reduced fear of humans changes intra-specific social behavior in red junglefowl—implications for chicken domestication. Genes 13, 43.

Harcourt, J.L., Ang, T.Z., Sweetman, G., Johnstone, R.A., Manica, A., 2009. Social feedback and the emergence of leaders and followers. Curr. Biol. 19, 248–252.

Ishiwata, T., Kilgour, R., Uetake, K., Eguchi, Y., Tanaka, T., 2007. Choice of attractive conditions by beef cattle in a Y-maze just after release from restraint. J. Anim. Sci. 85, 1080–1085.

Jean-Joseph, H., Dooey, G., Kotrschal, K., 2022. Diurnal activity patterns of equally socialized and kept wolves, Canis lupus, and dogs, Canis lupus familiaris. Anim. Behav. 190, 41–52. https://doi.org/10.1016/j.anbehav.2022.05.009.

Jean-Joseph, H., Kortekaas, K., Range, F., Kotrschal, K., 2020. Context-specific arousal during resting in wolves and dogs: effects of domestication? Front. Psychol. 11 https://www.frontiersin.org/articles/10.3389/fpsyg.2020.568199.

Jones, R.B., 1977. Open-field responses of domestic chicks in the presence or absence of familiar cues. Behav. Process. 2, 315–323.

Jones, R.B., Harvey, S., 1987. Behavioural and adrenocortical responses of domestic chicks to systematic reductions in group size and to sequential disturbance of companions by the experimenter. Behav. Process. 14, 291–303.

Jones, R.B., Satterlee, D.G., Ryder, F.H., 1992. Fear and distress in Japanese quail chicks of two lines genetically selected for low or high adrenocortical response to immobilization stress. Horm. Behav. 26, 385–393.

Katajamaa, R., Jensen, P., 2020. Selection for reduced fear in red junglefowl changes brain composition and affects fear memory. R. Soc. Open Sci. 7, 200628.

Kawamori, A., Matsushima, T., 2012. Sympatric divergence of risk sensitivity and diet menus in three species of tit. Animal Behaviour 84, 1001–1012. https://doi.org/10.1016/j.anbehav.2012.07.026.

Koolhaas, J.M., Korte, S.M., De Boer, S.F., Van Der Vegt, B.J., Van Reenen, C.G., Hopster, H., De Jong, I.C., Ruis, M.A.W., Blokhuis, H.J., 1999. Coping styles in animals: current status in behavior and stress-physiology. Neurosci. Biobehav. Rev. 23, 925–935.

Kortekaas, K., Kotrschal, K., 2019. Does socio-ecology drive differences in alertness between wolves and dogs when resting? Behavioural Processes 166, 103877. In: https://doi.org/10.1016/j.beproc.2019.05.024.

Kortekaas, K., Kotrschal, K., 2020. Social context influences resting physiology in dogs. Anim. 10 (12), 2214. https://doi.org/10.3390/ani10122214.

Künzl, C., Sachser, N., 1999. The behavioral endocrinology of domestication: a comparison between the domestic Guinea Pig (Cavia apereaf.porcellus) and Its Wild Ancestor, the Cavy (Cavia aperea). Horm. Behav. 35, 28–37.

Lawler, A., 2016. Why Did the Chicken Cross the World?: the Epic Saga of the Bird That Powers Civilization. Simon and Schuster.

Liebsch, G., Linthorst, A.C., Neumann, I.D., Reul, J.M., Holsboer, F., Landgraf, R., 1998. Behavioral, physiological, and neuroendocrine stress responses and differential sensitivity to diazepam in two Wistar rat lines selectively bred for high-and low-anxiety–related behavior. Neuropsychopharmacology 19, 381–396.

Lindqvist, C., Jensen, P., 2009. Domestication and stress effects on contrafreeloading and spatial learning performance in red jungle fowl (Gallus gallus) and White Leghorn layers. Behav. Process. 81, 80–84.

Marin, R.H., Freytes, P., Guzman, D., Bryan Jones, R., 2001. Effects of an acute stressor on fear and on the social reinstatement responses of domestic chicks to cagemates and strangers. Appl. Anim. Behav. Sci. 71, 57–66.

Marshall-Pescini, S., Cafazzo, S., Virányi, Z., Range, F., 2017. Integrating social ecology in explanations of wolf–dog behavioral differences. Curr. Opin. Behav. Sci. 16, 80–86.

Marshall-Pescini, S., Virányi, Z., Kubinyi, E., Range, F., 2017. Motivational factors underlying problem solving: comparing wolf and dog puppies' explorative and neophobic behaviors at 5, 6, and 8 weeks of age. Front. Psychol. 8, 180. https://doi.org/10.3389/fpsyg.2017.00180.

Mendl, M., 1999. Performing under pressure: stress and cognitive function. Appl. Anim. Behav. Sci. 65, 221–244.

Mettke-Hofmann, C., Winkler, H., Leisler, B., 2002. The Significance of Ecological Factors for Exploration and Neophobia in Parrots. Ethology 108, 249–272. https://doi.org/10.1046/j.1439-0310.2002.00773.x.

Mills, A., Faure, J., 1990. Panic and hysteria in domestic fowl: a review. Panic hysteria Domest. fowl: a Rev. 248–272.

Moretti, L., Hentrup, M., Kotrschal, K., Range, F., 2015. The influence of relationships on neophobia and exploration in wolves and dogs. Anim. Behav. 107, 159–173.

van Oers, K., Klunder, M., Drent, P.J., 2005. Context dependence of personalities: risk-taking behavior in a social and a nonsocial situation. Behavioral Ecology 16, 716–723. https://doi.org/10.1093/beheco/ari045.

Price, E.O., 1984. Behavioral aspects of animal domestication. Q. Rev. Biol. 59, 1–32.

Price, E.O. 2002. Pre-adaptations for Domestication Animal Domestication and Behaviour. CAB International Wallingford Oxon OX10 8DE UK: CABI Publishing.

Rault, J.-L., 2012. Friends with benefits: Social support and its relevance for farm animal welfare. Appl. Anim. Behav. Sci. 136, 1–14.

Ricci-Bonot, C., Romero, T., Nicol, C., Mills, D., 2021. Social buffering in horses is influenced by context but not by the familiarity and habituation of a companion. Sci. Rep. 11, 1–10.

Ross, M., Rausch, Q., Vandenberg, B., Mason, G., 2020. Hens with benefits: can environmental enrichment make chickens more resilient to stress? Physiol. Behav. 226, 113077.

Rushen, J., 1982a. Development of social behaviour in chickens: a factor analysis. Behav. Process. 7, 319–333.

Rushen, J., 1982b. The peck orders of chickens: how do they develop and why are they linear? Anim. Behav. 30, 1129–1137.

Satterlee, D., Cadd, G., Jones, R., 2000. Developmental instability in Japanese quail genetically selected for contrasting adrenocortical responsiveness. Poult. Sci. 79, 1710–1714.

Schütz, K., Kerje, S., Carlborg, O., Jacobsson, L., Andersson, L., Jensen, P., 2002. QTL analysis of a red junglefowl× White Leghorn intercross reveals trade-off in resource allocation between behavior and production traits. Behav. Genet. 32, 423–433.

Schütz, K.E., Jensen, P., 2001. Effects of resource allocation on behavioural strategies: a comparison of red junglefowl (Gallus gallus) and two domesticated breeds of poultry. Ethology 107, 753–765.

Schütz, K.E., Forkman, B., Jensen, P., 2001. Domestication effects on foraging strategy, social behaviour and different fear responses: a comparison between the red junglefowl (Gallus gallus) and a modern layer strain. Appl. Anim. Behav. Sci. 74, 1–14.

Schütz, K.E., Kerje, S., Jacobsson, L., Forkman, B., Carlborg, Ö., Andersson, L., Jensen, P., 2004. Major growth QTLs in fowl are related to fearful behavior: possible genetic links between fear responses and production traits in a red junglefowl× White Leghorn intercross. Behav. Genet. 34, 121–130.

Siegel, P.B., Haberfeld, A., Mukherjee, T.K., Stallard, L.C., Marks, H.L., Anthony, N.B., Dunnington, E.A., 1992. Jungle fowl–domestic fowl relationships: a use of DNA fingerprinting. World'S. Poult. Sci. J. 48, 147–155.

Solberg, M.F., Robertsen, G., Sundt-Hansen, L.E., Hindar, K., Glover, K.A., 2020. Domestication leads to increased predation susceptibility. Sci. Rep. 10, 1929.

Trimpop, R.M., 1994. The Psychology of Risk Taking Behavior. Elsevier.

Trut, L., Oskina, I., Kharlamova, A., 2009. Animal evolution during domestication: the domesticated fox as a model. Bioessays 31, 349–360.

Väisänen, J., Jensen, P., 2003. Social versus exploration and foraging motivation in young red junglefowl (Gallus gallus) and White Leghorn layers. Appl. Anim. Behav. Sci. 84, 139–158.

Väisänen, J., Jensen, P., 2004. Responses of young red jungle fowl (*Gallus gallus*) and White Leghorn layers to familiar and unfamiliar social stimuli. Poult. Sci. 83, 335–343.

Versace, E., Ragusa, M., Pallante, V., Wang, S., 2021. Attraction for familiar conspecifics in young chicks (Gallus gallus): an interbreed study. Behav. Process. 193, 104498.

Wang, M.-S., Thakur, M., Peng, M.-S., Jiang, Y., Frantz, L.A.F., Li, M., Zhang, J.-J., Wang, S., Peters, J., Otecko, N.O., 2020. 863 genomes reveal the origin and domestication of chicken. Cell Res. 30, 693–701.

Wilkins, A.S., Wrangham, R.W., Fitch, W.T., 2014. The "domestication syndrome" in mammals: a unified explanation based on neural crest cell behavior and genetics. Genetics 197, 795–808.

Wilson, E.O., 2000. Sociobiology: The New Synthesis. Harvard University Press.

Wirén, A., Wright, D., Jensen, P., 2013. Domestication-related variation in social preferences in chickens is affected by genotype on a growth QTL. Genes, Brain Behav. 12, 330–337.

Concluding Discussion|

Thesis Overview

It was the primary aim of my thesis to draw a broad picture of behavioural and emotional adaptations of dogs toward humans and their environment by testing their physiological and behavioural responses in various situations. The secondary aim of this thesis was to test how these reactions to human presence support or refute the domestication hypotheses pertinent to wolves/dog - human interaction.

