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Both humans and conspecifics provide social support to dog and wolf puppies

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Social support can play a crucial role in enabling individuals to cope better with environmental stressors when accompanied by a social partner, but this effect varies strongly across species and often with partner identity. While generally conspecifics can provide social support most effectively, domesticated species might benefit also from the presence of a human partner; even more than their intensively human-socialized wild relatives. Here we set out to compare stress support provided by conspecific and human partners in equally hand-raised and kept wolf, *Canis lupus*, and dog, *Canis lupus familiaris*, puppies. Given their similar developmental trajectories and evolutionary background, we expected a similar supportive role of conspecifics in both species. Moreover, we hypothesized that domestication has prepared dogs to benefit from the presence of a human more than wolves, which, however, may be masked when intensive socialization is provided to both species. Therefore, we expected a similar stress buffering effect of a human partner in both dog and wolf puppies. To test this, we had puppies of both species participate in two neophobia tasks and one isolation-reunion-separation task. Although we found no direct differences between the two species when tested with either a conspecific or a human partner, there were a few behavioural differences between wolf and dog puppies suggesting that dogs rely more on humans than wolves. Our present results provide evidence that stress buffering has not evolved anew during the process of domestication, but also that both socialization and domestication might play a role in shaping the extent to which young dogs and wolves rely on their human partners.

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Living in groups can provide many advantages for survival including social stress buffering (generally referred to as social support) which, through the mere presence of a social partner, can help an individual cope with external stressors, which leads to a detectable reduction of physiological and behavioural stress levels (DeVries et al., 2003; Rault, 2012; Wu, 2021). Many social species have been shown to benefit from stress buffering effects of conspecifics, with individuals showing decreased signs of stress and fear and increased proximity seeking towards their partner when facing a novel stimulus in their presence, as compared to being alone (Rault, 2012). Although most social species benefit from social support, variation has been seen depending on the social organization of the species (Hennessy et al., 2009), the identity of the partner and a number of other factors (Cimarelli et al., 2019; Cimarelli, Marshall-Pescini, et al., 2021; Hennessy et al., 2009).

It is usually assumed that conspecifics are the best partners for stress buffering, albeit research has shown that heterospecifics can also be a source of social support (Frigerio et al., 2003). This might be especially true in species living in mixed-species groups (Stensland et al., 2003), including domesticated species which may benefit from the presence of humans (Hennessy et al., 2009). However, to date it is unclear whether domesticated species are more prone to accept members of other species (especially humans) as social partners than non-domesticated species and whether domestication has affected

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the social buffering effects of conspecifics (Gjøen et al., 2023; Nowak & Boivin, 2015; Udell et al., 2010).

Domestic dogs are particularly interesting in this regard, as they have the longest domestication history (Perri et al., 2021) which has affected their intraspecific social ecology as well as allowed them to play diverse roles in human societies, demonstrating a level of embeddedness that no other species has reached. Not surprisingly, studies have shown that dogs benefit from the presence of a human to a similar or larger extent than from the presence of another dog when facing a variety of environmental stressors (Cimarelli et al., 2019; Gácsi et al., 2013; Pettijohn et al., 1977; Tuber et al., 1996). However, it has not been systematically investigated to what extent dogs' abilities to use humans as social support, possibly facilitated by their long domestication history, exceed wolves' similar capacities, especially in comparison to social support provided by conspecifics. Wolves clearly benefit from conspecific social support in cooperating over hunting, rearing offspring and defending their territory (Marshall-Pescini et al., 2017), which has been confirmed by experimental studies as well (Cimarelli, Marshall-Pescini, et al., 2021; Moretti et al., 2015). These two studies found that dogs and wolves can benefit to a similar extent from the presence of a conspecific in stressful situations, suggesting that domestication did not affect their reliance on conspecifics as social supporters. Hence, wolves may also be able to accept human social support when intensively and responsively socialized by humans, and the difference between wolves and dogs in this respect may rather be one of degree than of kind (Jean-Joseph et al., 2020).

Currently it is unknown whether humans can buffer stress in dogs and wolves to a similar extent, whether this role is comparable to that of conspecifics in both species and to what extent the process of domestication has changed these aspects. Asking these questions can further our understanding of sociality, bond formation and how domestication might shape them in different species, particularly when the bonds are between domesticated animals and humans, as compared to their ancestral forms. Such an investigation has also applied implications. For instance, a better understanding of the potential supportive role of humans might help design better management practices for both captive wild and domesticated species.

Addressing these questions requires comparisons between wolves and dogs similarly and intensively socialized with both humans and conspecifics. Here we set out to test the effects of social support by conspecifics and humans on wolf, *Canis lupus*, and dog, *Canis lupus familiaris*, puppies that had been human raised in peer groups and had therefore a similar amount of experience with both humans and their conspecific peers.

While domestication has altered the intraspecific social ecology of dogs (Marshall-Pescini et al., 2017), with the most prominent difference being a more general reliance on alloparental care in wolves than in dogs (Mech, 1999; Paul et al., 2014), the early social life (up until weaning) of dog and wolf puppies in relation to their littermates does not seem to have changed dramatically. In fact, in both species, mothers give birth to two to eight puppies per litter (Scott & Fuller, 1965), pups stay in the den until approximately 3 weeks of age when they start to spend more time at the rendezvous site (Packard et al., 1992; Scott & Fuller, 1965), and pups might be left alone for various amounts of time while the mother (and/or other adult members of the pack) go foraging (Mech, 1970; Pal, 2005). If confronted with potential environmental threats, puppies may activate behavioural patterns of distress, leading to proximity seeking towards the den/siblings (Scott, 1967; Sidorovich et al., 2017). These behavioural responses, at a proximate level, are likely mediated by the perception of social isolation as a stressor, and by the sense of security and support elicited by the presence of social partners (Kikusui et al., 2006). Consequently, we argue that the supportive role of conspecifics in young animals has not changed much during domestication (Cimarelli, Marshall-Pescini, et al., 2021). Hence, here we hypothesized that puppies of the two species at a preweaning age (less than 8 weeks old) do not show differences in the extent to which they rely on their littermates. Based on this, we predicted that puppies when tested in a stressful situation in the presence of a littermate would show fewer behavioural stress responses than when tested alone, with no difference between the two species.

If so, the question of whether humans are better stress buffers for dog puppies than for wolf puppies remains. In a human-dominated environment, where dogs typically live, humans often provide food and safety (Vanak & Gompper, 2009), although occasionally they may also be a source of danger (Paul et al., 2016). This ecological background might explain why both young and adult dogs rely on humans and why, if socialized, dogs may show distress in alignment with the definition of attachment behaviour, when separated from familiar humans: greet them upon reunion, seek proximity to them in times of distress and use them as a secure base to explore a novel environment (Gàcsi et al., 2013; Horn et al., 2013; Mariti et al., 2014; Solomon et al., 2019; Topál et al., 1998, 2005). Instead, relying on humans might not be necessary (or even dangerous, Bryan et al., 2015; Sidorovich et al., 2017) for wild wolves which might only rely on conspecific pack members for protection and support (Fox, 1973).

Based on this, we hypothesized that the process of domestication has allowed dogs to be socialized to humans more easily, as compared to wolves, resulting in dogs being more able to rely on humans in stressful situations than wolves (Topál et al., 2005). This predicts that humans would act as more efficient stress buffers for dogs than for wolves, and for dogs possibly even as more potent stress buffers than conspecifics. In contrast, for wolves, conspecifics should be better stress buffers than humans, even if they were as carefully and closely human-socialized as the dogs they are compared with.

In contrast, more recent studies have reported preferential contact seeking in a stressful situation and stress buffering linked to the presence of a hand-raiser also in young wolves (Hall et al., 2015; Hansen Wheat et al., 2022). These results indicate that in some situations intensive socialization by humans may enable wolf pups to benefit from emotional support by humans even to an extent comparable to dogs. Consequently, the authors argued that domestication did not significantly affect how dogs can benefit from human presence in stressful situations. This may indicate a lack of domestication effect, but it is also compatible with another hypothesis. These studies provided all animals with early and long persisting, exclusively positive and responsive human care, which may have allowed wolves to accept humans as social partners, while this might not be necessary for dogs (Gácsi et al., 2001). Hence, it may be that domestication has reduced the need for extended and sensitive socialization with humans required for dogs to use humans as stress buffering social partners, as compared to wolves. Note that, in contrast to the above domestication hypothesis, this suggests that the underlying mechanism enabling dogs to rely on the supportive role of conspecifics and humans is the same (Lenkei et al., 2020; Range & Virányi, 2015). Several studies have shown that wolves need to be hand-raised by humans from an early age to be comfortable around humans and remain so even when adult (Klinghammer & Goodmann, 1987; Lenkei et al., 2020), in contrast to dogs which seem to need only minimal socialization to form trustful relationships with humans. This different need for socialization to benefit from human presence would predict, that, if wolves and dogs are intensively socialized with humans, they would not differ in terms of stress buffering deriving from either conspecifics or humans.

Accordingly, the aim of this study was to test the outlined hypotheses by investigating whether wolf and dog pups, when socialized to a similar extent and intensively with both humans and conspecifics, can benefit from the presence of such partners in a stressful situation. First, we analysed the supportive role of a human caregiver in a novel object task (using two different objects potentially eliciting different degrees of neophobia). Second, we aimed at investigating whether the presence of a human caregiver would differ from that of a littermate in an isolation-reunion-separation task (Nowak & Boivin, 2015). We analysed behaviours previously linked to stress buffering and social support, such as stress-related behaviours, vocalizations, fear-related behaviours (expected to be reduced with an effective stress buffering effect), as well as proximity to the partner and interaction with the environment (expected to increase with an effective stress buffering effect, Rault, 2012).

GENERAL METHODS

Ethical Note

All procedures were noninvasive and in accordance with the European Union Directive on the protection of animals used for scientific purposes (EU Directive 2010/63/EU), as well as the ASAB/ABS Guidelines for the ethical treatment of nonhuman animals in research. No special permission for use of animals (wolves and dogs) in such noninvasive behavioural studies was required in Austria (Tierversuchsgesetz 2012—TVG 2012) at the time of testing. Animals' distress in the present experimental situations was minimized thanks to the socialization provided since early life (see below); the animals were familiar with the exposure to novel objects and environments, as well as with being separated from social siblings. Still, to reduce the potential distress associated with being exposed to novel stimuli, these were only applied for a short period of time (i.e. the exposure to the novel objects used in experiment 1 was for 1 min, and the isolation was carried for a maximum of 5 min in experiment 2, see below). All subjects returned to their routine daily life immediately after the experimental procedure.

Subjects

Thirty-five animals (18 wolves, 17 dogs; Table 1) were tested at the age of 5 and 7 weeks. All wolves and dogs had been hand-raised and were kept identically at the Wolf Science Center, Austria. The wolves were born in captivity in different facilities in North America (US and Canada). The mongrel dogs were obtained from animal shelters in Hungary. Usually only two pups were taken from each litter. Dogs and wolves were hand-raised with conspecifics in peer groups of four to six after being separated from their mothers in the first 10 days after birth. The animals were intensively socialized (continuous presence of humans who also bottle and hand fed them) with humans being continuously present during both day and night until approximately 4 months old. During the first weeks of raising, the pups were kept in a 20 m^2 room equipped with different toys. Starting at the age of 4–5 weeks, they had access to an outside enclosure of 3000 m^2. The pups were regularly (two to three times per week) exposed to unfamiliar people as well as novel objects and unfamiliar situations (e.g. experiencing

Table 1
Subjects' characteristics.