In chapter one, I investigated the physiological responses of equally raised and kept wolves to the presence of a familiar human during rest. Dogs were overall more relaxed than wolves at rest, whereas they were equally relaxed during inactive wakefulness. Looking across conditions, dogs were less relaxed when resting alone as compared to resting with a familiar human or their pack, whereas wolves were most relaxed when resting near their pack and the effect of the presence of a familiar human varied between individuals.

In chapter two, I observed the behavioural response of equally raised and kept dog and wolves to human presence during their daily activity. Dogs' and wolves' time budgets did not significantly differ and were both equally affected by light conditions and seasonality. However, dogs were more active than wolves when humans were close to their enclosure.

In chapter three, I investigated the behavioural and physiological responses of equally raised and kept wolves and dog to social support provided by a familiar human during a risk-taking paradigm. Wolves and dogs both showed similar behaviours towards familiar humans, but their presence did not seem to affect wolf or dog behaviours or physiology compared to the non-social condition, and dogs did not react more than wolves to the communicative gestures of the familiar human. In fact, age was the main factor affecting risk-proneness: the older the animals were, the faster they took the food, no matter whether wolf or dog.

In chapter four I turned to another classical domestication model, the chicken, to broaden my perspective on domestication-related behavioural effects. I investigated how the social environment influenced risk-taking behaviours of white leghorn chicks (a domestic breed; WL) compared to red junglefowl ones (the wild-type counterpart; RJF) in a paradigm similar to Chapter three. Domesticated chickens were less agitated, and less alert but faster to reach the food than their wild-type counterparts. However, the RJFs were more explorative than the domesticated WLs, approached the object earlier, and spent more time in its vicinity. Additionally, RJFs were also more socially motivated compared to WLs who were more food motivated.

To summarize, I found that wolves´ and dogs’ behaviours did not follow standard predictions of domestication hypotheses (Belyaev et al., 1985; Darwin, 1868; Wilkins et al., 2014) whereas chicken behaviours did.

Wolves and Dogs: a more nuanced interpretation of Domestication

To sum up, in my thesis I provide insight into the effects of domestication on different aspects of the domesticated animals' reaction to their environment with special regard to the role of humans by comparing them to their wild-type counterparts. I used behavioural experiments and observations as well as physiological measurements to investigate this topic. My results demonstrated that wolves’ and dogs’ behaviours did not exactly follow the standard predictions from domestication hypotheses (Belyaev et al., 1985; Darwin, 1868; Wilkins et al., 2014).

During my experiments, I found no evidence supporting the “emotional reactivity hypothesis” (Hare et al., 2005, 2012): Dogs were generally not less scared, or less reactive than socialized wolves. The only situation where they were found less alert (and therefore more relaxed) than wolves was at rest (Jean-Joseph et al., 2020). It contrasts with a previous resting study (Kortekaas & Kotrschal, 2019) where socialized wolves were generally more relaxed than dogs (Kortekaas & Kotrschal, 2019). However, this study didn't take into account the confounding factor of the unfamiliar human observing the animals. Hence, I would argue that in Kortekaas and Kotrschal’s study, dogs were more alert because they were focusing their attention on the unfamiliar human, unlike the wolves. Indeed, as evidenced by my second study (Jean-Joseph et al., 2022), dogs but not wolves seem to consider humans as social Zeitgeber (Grandin et al., 2006) and increase their activity when humans were present. Taken together, my two studies seem to partially support the “hypersociability hypothesis” (Bentosela et al., 2016; vonHoldt et al., 2017), as I found that compared to socialised wolves, dogs show increased sociability toward humans. This is further evidenced in chapter one, as most dogs were as relaxed around a familiar human as with their pack, whereas only one wolf (an older female) was more relaxed around a familiar human than in any other condition. Even socialized, wolves might be more selective with their human partner and hence show more variability in their response to humans than dogs do. Those results also agreed with a previous study comparing the behaviours of wolves and various populations of dogs toward humans: despite various degrees of socialisation (i.e., free-ranging dogs have less contact with humans than pet-dogs), all the dogs tested showed interest in interacting with humans (Lazzaroni et al., 2020).

In contrast to Chapter one and two results, Chapter three results (Jean-Joseph et al., submitted) do not support the “hypersociability hypothesis”(vonHoldt et al., 2017). Indeed, in this particular situation involving both risk-taking and foraging, dogs’ and wolves' behavioral and physiological reactions to a familiar human did not differ: they displayed similar behaviour toward the familiar humans and similar cardiac outputs. Moreover, the “deferential hypothesis”(Range et al., 2019) is not supported either as dogs did not follow the various communicative gestures of the familiar human more than wolves. Rather, these results support the “canine cooperation hypothesis” (Range & Virányi, 2015) and the “two-stage hypothesis” (Udell et al., 2010) as both socialized wolves and dogs demonstrated the same behaviours toward the human in this context.

There is a discrepancy between the two first chapters (that support the “hypersociability hypothesis”) and the third chapter (that does not). This discrepancy could be explained by how frightening, or not, the experiment was to the animals. Most likely, the object used in Chapter three was not scary enough and neither dogs nor wolves needed the support of the familiar human to overcome it. Indeed, older individuals solved the task faster than younger ones, which implies that their previous experience in other experimental settings might have helped them. Alternatively, the food reward might have been too distracting for the animals as wolves and dogs are both highly attracted to meat as a food reward (Rao et al., 2018). Hence, this paradigm might not be the best to test the “hypersociability hypothesis”.

In my thesis, I endeavoured to control for life experience and context effects when comparing wolves and dogs. Previous studies have demonstrated that life experience can influence behaviours similarly in domesticated and wild animals (Hecht et al., 2023). For example, Wirobski and colleagues demonstrated that even if wolves and dogs have different basal hormonal levels (Wirobski et al., 2021a), the hormonal reaction of similarly raised and kept wolves and dogs to interactions with humans do not differ (Wirobski et al., 2021b). Additionally, wild gerbils habituated to lab settings are as successful as domesticated gerbils as compared to wild non-habituated gerbils during a learning task (Stuermer & Wetzel, 2006).

Taken all together, my results showed that wolves’ and dogs’ behavioral and physiological differences are context-dependent and mostly related to reactions toward humans. Hence, it will be crucial for future studies to take into account potential confounding factors, such as life experience and the various contexts animals are tested in.

Comparing chickens, a classic example of domestication to wolves and dogs

Unlike the wolf/dog system, the results obtained from testing chickens followed the predictions based on selection for tameness (Belyaev, 1979), as domesticated chickens were less scared of a novel object than wild-type ones. Additionally, I observed an effect of the second selection for high production in the domestic chicken: white leghorns (WL) grew faster than red junglefowls (RJF) and fed more than their wild-type counterparts, a phenomenon observed in previous studies (Dudde et al., 2018; Schütz et al., 2001, 2002, 2004).

There are several possible explanations for these differences between wolves/dogs and chickens. First, they belong to very different amniote taxa, dogs and wolves being mammals whereas chickens are birds. Birds and mammals have diverged some 318 million years ago (Benton et al., 2015) which comes with obvious morphological, behavioral, and physiological differences (Scanes, 2020). Moreover, the differences between mammals' and birds' brains could contribute to these different results. For example, the mammalian pallial forebrain shows a cortical structure composed of columns, whereas the bird pallium shows a few relatively amorphous cell masses, Within the mammals, “big brained” species are less dependent on olfactory and hormonal cues and rely more on cognitive resources in reproduction and caregiving to offspring (Curley & Keverne, 2005) as compared to “small brained” mammals. Hence wolves and dogs could be less dependent on physiological mechanisms and at least socially more cognitively orientated than chicken (Broad et al., 2006). Second, wolves and dogs are predators whereas chickens are prey, which could affect their cognitive processing (Leavell & Bernal, 2019). For example, they could use different decision-making processes when facing a novel stimulus; I would expect predators to be more investigative than prey species. Third, the domestication process leading to domestic dogs and domestic chicken might have been different from the start. Wolves were domesticated first before humans became sedentary (Germonpré et al., 2009; Thalmann et al., 2013) whereas chickens and humans aligned after the latter became sedentary (Abdulwahid & Zhao, 2021), hence the methods used to domesticated them might have differ as well as the selective pressure applied to them. Additionally, the reason why dogs and chickens were domesticated might differ too, for example, wolves might have had the role of spiritual partners (Kotrschal, 2016) and may have hunted together with their human partners (Serpell, 2021; Shipman, 2015), whereas chickens were most likely food resources from the start (Lawler, 2016) and thus, different selective pressures would have led to different results. Lastly, I tested dogs and wolves in relation to human presence whereas chickens were only offered a conspecific as a social partner which could explain some of the differences as wolves and dogs might have reacted differently if offered the social support of their pack members. For example, offering a pack member or the whole pack as social support in Chapter three could have yielded different results similar to Moretti and colleagues’ ones (2015). Additionally, in wolves dogs and chicken there is factor that affect the quality of the social support an individual can offer, namely quality of the relationship (Cimarelli et al., 2021), or the reaction the supporter itself to the stimulus (Edgar et al., 2015).

Contribution to domestication debates

The results of my thesis projects emphasize that domestication might 1. be more nuanced (i.e., context-dependent) than previously thought, and 2. might not be responsible for all the differences observed between wolves and dogs; life experience also plays a role. For example, it was assumed that domestication produced a more reactive oxytocin system in dogs as compared to wolves (Nagasawa et al., 2015). However, recently Wirobski et al. (2021) showed that concentrations of oxytocin in equally raised and kept wolves and dogs did not increase after a petting session with their caregivers whereas it increased in pet dogs (Wirobski et al., 2021b). Hence, oxytocin increases in response to socio-positive interactions with humans can no longer be regarded as a basic wolf-dog difference but is rather due to the (social) context dogs (and wolves) are living in. Similar to the evidence by Wirobski et al. (2021), my results do not invalidate/falsify the classic domestication hypotheses but rather hint at the need for better control of confounding factors and parameters, such as life experience and context in future studies on domestication (Hecht et al., 2023; Range & Marshall-Pescini, 2022).

When assessing domesticated animals' behaviours, rather than focusing on an overall generalization of the phenomenon, one should acknowledge the potential differences in the life experiences and contexts in which the animals were tested. For example, Lord’s and colleagues’ critique (2020) question whether a domestication syndrome (Belyaev, 1979; Darwin, 1868; Wilkins et al., 2014) exists at all since not all of the features assigned to this syndrome are present in each domesticated species; some seem just breed-related (Lord et al., 2020). The same critique was made about the “neural crest hypothesis” (Wilkins, 2017, 2017, 2020; Wilkins et al., 2014, 2021), because as there is no evidences of pleiotropy (i.e., a gene or allele that affects several phenotypic traits; Paaby & Rockman, 2013) in the genes involved in domestication, the neural crest cannot be a unifiying meachanism for domestication syndrome (Johnsson et al., 2021). However, this may be a bit formalistic, as – for several reasons – it cannot be expected that all features of the syndrome will be equally expressed in each domesticated species. Indeed, domesticated animals are phylogenetically different. Hence, it could be expected to find the same variation in the DS features they displayed in accordance with their specificity (i.e., taxon, social-ecology, life experience). Studies have demonstrated life experience can affect the brain (Hecht et al., 2023). A comparison between wild, wild but lab-raised, and domesticated lab-raised gerbils revealed that early life experience rather than genetics affect success in an auditory learning task as both wild but lab-raised and domesticated gerbils performed better than wild gerbils (Stuermer & Wetzel, 2006). These results are comparable to my findings in Chapter Three (Jean-Joseph et al., submitted), where older and therefore more experienced dogs and wolves were more risk-prone than younger individuals.

Moreover, ecology could also matter. For example, chickens, as prey animals, might have perceived humans as predators during the early domestication process. Therefore, desensitisation to humans and their new human-dominated environment would have been essential to keep them captive and fit. However, in the case of wolves and later dogs, it might have not been the same process if, for example, they were initially used as hunting partners by hunter-gatherers (Coppinger & Coppinger, 2001; Driscoll et al., 2009; Grimm, 2015; Shipman, 2015). Since they were most likely kept to fulfill different purposes, they might have been subjected to slightly different selective pressures. Additionally, most of the extant domesticated species have undergone changing selection regimes. Farm animals, for example, may have initially been selected for tameness and later, high production (Brito et al., 2021; Oltenacu & Broom, 2010; Rauw et al., 1998). Dogs may also be the result of such a dual selection process (Miklósi et al., 2003; Pendleton et al., 2018; Udell et al., 2010). After an implicit selection of wolf-like dogs for tameness in the company of paleolithic hunter-gatherers (Mech & Janssens, 2022; Serpell, 2021), breeds have been purposefully selected (Kotrschal, 2018) after becoming sedentary and particularly, in the last 150 years, when many dogs are breed according to “standards” (CRUFTS: https://crufts.org.uk/, American Kennel Club: https://www.akc.org/dog-breeds/, LOF: https://www.centrale-canine.fr/articles/le-lof). Hence, phenotypic and behavioural differences observed in dog breeds could be input to the breed selection process, rather than to early domestication process (Gnanadesikan et al., 2020; MacLean et al., 2019). Recently, some breeds have been divided into different selective lines: show or work lines. Those dogs, despite being the same breed, have different behavioural dispositions (Fadel et al., 2016), which demonstrates that additional selection pressures can further alter behaviour in domesticated animals.

Hence, to be able to investigate domestication fairly, all of these confounding factors need to be accounted for in future studies. One has to keep in mind that most of the domesticated animals around today are the result of more than just selection for tameness.

Future research direction

Based on the results of my studies, I advocate for more attention to be given to the various contexts in future studies and to vary them as much as possible to obtain a comprehensive picture of potential domestication effects. It is crucial to always bear in mind the potential effects of life experience, and different social ecologies on the species that are investigated.

There are plenty of unanswered questions regarding dog domestication. For example, what was the mechanism involved in the early domestication process? Relevant research models for these questions about early domestication mechanisms could be red foxes (*Vulpes vulpes*) and coyotes (*Canis latrans*) that are currently thriving worldwide by adapting to live in urban environments (Gehrt et al., 2011; Kobryn et al., 2023; Padovani et al., 2021; Tolhurst et al., 2020). By comparing urban vs rural populations, the premises of the self-domestication hypothesis (Hare et al., 2012) versus the commensal hypothesis (Coppinger & Coppinger, 2001; Driscoll et al., 2009; Grimm, 2015) could be tested. Additionally, differences in urban coyotes' behaviours and genetics compared to rural ones have already been observed (Adducci et al., 2020; Breck et al., 2019). Hence, their adaptation to the human environment could elucidate if selection for adaptation to challenging environments (Hare et al., 2002) – or even some selection for tameness as a side effect – leads to domestication and the DS, which is another pending question of the domestication field.

Multiple cognitive and human-dog interaction studies on various populations of free-ranging dogs would also help to disentangle domestication from life experience's effects. It would also be great to bear in mind that most of the current wolf populations, notably in Eurasia, have been subject to drastic hunting pressure and, as a result, are shy and avoid human presence, whereas populations that were never hunted are bolder (Mech & Janssens, 2022). Most likely the wolf ancestor of modern dogs was bolder than modern wolves are, hence comparing this modern bolder population might be more relevant than testing Eurasian populations, at least for the question concerning the domestication process.

To further elucidate which feature of domestication are related to which mechanisms, it will be interesting to extend the range of animals used in domestication studies. For example, even if the early domestication of horses (*Equus caballus*) and the identification of an ancestor are still debated (Jansen et al., 2002; Kyselý & Peške, 2022; Taylor & Barrón-Ortiz, 2021; Warmuth et al., 2012), free-ranging horse populations do exist (Bhattacharyya et al., 2011; Girard et al., 2013; King, 2002) and would be a good mirror system to pet-dog vs free-ranging dog comparisons.

Furthermore, how domestication and/or life in close partnership with humans influence cognitive skills is another interesting question for the domestication field. Interesting species to further elucidate this question could be the domestic cats (*Felis catus*) and domestic rats (*Rattus norvegicus*). Indeed, domestic cats might also be a fair candidate species to disentangle life experience from domestication as they live more alongside us than with us, unlike pet dogs do. Cats most likely domesticated themselves (Hu et al., 2014) around early grain storage in the Near East and North Africa (Driscoll et al., 2007; Nilson et al., 2022). Studies of cats' socio-cognitive abilities are a recent field (Turner, 2021; Uccheddu et al., 2022; Vitale Shreve & Udell, 2015) with plenty of challenges left. It seems generally harder to work with cats than dogs because cats seem to have a much lower intrinsic motivation to cooperate (Uccheddu et al., 2022). So far, studies have already yielded interesting results concerning cats' socio-cognitive abilities. For example, cats read human gaze for referential information (Pongrácz et al., 2019) and they mentally map the position of their owners based on the latter's voices (Takagi et al., 2021), they succeed at the "do as I do" paradigm (Fugazza et al., 2021), they can use pointing gesture (Mäses & Wascher, 2023), and they bond with humans in a similar way to dogs (Vitale et al., 2019). Hence, domestic cats could well be a good challenger to definitively put to rest the so-called uniqueness of dogs' human-like socio-cognitive skills (Hare & Tomasello, 2005; Kaminski & Nitzschner, 2013; Miklósi & Topál, 2013) and tear apart what socio-cognitive skills could be due to domestication or living alongside humans (Miklósi et al., 2003; Miklósi & Topál, 2013), or even possibly to exposure to humans during early ontogeny and positive reinforcement (Udell et al., 2010).

Finally, rats could be another good candidate to disentangle the effects of domestication from life alongside humans. They are a highly social species and a well-known and studied model (Schweinfurth, 2020). Some populations are kept under standard conditions for scientific purposes, while others live as pets or are wild and thus considered pests (Himsworth et al., 2013; Moors et al., 1992; Pimentel et al., 2005). Overall, the situation of rats is quite similar to that of the dogs: some populations are kept as pets and are selected for particular phenotypic traits like coat color or ears shape, a situation comparable to breed selection in dogs. Some populations live in an urban environment mostly outside of humans control similar to free-ranging dogs, although human perception and tolerance of rats and free-ranging dogs might differ. Additionally, some populations are living completely under standard conditions in laboratories (Andrews, 1996; Himmler et al., 2013; Koolhaas, 2010). Hence, it would be interesting to study different rat populations' ability to apply their socio-cognitive skills to interaction with humans.

Taken together, my thesis supports the "hypersociability hypothesis" as well as the "canine cooperation hypothesis" and the "two-stage hypothesis". It adds to the literature by showing that dogs and wolves do not follow the classic prediction of selection for tameness and that life experience can alter the behaviours of domesticated and wild animals. Future work would benefit from focusing on the influence of life experience and other confounding factors when studying domestication.

References

Abdulwahid, A. M., & Zhao, J. B. (2021). China as a Center of Origin and Domestication of Chicken: A Review. *Agricultural Reviews*. https://arccjournals.com/journal/agricultural-reviews/R-206

Adducci, A., II, Jasperse, J., Riley, S., Brown, J., Honeycutt, R., & Monzón, J. (2020). Urban coyotes are genetically distinct from coyotes in natural habitats. *Journal of Urban Ecology*, *6*(1), juaa010. https://doi.org/10.1093/jue/juaa010

Andrews, J. S. (1996). Possible confounding influence of strain, age and gender on cognitive performance in rats. *Cognitive Brain Research*, *3*(3), 251–267. https://doi.org/10.1016/0926-6410(96)00011-0

Belyaev, D. K. (1979). Destabilizing selection as a factor in domestication. *Journal of Heredity*, *70*(5), Article 5. https://doi.org/10.1093/oxfordjournals.jhered.a109263

Belyaev, D. K., Plyusnina, I. Z., & Trut, L. N. (1985). Domestication in the silver fox (Vulpes fulvus Desm): Changes in physiological boundaries of the sensitive period of primary socialization. *Applied Animal Behaviour Science*, *13*(4), Article 4. https://doi.org/10.1016/0168-1591(85)90015-2

Benton, M. J., Donoghue, P. C. J., Asher, R. J., Friedman, M., Near, T. J., & Vinther, J. (2015). Constraints on the timescale of animal evolutionary history. *Palaeontologia Electronica*, *18*(1), 1–106. https://doi.org/10.26879/424

Bentosela, M., Wynne, C. D. L., D'Orazio, M., Elgier, A., & Udell, M. a. r. (2016). Sociability and gazing toward humans in dogs and wolves: Simple behaviors with broad implications. *Journal of the Experimental Analysis of Behavior*, *105*(1), Article 1. https://doi.org/10.1002/jeab.191

Bhattacharyya, J., Slocombe, D. S., & Murphy, S. D. (2011). The "Wild" or "Feral" Distraction: Effects of Cultural Understandings on Management Controversy Over Free-Ranging Horses (Equus ferus caballus). *Human Ecology*, *39*(5), 613–625. https://doi.org/10.1007/s10745-011-9416-9

Breck, S. W., Poessel, S. A., Mahoney, P., & Young, J. K. (2019). The intrepid urban coyote: A comparison of bold and exploratory behavior in coyotes from urban and rural environments. *Scientific Reports*, *9*(1), Article 1. https://doi.org/10.1038/s41598-019-38543-5

Brito, L. F., Bedere, N., Douhard, F., Oliveira, H. R., Arnal, M., Peñagaricano, F., Schinckel, A. P., Baes, C. F., & Miglior, F. (2021). Review: Genetic selection of high-yielding dairy cattle toward sustainable farming systems in a rapidly changing world. *Animal*, *15*, 100292. https://doi.org/10.1016/j.animal.2021.100292

Broad, K. d, Curley, J. p, & Keverne, E. b. (2006). Mother–infant bonding and the evolution of mammalian social relationships. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *361*(1476), 2199–2214. https://doi.org/10.1098/rstb.2006.1940

Cimarelli, G., Marshall-Pescini, S., Range, F., Berghänel, A., & Virányi, Z. (2021). Relationship quality affects social stress buffering in dogs and wolves. *Animal Behaviour*, *178*, 127–140. https://doi.org/10.1016/j.anbehav.2021.06.008

Coppinger, R., & Coppinger, L. (2001). *Dogs: A Startling New Understanding of Canine Origin, Behavior & Evolution*. Simon and Schuster.