Subject	Sex	Species	Year of birth	Birthplace
Amarok[a]	M	Wolf	2012	Minnesota Wildlife Connection, U.S.A.
Apache[b]	*M*	Wolf	2009	Zoo Basel, Swiss
Aragorn[c]	*M*	Wolf	2008	Game park Herberstein, Austria
Cherokee[b]	*M*	Wolf	2009	Zoo Basel, Swiss
Chitto[d]	*M*	Wolf	2012	Minnesota Wildlife Connection, U.S.A.
Geronimo[e]	*M*	Wolf	2009	Triple D Farm, Montana, U.S.A.
Kaspar[f]	*M*	Wolf	2008	Game park, Herberstein, Austria
Kay[g]	*F*	Wolf	2012	Haliburton Forest, Kanada
Kenai[j]	*M*	Wolf	2010	Parc Safari, Hemmingford, Canada
Nanuk	*M*	Wolf	2009	Triple D Farm, Montana, U.S.A.
Shima[c]	F	Wolf	2008	Game park Herberstein, Austria
Tala[a]	F	Wolf	2012	Minnesota Wildlife Connection, U.S.A.
Tatonga	F	Wolf	2009	Triple D Farm, Montana, U.S.A.
Taya[f]	F	Wolf	2008	Game park Herberstein, Austria
Una[d]	F	Wolf	2012	Minnesota Wildlife Connection, U.S.A.
Wamblee[g]	M	Wolf	2012	Haliburton Forest, Kanada
Wapi[j]	*M*	Wolf	2010	Parc Safari, Hemmingford, Canada
Yukon[e]	F	Wolf	2009	Triple D Farm, Montana, U.S.A.
Alika[1]	*F*	Dog	2009	Shelter, Hungary
Asali[2]	*M*	Dog	2010	Shelter, Hungary
Bashira[3]	*F*	Dog	2010	Shelter, Hungary
Binti[2]	*F*	Dog	2010	Shelter, Hungary
Doa[4]	*F*	Dog	2009	Shelter, Hungary
Hakima[3]	*M*	Dog	2010	Shelter, Hungary
Imani[5]	*M*	Dog	2009	Shelter, Hungary
Jini[4]	F	Dog	2009	Shelter, Hungary
Kali[6]	M	Dog	2011	Shelter, Hungary
Kilio[7]	M	Dog	2009	Shelter, Hungary
Maisha[7]	M	Dog	2009	Shelter, Hungary
Meru[8]	*M*	Dog	2010	Shelter, Hungary
Nuru[9]	*M*	Dog	2011	Shelter, Hungary
Rafiki[1]	M	Dog	2009	Shelter, Hungary
Tana[8]	M	Dog	2010	Shelter, Hungary
Uzima[5]	F	Dog	2009	Shelter, Hungary
Yera[6]	M	Dog	2011	Shelter, Hungary
Zuri[9]	F	Dog	2011	Shelter, Hungary

M: male; F: female. Siblings are indicated by matching superscripts to their name.

unfamiliar rooms, noises, being alone). They also received training using positive reinforcement at least once a day, and from the age of 6 weeks, they participated in leash walks two to three times per week. The basic principle of cooperative socialization and training was to build up exclusively positive associations with humans, by avoiding any competitive situations and conflicts with the animals. As a result of this socialization regime, the wolf puppies showed no sign of wariness or avoidance of humans but were keen to interact even with unfamiliar persons. Moreover, they were used to being separated from their social siblings.

Overall Design

We conducted a neophobia test at 5 and 7 weeks of age and an isolation-reunion-separation test (Nowak & Boivin, 2015) at 5 weeks of age. The two tests were performed between 0800 and 2000 hours on different days and in different familiar rooms. Tests were performed between 2008 and 2012.

EXPERIMENT 1: NEOPHOBIA TEST

Experimental Procedure

At the age of 5 weeks, subjects were confronted with two neophobia tasks, each consisting of two conditions. In the Alone condition, the subject was alone in the testing area, whereas in the Human condition, a human hand-raiser was present. Two different novel objects were used (i.e. yellow sponge ball and an alarm clock; Fig. 1). Each subject was first tested with the ball and then with the clock since the latter was expected to be scarier for the subjects, for a total of four test trials (e.g. ball Alone/ball with Human, clock Alone/clock with Human). The order of the two conditions for each object (Alone or Human) were counterbalanced across subjects. All four test trials were conducted on the same day, in the same room, with a few minutes break between trials.

At the age of 7 weeks, tests were repeated in the same testing area. The order of tests remained the same (first ball, then clock), whereas the order of conditions was reversed for each subject as compared to their 5-weeks test (that is, if tested first in the Alone and then in the Human condition at week 5, the subject was tested first in the Human and then in the Alone condition at week 7).

The experimental area (3×4 m) was empty during testing. It was separated from the rest of the room by a 1 m high opaque screen. Both stimuli were attached to a string that was held by an experimenter (E1) hiding behind the screen. E1 was responsible for having the object appear and move during testing. In the Ball test, the ball was slowly lowered to eye level of the subject at the beginning of the trial and then moved like a pendulum from left to right. In the Clock test, the alarm clock was lowered all the way to the ground, while ringing loudly for 10 s after appearance.

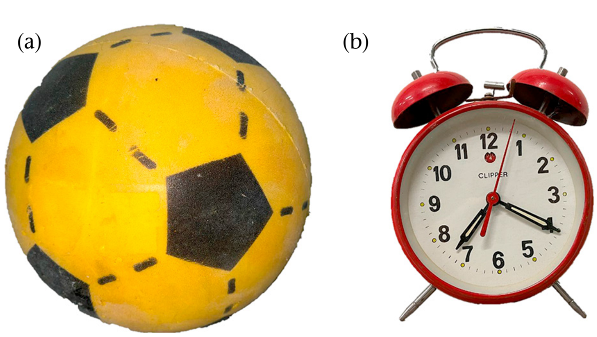

Figure 1. Objects used in the neophobia task. (a) A yellow sponge ball; (b) a red alarm clock.

In the Alone condition, a familiar experimenter (E2) carried the subject in her arms into the area and put it down in the middle at 1.5 m from the object location. After orienting the subject towards the object, E2 left the room, while the object appeared. After 1 min, the trial ended. In the Human condition, E2 brought the subject into the room in the same way but placed it on the lap of a hand-raiser (Hu), who was sitting on the ground with their back touching the screen at 1.5 m from the object. Hu held the subject with their hands for a few seconds, until E2 left the testing area and the object appeared, then Hu released the subject. This condition lasted 1 min.

In all but four cases (where puppies were tested in a room equipped with an automated video-recording system), the subject's behaviour was continuously recorded with a video camera (Handycam DCR SR35 Sony) held by a closely familiar experimenter, who was positioned behind an opaque barrier that covered the lower part of the body or who sat on a table with crossed legs. Hence, the camera-person was visible to the subjects, but not reachable. The camera-person was already present in the room before the puppies' arrival and remained silent during testing.

Behavioural Analysis

All videos were coded by using Solomon Coder (© András Peter) according to the ethogram reported in Table 2. Two independent observers (K.H. and G.C.) coded 65% (88% of the total dog videos and 57% of the total wolf videos) and 35% of the videos (12% of the total dog videos and 43% of the total wolf videos), respectively. To assess interrater reliability, both coders analysed 20% of the videos (52% of which were dog videos, while 48% were wolf videos). We ran two-way mixed-effects models to assess the absolute agreement between the two coders (Koo & Li, 2016). Interrater reliability resulted in moderate to excellent scores ('stress-related behaviours': intraclass correlation coefficient (ICC) = 0.705, $F_{17,18} = 5.78$, $P < 0.001$; 'vocalizations': ICC = 0.567, $F_{21,21.1} = 3.84$, $P = 0.002$; 'fearful posture/escaping attempts': ICC = 0.629, $F_{44,25.6} = 5.09$, $P < 0.001$ 'close to partner': ICC = 0.932, $F_{7,4.37} = 43.7$, $P < 0.001$; 'close to camera-person': ICC = 0.8878, $F_{45,45.1} = 15.1$, $P < 0.001$; 'exploration': ICC = 0.766, $F_{45,45.3} = 7.43$, $P < 0.001$; 'close to object': ICC = 0.813, $F_{45,30.4} = 10.9$, $P < 0.001$; 'interacting with object': ICC = 1, $F_{45} = \text{Inf}$, $P = 0$).

Statistical Analyses

Owing to health problems, some animals were not tested in all conditions, and corruption of some video files meant the actual number of individuals whose tests could be analysed varied between tests. The exact numbers are reported in Table 3.

We ran GLMMs (generalized linear mixed models, Baayen, 2008) with either beta distribution using the function glmmTMB of the package glmmTMB (for all variables coded as duration proportions; package version 1.0.2.1, Brooks et al., 2017), Poisson distribution and log link function (for 'stress', coded as counts) or binomial distribution and logit link function (for the variable 'interact with object', coded as an occurrence) using the function glmer of the package lme4 (package version 1.1–23, Bates et al., 2015). For all models, to reduce the likelihood of committing a Type 1 error, we used a likelihood ratio test to compare the full model versus a null model containing the same random structure and control variables but not the test predictors (Dobson, 2002; Forstmeier & Schielzeth, 2011). When the null–full model comparison was significant, we used a likelihood ratio test to determine the significance of individual effects by comparing likelihoods of models containing or not the specific effect (Barr et al., 2013). In all models, we z-transformed all continuous predictors to a mean of zero and a standard deviation of one to obtain more easily interpretable model estimates (Schielzeth, 2010) and ease model convergence.

Table 2
Behavioural variables coded during the NT and the IRST.

Variable	Description	Test	Type
Stress-related behaviours (summed)	Defecation: to evacuate solid waste	NT, IRST	Count
	Freezing: to look at the object without moving for at least 3 s. Muscles are tense, ears are erected, tail is either tucked in or held horizontally. A bout was from when the animal stopped for longer than 3 s until it started moving again	NT, IRST	Count
	Lips/nose licking: tongue moved over the lips/nose	NT, IRST	Count
	Panting: to gasp for breath. The tongue is visibly moving in and out the mouth. A bout was from when the animal opened its mouth to when it closed it again	NT, IRST	Count
	Peeing: to urinate with both hindlegs on the ground	NT, IRST	Count
	Scratching: ro nibble (autogrooming) or scratch different body parts with front or hind paws. A bout was from when the animal started autogrooming or scratching until it stopped doing so for at least 2 s	NT, IRST	Count
	Shaking: to wiggle the whole body, starting with the head and finishing with the hind part of the body	NT, IRST	Count
	Yawning: to open the mouth wide, slightly close the eyes and turn the ears backwards. Sometimes accompanied by yawning noises	NT, IRST	Count
Vocalizations	To whine, whimper or howl	NT, IRST	Count, Duration
Fearful posture/escaping attempts	To walk or run with tail tucked and often body moved away from the source of fear (e.g. object). A tense, crouched body posture often combined with lowered head and firmly backward-facing ears. To climb on the wall, door or exit construction	NT, IRST	Duration
Close to partner	The subject is within 30 cm of the partner (hand-raiser/conspecific) with any part of the body	NT, IRST	Duration
Close to camera-person	The subject is within 30 cm from where the camera-person was positioned (either the opaque barrier or the table on which they were sitting)	NT, IRST	Duration
Exploration	To walk or run, including sniffing, distal and close visual inspection or oral examination, directed towards the environment (object, camera-person, experimenter or human partner), in a relaxed manner. That is, tail is either wagging perpendicularly or held in a neutral position, ears are pointed forward, body posture is relaxed	NT, IRST	Duration
Close to object	The subject is within 30 cm of the object with any part of the body	NT	Duration
Interacting with object	To run around the object, snapping, jumping, pawing or barking at it, accompanied by erected ears and often tail wagging	NT	Likelihood

NT: neophobia test; IRST: isolation-reunion-separation test.