Curley, J. P., & Keverne, E. B. (2005). Genes, brains and mammalian social bonds. *Trends in Ecology & Evolution*, *20*(10), 561–567. https://doi.org/10.1016/j.tree.2005.05.018

Darwin, C. (1868). *The Variation of Animals and Plants Under Domestication*. O. Judd.

Driscoll, C. A., Macdonald, D. W., & O'Brien, S. J. (2009). From wild animals to domestic pets, an evolutionary view of domestication. *Proceedings of the National Academy of Sciences*, *106*(supplement_1), 9971–9978. https://doi.org/10.1073/pnas.0901586106

Driscoll, C. A., Menotti-Raymond, M., Roca, A. L., Hupe, K., Johnson, W. E., Geffen, E., Harley, E. H., Delibes, M., Pontier, D., Kitchener, A. C., Yamaguchi, N., O'Brien, S. J., & Macdonald, D. W. (2007). The Near Eastern Origin of Cat Domestication. *Science*, *317*(5837), 519–523. https://doi.org/10.1126/science.1139518

Dudde, A., Schrader, L., Weigend, S., Matthews, L. R., & Krause, E. T. (2018). More eggs but less social and more fearful? Differences in behavioral traits in relation to the phylogenetic background and productivity level in laying hens. *Applied Animal Behaviour Science*, *209*, 65–70. https://doi.org/10.1016/j.applanim.2018.08.017

Edgar, J., Held, S., Paul, E., Pettersson, I., I'Anson Price, R., & Nicol, C. (2015). Social buffering in a bird. *Animal Behaviour*, *105*, 11–19. https://doi.org/10.1016/j.anbehav.2015.04.007

Fadel, F. R., Driscoll, P., Pilot, M., Wright, H., Zulch, H., & Mills, D. (2016). Differences in Trait Impulsivity Indicate Diversification of Dog Breeds into Working and Show Lines. *Scientific Reports*, *6*(1), 22162. https://doi.org/10.1038/srep22162

Fugazza, C., Sommese, A., Pogány, Á., & Miklósi, Á. (2021). Did we find a copycat? Do as I Do in a domestic cat (Felis catus). *Animal Cognition*, *24*(1), 121–131. https://doi.org/10.1007/s10071-020-01428-6

Gehrt, S., Brown, J., & Anchor, C. (2011). Is the Urban Coyote a Misanthropic Synanthrope? The Case from Chicago. *Cities and the Environment (CATE)*, *4*(1). https://digitalcommons.lmu.edu/cate/vol4/iss1/3

Germonpré, M., Sablin, M. V., Stevens, R. E., Hedges, R. E. M., Hofreiter, M., Stiller, M., & Després, V. R. (2009). Fossil dogs and wolves from Palaeolithic sites in Belgium, the Ukraine and Russia: Osteometry, ancient DNA and stable isotopes. *Journal of Archaeological Science*, *36*(2), Article 2. https://doi.org/10.1016/j.jas.2008.09.033

Girard, T. L., Bork, E. W., Nielsen, S. E., & Alexander, M. J. (2013). Seasonal Variation in Habitat Selection by Free-Ranging Feral Horses Within Alberta's Forest Reserve. *Rangeland Ecology & Management*, *66*(4), 428–437. https://doi.org/10.2111/REM-D-12-00081.1

Gnanadesikan, G. E., Hare, B., Snyder-Mackler, N., Call, J., Kaminski, J., Miklósi, Á., & MacLean, E. L. (2020). Breed Differences in Dog Cognition Associated with Brain-Expressed Genes and Neurological Functions. *Integrative and Comparative Biology*, *60*(4), 976–990. https://doi.org/10.1093/icb/icaa112

Grandin, L. D., Alloy, L. B., & Abramson, L. Y. (2006). The social zeitgeber theory, circadian rhythms, and mood disorders: Review and evaluation. *Clinical Psychology Review*, *26*(6), Article 6. https://doi.org/10.1016/j.cpr.2006.07.001

Grimm, D. (2015). Dawn of the dog. *Science*, *348*(6232), 274–279. https://doi.org/10.1126/science.348.6232.274

Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The Domestication of Social Cognition in Dogs. *Science*, *298*(5598), Article 5598. https://doi.org/10.1126/science.1072702

Hare, B., Plyusnina, I., Ignacio, N., Schepina, O., Stepika, A., Wrangham, R., & Trut, L. (2005). Social Cognitive Evolution in Captive Foxes Is a Correlated By-Product of Experimental Domestication. *Current Biology*, *15*(3), 226–230. https://doi.org/10.1016/j.cub.2005.01.040

Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Sciences*, *9*(9), Article 9. https://doi.org/10.1016/j.tics.2005.07.003

Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour*, *83*(3), Article 3. https://doi.org/10.1016/j.anbehav.2011.12.007

Hecht, E. E., Barton, S. A., Rogers Flattery, C. N., & Meza Meza, A. (2023). The evolutionary neuroscience of domestication. *Trends in Cognitive Sciences*, *27*(6), 553–567. https://doi.org/10.1016/j.tics.2023.03.008

Himmler, B. T., Stryjek, R., Modlinska, K., Derksen, S. M., Pisula, W., & Pellis, S. M. (2013). How domestication modulates play behavior: A comparative analysis between wild rats and a laboratory strain of Rattus norvegicus. *Journal of Comparative Psychology*, *127*(4), 453–464. https://doi.org/10.1037/a0032187

Himsworth, C. G., Parsons, K. L., Jardine, C., & Patrick, D. M. (2013). Rats, Cities, People, and Pathogens: A Systematic Review and Narrative Synthesis of Literature Regarding the Ecology of Rat-Associated Zoonoses in Urban Centers. *Vector-Borne and Zoonotic Diseases*, *13*(6), 349–359. https://doi.org/10.1089/vbz.2012.1195

Hu, Y., Hu, S., Wang, W., Wu, X., Marshall, F. B., Chen, X., Hou, L., & Wang, C. (2014). Earliest evidence for commensal processes of cat domestication. *Proceedings of the National Academy of Sciences*, *111*(1), 116–120. https://doi.org/10.1073/pnas.1311439110

Jansen, T., Forster, P., Levine, M. A., Oelke, H., Hurles, M., Renfrew, C., Weber, J., & Olek, K. (2002). Mitochondrial DNA and the origins of the domestic horse. *Proceedings of the National Academy of Sciences*, *99*(16), 10905–10910. https://doi.org/10.1073/pnas.152330099

Jean-Joseph, H., Dooey, G., & Kotrschal, K. (2022). Diurnal activity patterns of equally socialized and kept wolves, Canis lupus, and dogs, Canis lupus familiaris. *Animal Behaviour*, *190*, 41–52. https://doi.org/10.1016/j.anbehav.2022.05.009

Jean-Joseph, H., Kortekaas, K., Range, F., & Kotrschal, K. (2020). Context-Specific Arousal During Resting in Wolves and Dogs: Effects of Domestication? *Frontiers in Psychology*, *11*. https://www.frontiersin.org/articles/10.3389/fpsyg.2020.568199

Jean-Joseph, H., Kortekaas, K., Range, F., & Kotrschal, K. (submitted). Equally raised and kept wolves and dogs show similar risk-proneness – no matter whether alone or with a familiar human. *PLOS ONE*.

Johnsson, M., Henriksen, R., & Wright, D. (2021). The neural crest cell hypothesis: No unified explanation for domestication. *Genetics*, *219*(1), iyab097. https://doi.org/10.1093/genetics/iyab097

Kaminski, J., & Nitzschner, M. (2013). Do dogs get the point? A review of dog–human communication ability. *Learning and Motivation*, *44*(4), Article 4. https://doi.org/10.1016/j.lmot.2013.05.001

King, S. R. B. (2002). Home range and habitat use of free-ranging Przewalski horses at Hustai National Park, Mongolia. *Applied Animal Behaviour Science*, *78*(2), 103–113. https://doi.org/10.1016/S0168-1591(02)00087-4

Kobryn, H. T., Swinhoe, E. J., Bateman, P. W., Adams, P. J., Shephard, J. M., & Fleming, P. A. (2023). Foxes at your front door? Habitat selection and home range estimation of suburban red foxes (Vulpes vulpes). *Urban Ecosystems*, *26*(1), 1–17. https://doi.org/10.1007/s11252-022-01252-5

Koolhaas, J. M. (2010). The laboratory rat. *The UFAW Handbook on the Care and Management of Laboratory and Other Research Animals*, *8*, 311–326.

Kortekaas, K., & Kotrschal, K. (2019). Does socio-ecology drive differences in alertness between wolves and dogs when resting? *Behavioural Processes*, *166*, 103877. https://doi.org/10.1016/j.beproc.2019.05.024

Kotrschal, K. (2016). *Hund & Mensch: Das Geheimnis unserer Seelenverwandtschaft*. Christian Brandstätter Verlag.

Kotrschal, K. (2018). How Wolves Turned into Dogs and How Dogs Are Valuable in Meeting Human Social Needs. *People and Animals: The International Journal of Research and Practice*, *1*(1), Article 1. https://docs.lib.purdue.edu/paij/vol1/iss1/6

Kyselý, R., & Peške, L. (2022). New discoveries change existing views on the domestication of the horse and specify its role in human prehistory and history – a review. *Archeologické Rozhledy*, *74*(3), Article 3. https://doi.org/10.35686/AR.2022.15

Lawler, A. (2016). *Why Did the Chicken Cross the World?: The Epic Saga of the Bird that Powers Civilization*. Simon and Schuster.

Lazzaroni, M., Range, F., Backes, J., Portele, K., Scheck, K., & Marshall-Pescini, S. (2020). The Effect of Domestication and Experience on the Social Interaction of Dogs and Wolves With a Human Companion. *Frontiers in Psychology*, *11*, 785. https://doi.org/10.3389/fpsyg.2020.00785

Leavell, B. C., & Bernal, X. E. (2019). The Cognitive Ecology of Stimulus Ambiguity: A Predator–Prey Perspective. *Trends in Ecology & Evolution*, *34*(11), 1048–1060. https://doi.org/10.1016/j.tree.2019.07.004

Lord, K. A., Larson, G., Coppinger, R. P., & Karlsson, E. K. (2020). The History of Farm Foxes Undermines the Animal Domestication Syndrome. *Trends in Ecology & Evolution*, *35*(2), 125–136. https://doi.org/10.1016/j.tree.2019.10.011

MacLean, E. L., Snyder-Mackler, N., vonHoldt, B. M., & Serpell, J. A. (2019). Highly heritable and functionally relevant breed differences in dog behaviour. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1912), 20190716. https://doi.org/10.1098/rspb.2019.0716

Mäses, M., & Wascher, C. A. F. (2023). Assessing cats' (Felis catus) sensitivity to human pointing gestures. *Journal of Comparative Psychology*, *137*(1), 38–44. https://doi.org/10.1037/com0000338

Mech, L. D., & Janssens, L. A. A. (2022). An assessment of current wolf Canis lupus domestication hypotheses based on wolf ecology and behaviour. *Mammal Review*, *52*(2), 304–314. https://doi.org/10.1111/mam.12273

Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., & Csányi, V. (2003). A simple reason for a big difference: Wolves do not look back at humans, but dogs do. *Current Biology*, *13*(9), Article 9.

Miklósi, Á., & Topál, J. (2013). What does it take to become 'best friends'? Evolutionary changes in canine social competence. *Trends in Cognitive Sciences*, *17*(6), Article 6. https://doi.org/10.1016/j.tics.2013.04.005

Moors, P. J., Atkinson, I. a. E., & Sherley, G. H. (1992). Reducing the rat threat to island birds. *Bird Conservation International*, *2*(2), 93–114. https://doi.org/10.1017/S0959270900002331

Moretti, L., Hentrup, M., Kotrschal, K., & Range, F. (2015). The influence of relationships on neophobia and exploration in wolves and dogs. *Animal Behaviour*, *107*(Supplement C), Article Supplement C. https://doi.org/10.1016/j.anbehav.2015.06.008

Nagasawa, M., Mitsui, S., En, S., Ohtani, N., Ohta, M., Sakuma, Y., Onaka, T., Mogi, K., & Kikusui, T. (2015). Oxytocin-gaze positive loop and the coevolution of human-dog bonds. *Science*, *348*(6232), 333–336. https://doi.org/10.1126/science.1261022

Nilson, S. M., Gandolfi, B., Grahn, R. A., Kurushima, J. D., Lipinski, M. J., Randi, E., Waly, N. E., Driscoll, C., Murua Escobar, H., Schuster, R. K., Maruyama, S., Labarthe, N., Chomel, B. B., Ghosh, S. K., Ozpinar, H., Rah, H.-C., Millán, J., Mendes-de-Almeida, F., Levy, J. K., … Lyons, L. A. (2022). Genetics of randomly bred cats support the cradle of cat domestication being in the Near East. *Heredity*, *129*(6), Article 6. https://doi.org/10.1038/s41437-022-00568-4

Oltenacu, P. A., & Broom, D. M. (2010). The impact of genetic selection for increased milk yield on the welfare of dairy cows. *Animal Welfare*, *19*(S1), 39–49. https://doi.org/10.1017/S0962728600002220

Paaby, A. B., & Rockman, M. V. (2013). The many faces of pleiotropy. *Trends in Genetics*, *29*(2), 66–73. https://doi.org/10.1016/j.tig.2012.10.010

Padovani, R., Shi, Z., & Harris, S. (2021). Are British urban foxes (Vulpes vulpes) “bold”? The importance of understanding human–wildlife interactions in urban areas. *Ecology and Evolution*, *11*(2), Article 2. https://doi.org/10.1002/ece3.7087

Pendleton, A. L., Shen, F., Taravella, A. M., Emery, S., Veeramah, K. R., Boyko, A. R., & Kidd, J. M. (2018). Comparison of village dog and wolf genomes highlights the role of the neural crest in dog domestication. *BMC Biology*, *16*(1), 64. https://doi.org/10.1186/s12915-018-0535-2

Pimentel, D., Zuniga, R., & Morrison, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, *52*(3), 273–288. https://doi.org/10.1016/j.ecolecon.2004.10.002

Pongrácz, P., Szapu, J. S., & Faragó, T. (2019). Cats (Felis silvestris catus) read human gaze for referential information. *Intelligence*, *74*, 43–52. https://doi.org/10.1016/j.intell.2018.11.001

Range, F., & Marshall-Pescini, S. (2022). Taking confounding factors and life experience seriously. *Trends in Cognitive Sciences*, *26*(9), 730–731. https://doi.org/10.1016/j.tics.2022.06.007

Range, F., Marshall-Pescini, S., Kratz, C., & Virányi, Z. (2019). Wolves lead and dogs follow, but they both cooperate with humans. *Scientific Reports*, *9*(1), Article 1. https://doi.org/10.1038/s41598-019-40468-y

Range, F., & Virányi, Z. (2015). Tracking the evolutionary origins of dog-human cooperation: The “Canine Cooperation Hypothesis.” *Frontiers in Psychology*, *5*. https://doi.org/doi.org/10.3389/fpsyg.2014.01582

Rao, A., Range, F., Kadletz, K., Kotrschal, K., & Marshall-Pescini, S. (2018). Food preferences of similarly raised and kept captive dogs and wolves. *PLOS ONE*, *13*(9), Article 9. https://doi.org/10.1371/journal.pone.0203165

Rauw, W. M., Kanis, E., Noordhuizen-Stassen, E. N., & Grommers, F. J. (1998). Undesirable side effects of selection for high production efficiency in farm animals: A review. *Livestock Production Science*, *56*(1), 15–33. https://doi.org/10.1016/S0301-6226(98)00147-X

Scanes, C. G. (2020). Avian Physiology: Are Birds Simply Feathered Mammals? *Frontiers in Physiology*, *11*. https://www.frontiersin.org/articles/10.3389/fphys.2020.542466

Schütz, K. E., Forkman, B., & Jensen, P. (2001). Domestication effects on foraging strategy, social behaviour and different fear responses: A comparison between the red junglefowl (Gallus gallus) and a modern layer strain. *Applied Animal Behaviour Science*, *74*(1), 1–14. https://doi.org/10.1016/S0168-1591(01)00156-3

Schütz, K. E., Kerje, S., Carlborg, Ö., Jacobsson, L., Andersson, L., & Jensen, P. (2002). QTL Analysis of a Red Junglefowl × White Leghorn Intercross Reveals Trade-Off in Resource Allocation Between Behavior and Production Traits. *Behavior Genetics*, *32*(6), 423–433. https://doi.org/10.1023/A:1020880211144

Schütz, K. E., Kerje, S., Jacobsson, L., Forkman, B., Carlborg, Ö., Andersson, L., & Jensen, P. (2004). Major Growth QTLs in Fowl Are Related to Fearful Behavior: Possible Genetic Links Between Fear Responses and Production Traits in a Red Junglefowl × White Leghorn Intercross. *Behavior Genetics*, *34*(1), 121–130. https://doi.org/10.1023/B:BEGE.0000009481.98336.fc

Schweinfurth, M. K. (2020). The social life of Norway rats (Rattus norvegicus). *ELife*, *9*, e54020. https://doi.org/10.7554/eLife.54020

Serpell, J. A. (2021). Commensalism or Cross-Species Adoption? A Critical Review of Theories of Wolf Domestication. *Frontiers in Veterinary Science*, *8*. https://www.frontiersin.org/articles/10.3389/fvets.2021.662370

Shipman, P. (2015). *The Invaders: How Humans and Their Dogs Drove Neanderthals to Extinction*. Harvard University Press.

Stuermer, I. W., & Wetzel, W. (2006). Early experience and domestication affect auditory discrimination learning, open field behaviour and brain size in wild Mongolian gerbils and domesticated Laboratory gerbils (Meriones unguiculatus forma domestica). *Behavioural Brain Research*, *173*(1), 11–21. https://doi.org/10.1016/j.bbr.2006.05.025

Takagi, S., Chijiiwa, H., Arahori, M., Saito, A., Fujita, K., & Kuroshima, H. (2021). Socio-spatial cognition in cats: Mentally mapping owner's location from voice. *PLOS ONE*, *16*(11), e0257611. https://doi.org/10.1371/journal.pone.0257611

Taylor, W. T. T., & Barrón-Ortiz, C. I. (2021). Rethinking the evidence for early horse domestication at Botai. *Scientific Reports*, *11*(1), 7440. https://doi.org/10.1038/s41598-021-86832-9

Thalmann, O., Shapiro, B., Cui, P., Schuenemann, V. J., Sawyer, S. K., Greenfield, D. L., Germonpré, M. B., Sablin, M. V., López-Giráldez, F., Domingo-Roura, X., Napierala, H., Uerpmann, H.-P., Loponte, D. M., Acosta, A. A., Giemsch, L., Schmitz, R. W., Worthington, B., Buikstra, J. E., Druzhkova, A., … Wayne, R. K. (2013). Complete Mitochondrial Genomes of Ancient Canids Suggest a European Origin of Domestic Dogs. *Science*, *342*(6160), Article 6160. https://doi.org/10.1126/science.1243650