In all cases, we assessed overdispersion, which was acceptable. In particular, we ran models (separately for the Ball and the Clock test) with stress-related behaviours, vocalizations, fearful posture/escaping attempts, proximity to the camera-person, exploration, proximity to the object, and the likelihood of interacting with the object as response variables. We included species (dogs versus wolves), condition (Alone versus Human) and age (5 versus 7 weeks) as predictors, as well as the three-way interaction between them. However, the stability of the models comprising the three-way interaction was very low; hence we conducted models including the two-way interaction between species and condition (to test our hypotheses) and the two-way interaction between species and age to control for potential developmental differences between dogs and wolves. Nonsignificant interactions were removed from the final model. Order of testing and cohort (year of testing) were included as control variables (that is, we did not consider their significance). The identity of the subject and the identity of the coder were included as random effects. The model with proximity to the human partner was similar to the previous ones with the only difference that condition (hence, the interaction between species and condition) was not included in the list of predictors (as this behaviour was only coded in the condition in which the human was present). Whenever an interaction was significant, we analysed pairwise comparisons using the function emmeans of the package emmeans, adjusting for multiple testing using the Tukey method (package version 1.8.0, Searle et al., 1980). All statistical analyses were performed using R 4.3.1 (R Core Team, 2021).

Results

In the Ball test, puppies showed more stress-related behaviours in the Alone than in the Human condition ($X^2_1 = 6.28$, $P = 0.01$; Fig. 2a), while the opposite was true in the Clock test ($X^2_1 = 23.28$, $P < 0.001$; Fig. 2b). They also vocalized more in the Alone than in the Human condition in the Ball test ($X^2_1 = 9.08$, $P = 0.003$; Fig. 2c), while in the Clock test we found a significant species*condition interaction ($X^2_1 = 9.79$, $P = 0.002$; Fig. 2d). In the Clock test, dogs vocalized more in the Alone than in the Human condition (estimates ± SE = 1.28 ± 0.24, z-ratio = 5.23, $P < 0.001$), while no difference between the two conditions was observed in wolves (estimates ± SE = 0.30 ± 0.19, z-ratio = 1.58, $P = 0.11$). When comparing whether dogs and wolves differed in each condition, we found no differences (Alone condition, dogs versus wolves: estimates ± SE = 0.42 ± 0.33, z-ratio = 1.26, $P = 0.21$; Human condition, dogs versus wolves: estimates ± SE = −0.56 ± 0.38, z-ratio = −1.48, $P = 0.14$).

In the Ball test (species*condition interaction: $X^2_1 = 7.80$, $P = 0.01$), dogs showed fearful behaviours for longer in the Alone than in the Human condition (estimates ± SE = 1.49 ± 0.34, z-ratio = 4.34, $P < 0.001$), while this was not true for wolves (estimates ± SE = 0.29 ± 0.29, z-ratio = 1.00, $P = 0.32$; Fig. 2e). When comparing the two species in each condition, we found no significant differences (Alone condition, dogs versus wolves: estimates ± SE = 0.47 ± 0.37, z-ratio = 1.29, $P = 0.20$; Human condition, dogs versus wolves: estimates ± SE = −0.73 ± 0.39, z-ratio = −1.89, $P = 0.06$). In the Clock test, puppies showed more fear in the Alone than in the Human condition ($X^2_1 = 18.76$, $P < 0.001$; Fig. 2f).

In both tests, dogs spent more time close to the Human partner than wolves (Ball test: $X^2_1 = 7.46$, $P = 0.01$, estimates ± SE = 0.91 ± 0.33, z-value = 2.71, $P = 0.01$; Fig. 3a; Clock test: $X^2_1 = 17.80$, $P < 0.001$, estimates ± SE = 1.52 ± 0.32, z-value = 4.73, $P < 0.001$; Fig. 3b).

Table 3
Number of subjects tested in each condition

	Wolves	Dogs
5 weeks	Ball Alone: $N = 12$	Ball Alone: $N = 14$
	Ball with Human: $N = 13$	Ball with Human: $N = 14$
	Clock Alone: $N = 16$	Clock Alone: $N = 14$
	Clock with Human: $N = 15$	Clock with Human: $N = 14$
7 weeks	Ball Alone: $N = 17$	Ball Alone: $N = 13$
	Ball with Human: $N = 18$	Ball with Human: $N = 13$
	Clock Alone: $N = 17$	Clock Alone: $N = 11$
	Clock with Human: $N = 18$	Clock with Human: $N = 13$

In both tests, in the models for proximity to the camera-person, the species*condition interaction was significant (Ball test: $X^2_1 = 4.70$, $P = 0.01$; Clock test: $X^2_1 = 7.71$, $P = 0.01$). In particular, both dogs (Ball test: estimates ± SE = 1.54 ± 0.36, z-ratio = 4.27, $P < 0.001$; Clock test: estimates ± SE = 1.85 ± 0.39, z-ratio = 4.72, $P < 0.001$) and wolves (Ball test: estimates ± SE = 0.61 ± 0.29, z-ratio = 2.10, $P = 0.32$; Clock test: estimates ± SE = 0.55 ± 0.26, z-ratio = 2.14, $P = 0.03$) spent more time close to the camera-person in the Alone than in the Human condition (Fig. 3c and d). When comparing the two species in each condition, we found no significant difference in the Alone condition (dogs versus wolves, Ball test: estimates ± SE = 0.26 ± 0.28, z-ratio = 0.96, $P = 0.34$; Clock test: estimates ± SE = 0.36 ± 0.33, z-ratio = 1.09, $P = 0.28$) but we found that dogs spent less time close to the camera-person than wolves in the Human condition (dogs versus wolves, Ball test: estimates ± SE = −0.67 ± 0.32, z-ratio = −2.10, $P = 0.04$; Clock test: estimates ± SE = −0.94 ± 0.39, z-ratio = −2.38, $P = 0.02$).

In the Ball test, none of the variables of interest influenced subjects' explorative behaviour (null-full model comparison: $X^2_5 = 2.08$, $P = 0.83$; Fig. 3e). In the Clock test, however, dogs and wolves differed depending on the condition (species*condition interaction: $X^2_1 = 5.91$, $P = 0.02$, Fig. 3f). While dogs tended to explore more in the Alone condition than in the Human one (estimates ± SE = 0.60 ± 0.30, z-ratio = 2.00, $P = 0.05$), wolves did not differ between the two conditions (estimates ± SE = −0.43 ± 0.28, z-ratio = −1.51, $P = 0.13$). Dogs explored more than wolves in the Alone condition (estimates ± SE = 0.95 ± 0.37, z-ratio = 2.57, $P = 0.01$), while this difference was not significant in the Human condition (estimates ± SE = −0.07 ± 0.36, z-ratio = −0.20, $P = 0.84$).