Tolhurst, B. A., Baker, R. J., Cagnacci, F., & Scott, D. M. (2020). Spatial Aspects of Gardens Drive Ranging in Urban Foxes (Vulpes vulpes): The Resource Dispersion Hypothesis Revisited. *Animals*, *10*(7), Article 7. https://doi.org/10.3390/ani10071167

Turner, D. C. (2021). The Mechanics of Social Interactions Between Cats and Their Owners. *Frontiers in Veterinary Science*, *8*. https://www.frontiersin.org/articles/10.3389/fvets.2021.650143

Uccheddu, S., Miklósi, Á., Gintner, S., & Gácsi, M. (2022). Comparing Pears to Apples: Unlike Dogs, Cats Need Habituation before Lab Tests. *Animals*, *12*(21), Article 21. https://doi.org/10.3390/ani12213046

Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2010). What did domestication do to dogs? A new account of dogs' sensitivity to human actions. *Biological Reviews*, *85*(2), Article 2. https://doi.org/10.1111/j.1469-185X.2009.00104.x

Vitale, K. R., Behnke, A. C., & Udell, M. A. R. (2019). Attachment bonds between domestic cats and humans. *Current Biology*, *29*(18), R864–R865. https://doi.org/10.1016/j.cub.2019.08.036

Vitale Shreve, K. R., & Udell, M. A. R. (2015). What's inside your cat's head? A review of cat (Felis silvestris catus) cognition research past, present and future. *Animal Cognition*, *18*(6), 1195–1206. https://doi.org/10.1007/s10071-015-0897-6

vonHoldt, B. M., Shuldiner, E., Koch, I. J., Kartzinel, R. Y., Hogan, A., Brubaker, L., Wanser, S., Stahler, D., Wynne, C. D. L., Ostrander, E. A., Sinsheimer, J. S., & Udell, M. A. R. (2017). Structural variants in genes associated with human Williams-Beuren syndrome underlie stereotypical hypersociability in domestic dogs. *Science Advances*, *3*(7), Article 7. https://doi.org/10.1126/sciadv.1700398

Warmuth, V., Eriksson, A., Bower, M. A., Barker, G., Barrett, E., Hanks, B. K., Li, S., Lomitashvili, D., Ochir-Goryaeva, M., Sizonov, G. V., Soyonov, V., & Manica, A. (2012). Reconstructing the origin and spread of horse domestication in the Eurasian steppe. *Proceedings of the National Academy of Sciences*, *109*(21), 8202–8206. https://doi.org/10.1073/pnas.1111122109

Wilkins, A. S. (2017). Revisiting two hypotheses on the “domestication syndrome” in light of genomic data. *Vavilov Journal of Genetics and Breeding*, *21*(4), Article 4. https://doi.org/10.18699/VJ17.262

Wilkins, A. S. (2020). A striking example of developmental bias in an evolutionary process: The “domestication syndrome.” *Evolution & Development*, *22*(1–2), 143–153. https://doi.org/10.1111/ede.12319

Wilkins, A. S., Wrangham, R., & Fitch, W. T. (2021). The neural crest/domestication syndrome hypothesis, explained: Reply to Johnsson, Henriksen, and Wright. *Genetics*, *219*(1), iyab098. https://doi.org/10.1093/genetics/iyab098

Wilkins, A. S., Wrangham, R. W., & Fitch, W. T. (2014). The “Domestication Syndrome” in Mammals: A Unified Explanation Based on Neural Crest Cell Behavior and Genetics. *Genetics*, *197*(3), Article 3. https://doi.org/10.1534/genetics.114.165423

Wirobski, G., Range, F., Schaebs, F. S., Palme, R., Deschner, T., & Marshall-Pescini, S. (2021a). Endocrine changes related to dog domestication: Comparing urinary cortisol and oxytocin in hand-raised, pack-living dogs and wolves. *Hormones and Behavior*, *128*, 104901. https://doi.org/10.1016/j.yhbeh.2020.104901

Wirobski, G., Range, F., Schaebs, F. S., Palme, R., Deschner, T., & Marshall-Pescini, S. (2021b). Life experience rather than domestication accounts for dogs’ increased oxytocin release during social contact with humans. *Scientific Reports*, *11*(1), 14423. https://doi.org/10.1038/s41598-021-93922-1

Appendix|

Supplementary material from Chapter 1

Supplementary Materials

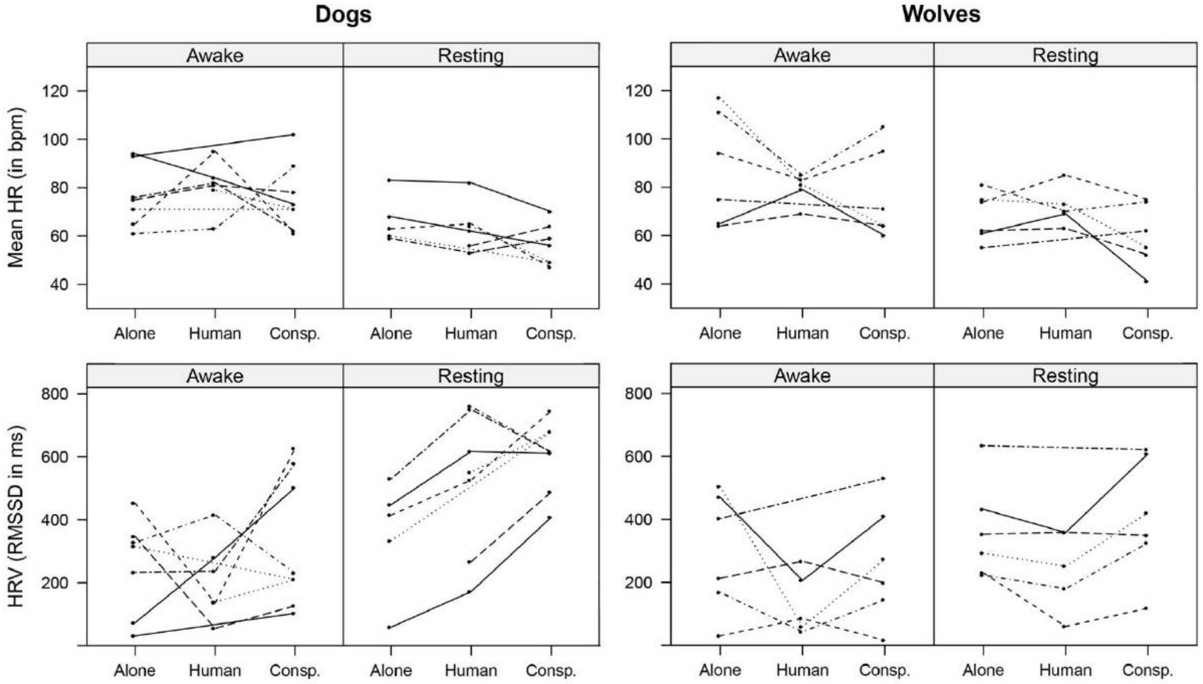


Figure 1: Plot of the individual data. A) Individual mean HR of dogs when resting or awake. B) Individual mean HR of wolves when resting or awake. C) Individual RMSSD of dogs when resting or awake. D) Individual RMSSD of wolves when resting or awake. Each line style represent a different individual.

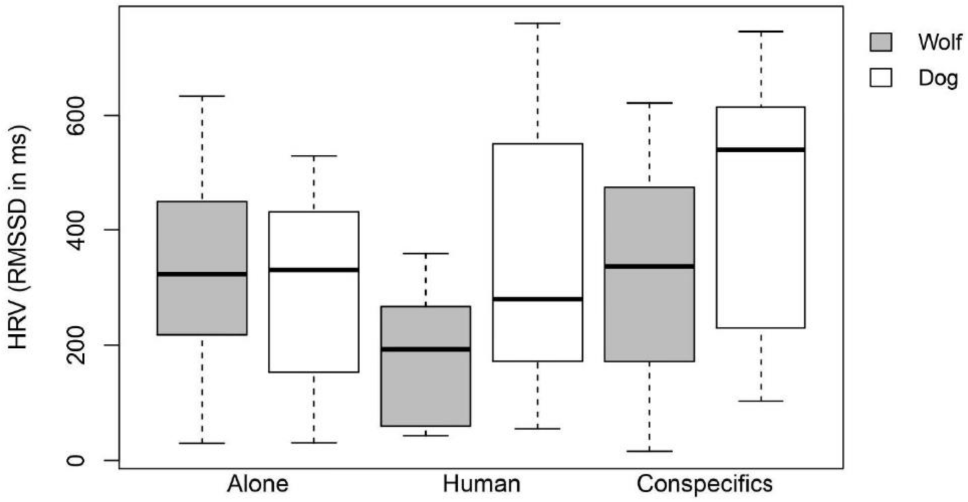


Figure 2: Boxplot of HRV representing the interaction between species and condition. The different level of the activity factor (resting or awake inactive) are both included in this boxplot.

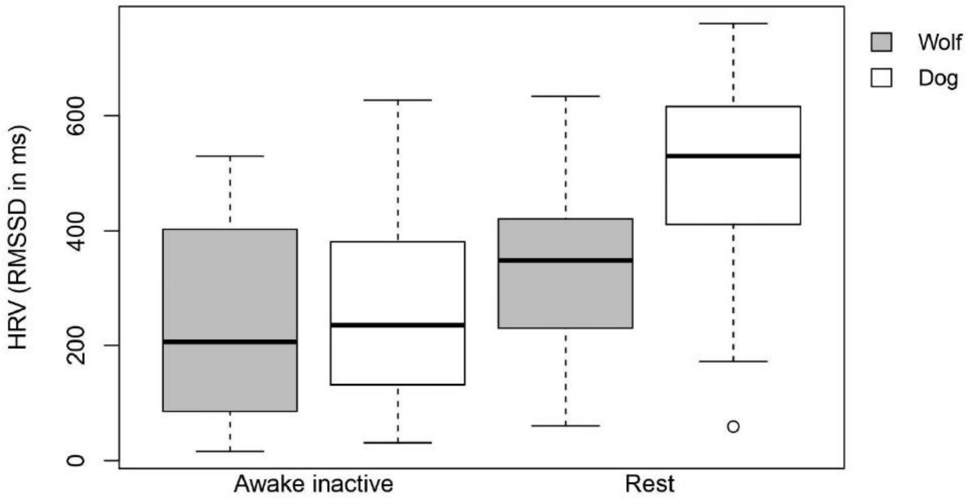


Figure 3: Boxplot of HRV representing the interaction between species and activity. The different level of the condition factor (alone, with a familiar human or with pack members) are all included in this boxplot.