Wolf puppies spent more time close to the ball than dogs ($X^2_1 = 11.84$, $P < 0.001$), while no difference between the two species was found in the Clock test (null−full model comparison: $X^2_5 = 6.75$, $P = 0.24$). None of the variables of interest affected the likelihood of interacting with the ball (null−full model comparison: $X^2_5 = 10.29$, $P = 0.07$), and in the case of the Clock test, too few subjects interacted with the clock to be able to run a model (one dog and four wolves).

Complete results can be found in the Supplementary Material. All significant results are summarized in Table 4.

EXPERIMENT 2: ISOLATION-REUNION-SEPARATION TEST

Experimental Set-Up

At the age of 5 weeks, all 35 animals participated in a social separation experiment consisting of three phases: isolation in an unfamiliar room for 5 min (Phase 1), then addition of a social partner for 5 min (Phase 2) before being separated for another 5 min (Phase 3). Each subject was tested in two conditions: with a hand-raiser (Human) or with a conspecific as a partner (Conspecific). The two conditions were conducted for each subject in the same room on the same day with a 30 min break between tests and in a counterbalanced order. During the experiment, the test room was empty, except for a camera-person who was separated from the subject (as in experiment 1).

Experimental Procedure

A familiar experimenter carried the subject into the test room, placed it in the middle of the room and then left. After the subject had been alone for 5 min, in the Human condition, a hand-raiser entered and sat down in the middle of the room. Whenever the pup approached to within arm-reach, the hand-raiser was allowed to talk to the subject and pet it without restricting the pup's movements. After 5 min, the hand-raiser left the room. In the Conspecific condition, the experimenter silently entered the room carrying the conspecific in their hands, placed it in the middle of the test room and left again. Since the conspecific was not restrained during the test, the one least active (among all available puppies) at the time of the test was chosen as a partner. Relatedness was not taken into account when choosing the partner since pups were raised as groups even if they originated from different litters. In total, four of 18 dogs were tested with relatives, while seven of 17 wolves were. A Fisher's exact test reveals the two species did not differ in their likelihood of being tested with a relative ($P = 0.50$). After 5 min, the experimenter silently entered the room, quickly picked the conspecific up and left without interacting with the subject. In the last phase, the subject was again alone for 5 min, before the experimenter entered the room and tried to attract the pup's attention by gently trampling with their feet. If the pup approached them, they picked the pup up without talking to it. If the pup did not react to the entering experimenter within 10 s, the experimenter slowly approached the subject, stroked the animal and lifted it up.

Behavioural Analysis

Videos were coded using the same ethogram of the neophobia test (Table 2). We also scored the behavioural stress levels of the conspecific partner used in the Conspecific condition on a scale from one to five to control for it in the analyses (subjective scale based on the occurrence and intensity of behaviours such as vocalizations, pacing, and stress-related behaviours such as defecation, freezing, lips/nose licking, panting, peeing, scratching, shaking, yawning). Two observers (K.H. and G.C.) coded 57% (67% of the total dog videos, 47% of the total wolf videos) and 43% of the videos (33% of the total dog videos and 53% of the total wolf videos) independently. Fourteen per cent of the videos (40% were dog videos and 60% were wolf videos) were coded by both to assess interrater reliability. We ran two-way mixed-effects models to assess the absolute agreement between the two coders (Koo & Li, 2016). Interrater reliability resulted in scores of good to excellent ('stress-related behaviours': ICC = 0.825, $F_{27,27.9} = 10.8$, $P < 0.001$; 'vocalizations': ICC = 0.838, $F_{27,28} = 11.3$, $P < 0.001$; 'fearful posture/escaping attempts': ICC = 0.62, $F_{27,8.24} = 6.12$, $P = 0.005$; 'close to partner': ICC = 0.88, $F_{9,4.75} = 24.4$, $P = 0.002$; 'close to camera-person': ICC = 0.735, $F_{27,15.9} = 7.91$, $P < 0.001$; 'exploration': ICC = 0.78, $F_{27,14} = 9.84$, $P < 0.001$).

Statistical Analysis

We ran GLMMs (Baayen, 2008) with either beta distribution using the function glmmTMB of the package glmmTMB (for all variables coded as duration proportions; package version 1.0.2.1, Brooks et al., 2017), Poisson distribution and log link function (for 'stress', coded as counts) using the function glmer of the package lme4 (package version 1.1−23, Bates et al., 2015). For all models, to