Supplementary Material

Table S1: Estimates, standard errors, lower an upper confidence interval and minimum and maximum values of the HR model

	Estimate	SE	Lower CI	Upper CI	min	max
Intercept	97.245	6.440	81.185	111.183	85.316	127.884
Species (0: dog; 1: wolf)	-25.237	9.604	-48.329	0.340	-67.823	-12.218
Human	9.908	4.123	2.100	19.327	6.189	13.864
Conspecifics	3.002	5.315	-7.937	14.480	-0.668	6.901
Activity (0: awake; 1: rest)	-11.773	3.560	-18.843	-4.828	-14.294	-8.874
Body mass[1]	10.706	3.585	1.190	19.384	7.685	29.470
Temperature[1]	-2.027	1.016	-4.405	0.441	-4.083	-0.897
Age[1]	15.248	2.402	9.001	20.828	6.113	23.909
Sex (0: F; 1: M)	-5.251	2.470	-11.713	1.534	-11.107	-0.461
Wolf:Human	-21.823	6.053	-34.864	-9.783	-26.241	-16.480
Wolf:Conspecifics	-16.729	7.465	-32.717	-1.932	-20.688	-7.496
Wolf:Rest	-7.956	4.942	-17.334	2.666	-11.249	-3.609
C.human:Rest	-9.627	4.448	-18.841	-1.156	-12.799	-5.370
Conspecifics:Rest	-7.030	4.361	-15.656	2.223	-10.718	-4.177
Wolf:Human:Rest	22.889	6.490	9.816	35.788	18.818	26.666
Wolf:Conspecifics:Rest	10.030	6.185	-2.276	21.923	4.199	13.718

[1] predictors were z-transformed to a mean of zero and a standard deviation of one; original means (sd) were weight: 32.98 (9.49) kg , temperature: 22.41 (7.18) °C and age 2440.23 (801.93) days.

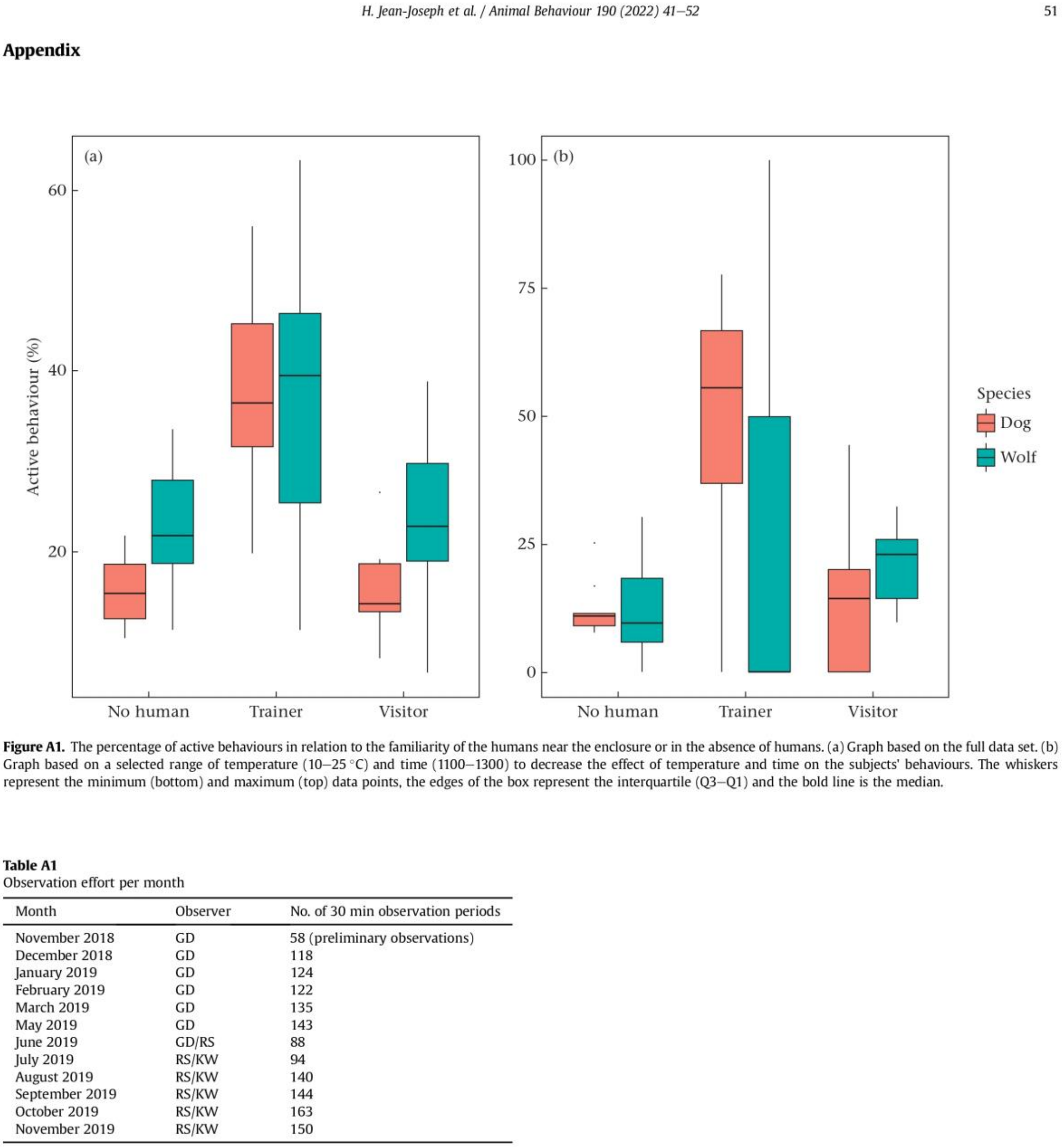
Supplementary Material

Table S2: Estimates, standard errors, lower and upper confidence intervals and minimum and maximum values of the HRV model

	Estimate	SE	Lower CI	Upper CI	min	max
Intercept	270.451	88.462	99.519	439.275	-44.198	383.619
Species (0: dog; 1: wolf)	80.431	133.413	-184.605	348.774	-115.856	567.343
Human	-24.868	57.153	-148.773	88.136	-56.304	19.503
Conspecifics	122.402	44.987	32.197	208.489	84.807	154.112
Activity (0: awake; 1: rest)	149.889	43.636	62.819	237.507	128.940	180.957
Body mass[1]	80.874	60.934	-39.359	207.593	-153.117	173.482
Temperature[1]	-5.988	14.578	-33.678	23.122	-19.428	21.783
Age[1]	-103.540	41.188	-187.868	-21.468	-137.475	-73.401
Sex (0: F; 1:M)	-68.764	69.425	-197.447	62.918	-151.351	51.167
Wolf:Human	-163.474	76.643	-319.109	-16.261	-193.285	-128.575
Wolf:Conspecifics	-168.204	53.965	-280.68	-62.354	-219.126	-143.187
Wolf:Rest	-130.650	42.885	-212.010	-43.779	-147.159	-120.729
Human:Rest	150.712	53.755	45.197	259.557	117.884	184.879
Conspecifics:Rest	114.564	51.403	11.684	216.154	85.006	145.558

[1] predictors were z-transformed to a mean of zero and a standard deviation of one;
original means (sd) were weight: 32.98 (9.49) kg , temperature: 22.41 (7.18) °C and age 2440.23 (801.93) days.

Supplementary material from Chapter 2



Appendix

Figure A1. The percentage of active behaviours in relation to the familiarity of the humans near the enclosure or in the absence of humans. (a) Graph based on the full data set. (b) Graph based on a selected range of temperature (10–25 °C) and time (1100–1300) to decrease the effect of temperature and time on the subjects' behaviours. The whiskers represent the minimum (bottom) and maximum (top) data points, the edges of the box represent the interquartile (Q3–Q1) and the bold line is the median.

Table A1
Observation effort per month

Month	Observer	No. of 30 min observation periods
November 2018	GD	58 (preliminary observations)
December 2018	GD	118
January 2019	GD	124
February 2019	GD	122
March 2019	GD	135
May 2019	GD	143
June 2019	GD/RS	88
July 2019	RS/KW	94
August 2019	RS/KW	140
September 2019	RS/KW	144
October 2019	RS/KW	163
November 2019	RS/KW	150

Table A2
Percentage occurrence of each behaviour for the overall data set and when humans were present or absent

Behaviours	Overall		Human present[1]		Human absent[1]	
	Wolves	Dogs	Wolves	Dogs	Wolves	Dogs
Cantering	0.09	0.19	0.23	1.02	0.05	0.03
Defecating	0.02	0.01	0.01	0	0.03	0.02
Digging	0.01	0.30	0	0.57	0.02	0.27
Drinking	0.20	0.22	0.27	0.28	0.18	0.22
Eating	0.61	0.23	0.69	0.60	0.61	0.16
Foraging	1.82	4.43	1.29	4.86	2.05	4.55
Hunting	<0.01	0.01	0.01	0	<0.01	0.02
Lying	15.97	19.88	16.68	15.56	16.28	21.68
Sitting	0.58	7.93	0.48	7.36	0.63	8.42
Standing	18.83	19.58	20.76	36.96	18.86	16.89
Maintenance	1.23	1.63	1.49	0.67	1.19	1.91
Not visible	2.50	3.64	0.01	0	<0.01	0
Object manipulation	0.05	1.06	0.05	1.04	0.05	1.12
Resting	5.06	5.28	5.57	2.66	5.07	6.06
Sexual	0.07	0	0.12	0	0.06	0
Sleeping	33.38	25.70	26.75	6.28	36.62	30.88
Social	1.04	0.89	1.44	1.80	0.95	0.74
Stress	<0.01	0	<0.01	0	0	0
Trotting	3.79	2.05	5.68	5.65	3.32	1.40
Urinating	0.04	0.06	0.03	0.04	0.05	0.06
Vocalizing	2.62	2.31	2.20	8.69	2.84	1.10
Walking	12.03	4.54	16.20	5.95	11.11	4.46
Inactive	73.83	78.39	70.24	68.81	77.46	83.93
Active	26.17	21.61	29.76	31.19	22.54	16.07

[1] The data do not include the observations where the presence or absence of humans was not available (3328 occasions out of 113 507). Behaviours in italic are those considered as inactive.