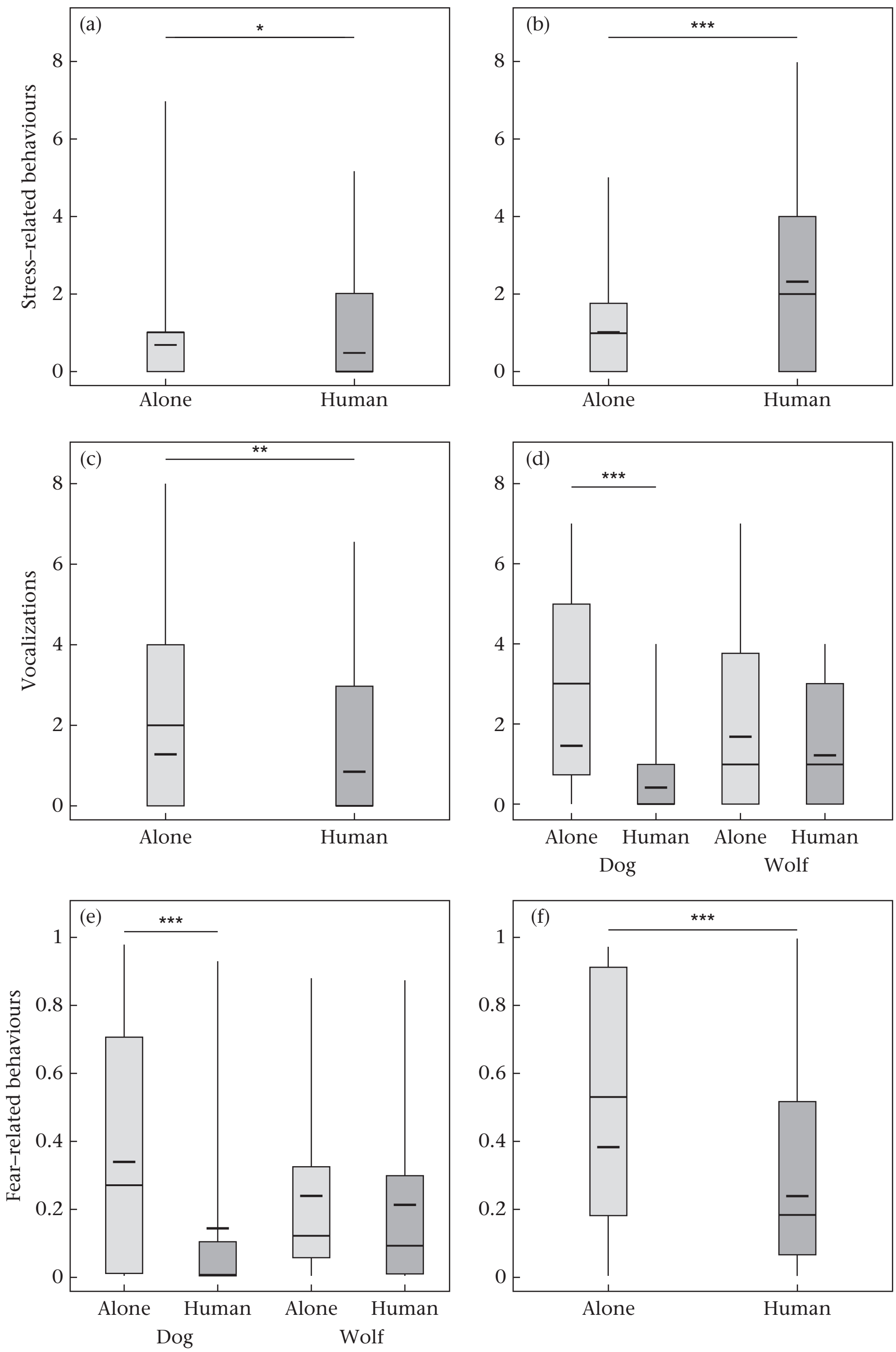

Figure 2. Results of the neophobia test: number of stress-related behaviours across conditions during the (a) Ball and (b) Clock tests; number of vocalizations across species and conditions during the (c) Ball and (d) Clock tests; and proportion of time spent showing fearful posture/escape attempts across species and conditions during the (e) Ball and (f) Clock tests. Box plots show the median (thin horizontal line) and interquartile range (IQR; represented by the box), 25th percentile + 1.5 IQR and 75th percentile − 1.5 IQR (represented by the lower and the upper whiskers, respectively). Fitted values extracted from the model are represented by the thick, short horizontal lines. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

reduce the likelihood of committing a Type 1 error, we used a likelihood ratio test to compare the full model versus a null model containing the same random structure and control variables but not the test predictors (Dobson, 2002; Forstmeier & Schielzeth, 2011). When the null−full model comparison was significant, we used a likelihood ratio test to determine the significance of individual effects by comparing likelihoods of models containing or not the specific effect (Barr et al., 2013). In all models, we z-transformed all continuous predictors to a mean of zero and a standard deviation of one to obtain more easily interpretable model estimates (Schielzeth, 2010) and ease model convergence. In all cases, we assessed overdispersion, which was acceptable. In particular, we