Table A3
Percentage occurrence of the conditions no human present and familiar (trainer) or unfamiliar (visitor) human present

	No human	Trainer	Visitor	Mixed group
Dog	82.90	6.57	3.35	7.18
Wolf	75.83	2.82	14.90	6.45

Table A4
Individuals' count and activity score (%) in relation to the conditions no human present and familiar (trainer) or unfamiliar (visitor) human present

Individual	No human		Trainer		Visitor	
	Count	%	Count	%	Count	%
Wolves						
Amarok	980	28.34	37	47.43	166	23.41
Aragorn	480	12.37	32	19.63	16	16.33
Chitto	619	21.57	22	29.33	244	31.16
Etu	1043	28.90	20	26.31	227	32.15
Geronimo	696	21.87	78	37.14	147	21.06
Kaspar	739	19.08	81	46.02	29	29.29
Kenai	816	22.84	50	63.29	166	21.40
Maikan	999	27.74	14	19.82	189	26.18
Nanuk	405	11.29	47	35.88	106	13.96
Shima	303	17.54	14	22.58	3	6.67
Taima	938	29.55	47	48.86	372	35.26
Tala	516	18.84	9	11.25	145	19.73
Tekoa	1067	29.55	51	54.84	404	38.80
Una	651	18.05	56	42.10	184	24.73
Wamblee	676	21.69	95	44.39	100	15.15
Yukon	868	27.36	86	41.95	150	22.15
Dogs						
Asali	679	16.03	102	41.63	9	8.11
Bora	915	21.80	105	46.46	30	26.55
Enzi	435	12.51	130	47.27	158	13.29
Gombo	182	10.76	19	35.18	25	14.20
Hiari	374	10.40	349	19.77	8	11.27
Imara	581	14.60	358	29.89	13	19.12
Layla	735	21.51	154	56.00	32	17.02
Meru	327	12.58	105	30.88	4	13.34
Panya	596	17.22	105	37.77	25	14.12
Zuri	657	18.99	103	33.77	55	19.16

Supplementary material from Chapter 3

APPENDIX

Table S1: Number of approaches

		Non-social condition		Social condition		Both	
		Food	Apparatus	Food	Apparatus	Food	Apparatus
Never approached	Wolves	4	11	3	11	3	9
	Dogs	3	13	8	11	1	11
Approached at least once	Wolves	7	1	10	3	7	0
	Dogs	6	2	13	3	6	1

Table S2: Supplementary material; Descriptive statistic of the HR model

	Estimate	Std. Error	t value	X2.5.	X97.5.	min	max
(Intercept)	163.114	21.406	7.62	119.859	205.076	151.016	173.717
Species (Wolf; Dog)	-10.21	13.621	-0.75	-38.604	16.415	-29.195	-1.557
Conditions (S; NS)	-1.185	6.325	-0.187	-13.281	10.957	-4.287	3.75
Temperature	-0.145	0.553	-0.262	-1.284	0.941	-0.387	0.081
Order (1; 2)	-6.655	6.049	-1.1	-18.45	5.463	-9.565	-4.355
Age	-1.89	1.138	-1.661	-4.164	0.36	-2.518	-1.194
Sex (M; F)	-3.193	7.816	-0.409	-18.881	12.084	-12.709	-0.213
Weight	-0.209	0.803	-0.26	-1.726	1.421	-0.623	0.79
Success (Yes; No)	2.325	6.68	0.348	-10.135	15.27	-3.969	6.064
HR Stage	-22.622	5.621	-4.025	-33.467	-12.175	-26.069	-19.117
	-14.495	4.751	-3.051	-23.586	-5.233	-16.835	-11.052
Species x Conditions	10.536	10.223	1.031	-9.01	30.736	4.529	16.721

Supplementary material from Chapter 4

Appendix A. Supplementary Materials

Table A.1: Results of the Agitated behaviours model

	Estimate	SE	X^2	df	P
(Intercept)	102.69	17.52			
Species	-76.51	25.13			
Condition	-69.56	12.74			
Weight	21.15	12.34	2.70	1	0.100
Order	-20.21	10.72	3.25	1	0.071
Species x Condition	50.49	18.13	7.02	1	0.008

Table A.2: Results of the alert behaviours model

	Estimate	SE	X^2	df	P
(Intercept)	177.44	26.44			
Species	9.61	37.12	0.07	1	0.80
Condition	-57.52	12.74	14.51	1	<0.001
Weight	-23.30	18.92	1.50	1	0.22
Order	-17.03	16.20	1.10	1	0.29

Table A.3: Results of the relaxed behaviours model

	Estimate	SE	X^2	df	P
(Intercept)	0.32	10.64			
Species	6.18	15.22			
Condition	34.128	7.96			
Weight	-4.29	7.50	0.33	1	0.57
Order	3.30	6.65	0.25	1	0.64

Species x Condition	-30.57	11.32	6.97	1	0.008

Table A.4: Results of the foraging behaviours model

	Estimate	SE	X^2	df	P
(Intercept)	76.13	21.06			
Species	-48.29	29.62	2.61	1	0.106
Condition	29.30	10.71	6.79	1	0.009
Weight	73.48	14.99	20.68	1	<0.001
Order	26.70	2.10	4.20	1	0.04

Table A.5: Results of the latency to 1st approach to the food model

	Estimate	SE	Z	P
Species	3.24	0.84	3.88	<0.001
Condition	1.60	0.75	2.13	0.03
Order	1.38	0.39	3.52	<0.001
Species x Condition	-1.29	0.28	-1.51	0.13

Table A.6: Results of the object investigation model

	Estimate	SE	X^2	df	P
(Intercept)	-4.48	6.33			
Species	10.89	9.11	1.41	1	0.23
Condition	8.78	3.11	7.28	1	0.007
Weight	-5.38	4.60	1.35	1	0.24
Order	2.35	3.81	0.38	1	0.54

Table A.7: Results of the latency to 1st approach the object

	Estimate	SE	Z	P
Species	-1.54	0.71	-2.18	0.03
Condition	-1.60	0.68	-2.35	0.02
Order	-0.19	0.41	0.46	0.65
Species x Condition	50.49	0.95	3.27	0.001

Table A.8: Results of the proximity to partner model

	Estimate	SE	X^2	df	P
(Intercept)	315.49	47.50			
Species	-167.73	73.79	4.68	1	0.03
Weight	80.46	37.49	4.07	1	0.04
Order	-53.36	32.07	2.19	1	0.14

Abstract

Humans and wolves/dogs are together since Paleolithic times. Along the way, domestication had made dogs to differ from wolves. This may include a changed perception of humans and their ability to interact and bond with them. In my PhD thesis, I aimed to test wolves' and dogs' behavioural and physiological reactions to familiar humans in different contexts to elucidate how equally raised and kept wolves and dogs perceived humans. In Chapter 1, I compared wolves' and dogs' cardiac output during rest. Humans and conspecifics had a similar relaxing effect on dogs whereas in wolves, only conspecifics had this effect. In Chapter 2, I compared wolves' and dogs’ diurnal time budgets and the impact of humans’ presence on their activity levels. Despite similar time budgets, dogs reacted more to the presence of humans than wolves. In Chapter 3, I used a risk-taking paradigm to compare wolves' and dogs' risk-proneness and responses to familiar humans providing social support. Surprisingly, age was the main factor affecting risk-proneness in both, wolves and dogs, and social support by a familiar human had no effect. Finally, in Chapter 4, I broadened the topic of my thesis by extending my research to a bird species and compared domesticated chicks to a wild-type strain in a risk-taking paradigm similar to the one used in Chapter 3. Agreeing with current domestication hypotheses – but contrasting with my results in wolves and dogs, domesticated chicks were more food-motivated and less scared than their wild-type relatives. Altogether, my results indicate that dogs and wolves do perceive humans somewhat differently. However, those differences may be more context-dependent than mainstream domestication hypotheses claim. Hence domestication might have more subtle, diversified, and context-dependent effects than previously thought. Future domestication research could therefore benefit by heeding more the context in experimental paradigms.

Zusammenfassung

Bereits in der Altsteinzeit fanden Menschen und Wölfe/Hunde zusammen. Seitdem entwickelten sich durch den Domestikationsprozess Hunde unterschiedlich von Wölfen. Dies mag eine veränderte Sicht auf die Menschenpartner, sicherlich aber die Fähigkeit der Hunde, mit Menschen zu interagieren mit einschließen. Ziel meines PhD Projekts war es, verhaltens- und physiologische Reaktionen von gleichartig aufgezogenen Wölfen und Hunden in bestimmten Kontexten und den Einfluss ihnen bekannter Menschen zu untersuchen. Im ersten Kapitel vergleiche ich die Herztätigkeit von Wölfen und Hunden während der Ruhephase. Dabei hatten Menschen und Artgenossen ähnliche entspannende Effekte auf die Hunde, auf die Wölfe nur die Artgenossen. Im zweiten Kapitel berichte ich über einen Vergleich des Tages-Zeitbudgets von Wölfen und Hunden bei An- und Abwesenheit von Menschen. Trotz erstaunlich ähnlicher Zeitbudgets reagierten Hunde stärker auf die Anwesenheit der Menschen, als Wölfe. Im dritten Kapitel nutzte ich ein Paradigma für Risikobereitschaft, um Wölfe und Hundediesbezüglich im Zusammenhang mit Nahrung zu testen, sowie ihrer Reaktionen auf die Anwesenheit bekannter, potentiell emotional sozial unterstützender Menschen zu vergleichen. Überraschenderweise stieg die Risikobereitschaft der Wölfe und Hunde in ähnlicher Weise mit zunehmendem Alter, aber soziale Unterstützung durch bekannte Menschen zeigte keine signifikanten Effekte. Im letzten Kapitel vergleiche ich mittels eines Paradigmas für Risikobereitschaft – vergleichbar mit dem Ansatz in Kapitel 3 – domestizierte Hühner mit einem Wildtypstamm. Übereinstimmend mit aktuellen Hypothesen zur Domestikation, jedoch im Gegensatz zu meinen Ergebnissen von den Wölfen und Hunden, zeigten sich domestizierte Hühner als futtermotivierter und weniger ängstlich als Wildtyp-Hühner. Meine Ergebnisse belegen, dass Hunde und Wölfe die Menschen etwas unterschiedlich wahrnehmen. Allerdings scheinen diese Unterschiede weniger stark und wesentlich kontextabhängiger ausgeprägt zu sein als gängige Domestikationshypothesen bisher vermuten lassen. Zukünftige Untersuchungen zur Domestikation sollten also stärker als bisher in den experimentellen Paradigmen auf die genauen Kontexte achten.