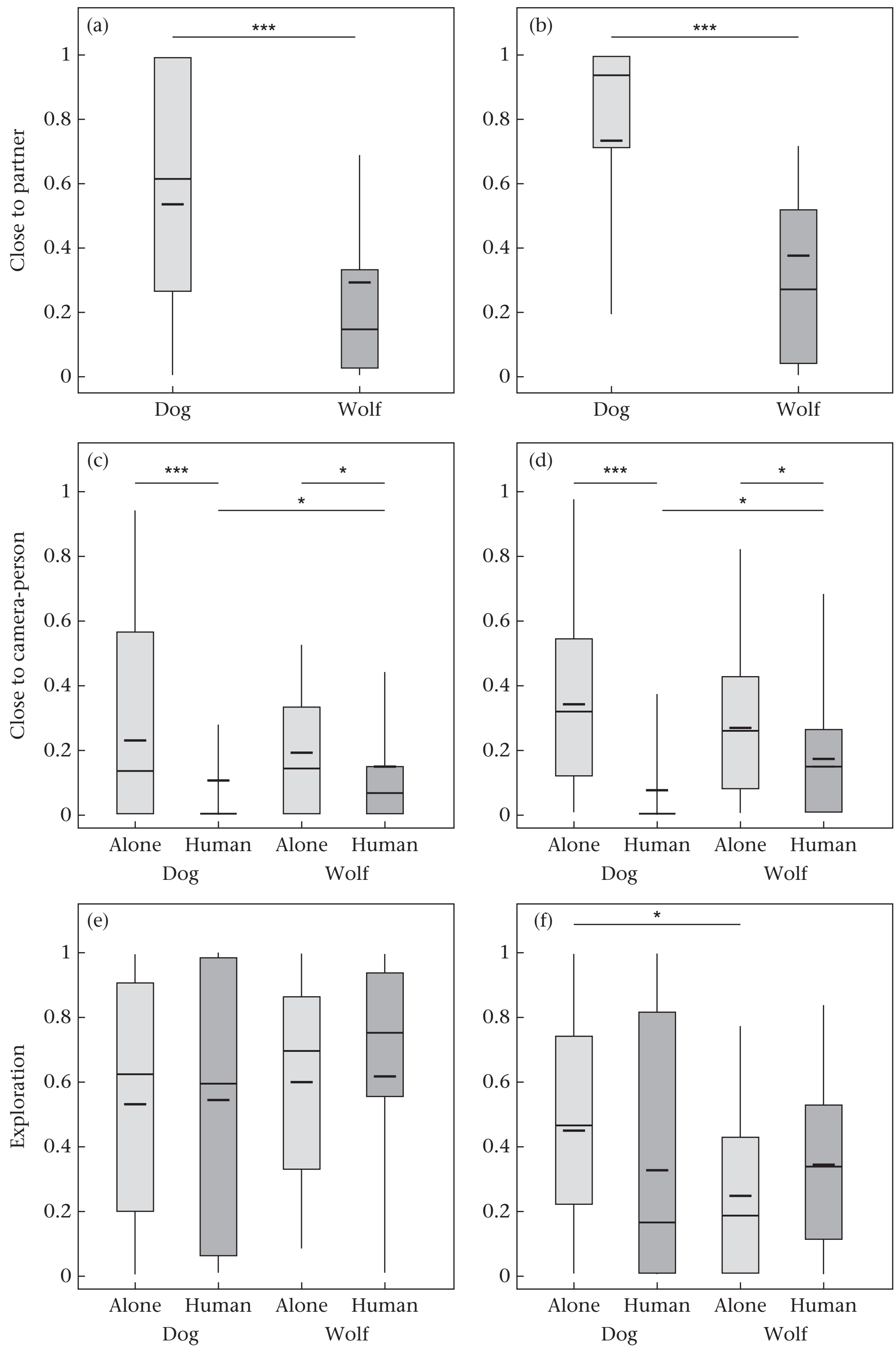

Figure 3. Results of the neophobia test: proportion of time spent close to the partner across species during the (a) Ball and (b) Clock tests; proportion of time spent close to the camera-person across species and conditions during the (c) Ball and (d) Clock tests; and proportion of time spent exploring across species and conditions during the (e) Ball and (f) Clock tests. Median (thin horizontal line) and interquartile range (IQR; represented by the box), 25th percentile + 1.5 IQR, and 75th percentile − 1.5 IQR (represented by the lower and the upper whiskers, respectively). Fitted values extracted from the model are represented by the thick, short horizontal lines. *$P < 0.05$; ***$P < 0.001$.

ran models with stress-related behaviours, vocalizations, fearful posture/escaping attempts, close to camera-person and exploration as response variables. We included species (dogs versus wolves), condition (Human versus Conspecific) and phase (1 versus 2 versus 3) as well as the three-way interaction between them as predictors. However, the stability of the models including the three-way interaction was low; hence, we ran reduced models with the two-way interactions between species and condition, and between species and phase, as predictors. We focused on these two-way interactions as they allowed us to test our hypotheses related to potential differences between the two species depending on the partner present or the experimental phase. Order of testing, cohort

Table 4
Summary of significant results

Test	Ball test		Clock test		Isolation-reunion-separation test		
Predictors	Species*	Condition	Species*	Condition	Species*	Condition	Phase
Behaviour							
Stress-related behaviours		Al > Hu		Hu > Al	**W > D**	Co > Hu	
Vocalizations		Al > Hu	**D:** Al > Hu **W:** Hu > Al		**D > W**(Phase 1)**W > D**(Phase 2 & 3)W: Phase 3 > 1		
Fearful posture/escaping attempts	**D:** Al > Hu			Al > Hu	**W > D**(Phase 3)W & D: Phase 1, 3 > 2		
Close to partner	**D > W**	/	**D > W**	/			/
Close to camera-person	**W > D**(Hu)		**W > D**(Hu)				3 > 1 > 2
Exploration			**D > W** (Al) **D:** Al > Hu				1 & 2 > 3
Close to object	**W > D**				/	/	/
Interacting with object					/	/	/

D: dogs; W: wolves; Hu: human; Al: alone; Co: conspecific. Asterisks indicate interactions.

(year of testing) and the behaviour of the partner (stress levels on a five-point scale) were included as control variables (that is, we did not consider their significance). The identities of the subject, partner, dyad and coder were included as random effects. In the case of the model for fear-related behaviours, the model with the identity of the coder as random effect failed to converge; hence this variable was included as control predictor in the fixed effect part. As proximity to partner was only coded during the reunion phase, we ran a similar model to those above for this variable with the only difference that phase was not among the predictors (including the interaction between species and phase). Nonsignificant interactions were removed from the final model. We analysed pairwise comparisons using the function emmeans of the package emmeans, adjusting for multiple testing using the Tukey method (package version 1.8.0, Searle et al., 1980). All statistical analyses were performed using R 4.3.1 (R Core Team, 2021).

Results

Wolves showed more stress-related behaviours than dogs, irrespective of condition and phase ($X^2_1 = 9.16$, $P = 0.002$; Fig. 4a), and puppies showed more stress-related behaviours in the Conspecific than in the Human condition ($X^2_1 = 5.81$, $P = 0.02$; Fig. 4b).

For vocalizations, the interaction between species and phase was significant ($X^2_2 = 12.38$, $P = 0.002$). While dog and wolf puppies were not different in the first (dog versus wolf: estimate $\pm$ SE $= 0.56 \pm 0.51$, z-ratio $= 1.09$, $P = 0.27$) and in the second phase (dog versus wolf: estimate $\pm$ SE $= -0.87 \pm 0.51$, z-ratio $= -1.70$, $P = 0.09$), wolf puppies vocalized more than dogs in the third phase (dog versus wolf: estimate $\pm$ SE $= -1.15 \pm 0.53$, z-ratio $= -2.17$, $P = 0.03$; Fig. 4c). Moreover, while dog puppies did not vocalize significantly differently across phases (dogs: all $P > 0.05$), wolf puppies showed an increase in vocalizations throughout the different phases (wolves: phase 1 versus phase 2: estimate $\pm$ SE $= -0.68 \pm 0.30$, z-ratio $= -2.28$, $P = 0.06$; phase 1 versus phase 3: estimate $\pm$ SE $= -1.03 \pm 0.34$, z-ratio $= -3.03$, $P = 0.01$; phase 2 versus phase 3: estimate $\pm$ SE $= -0.35 \pm 0.34$, z-ratio $= -1.02$, $P = 0.56$).

Wolves and dogs differed in the duration of fearful behaviours expressed across phases (species*phase interaction: $X^2_2 = 9.12$, $P = 0.01$). Although puppies showed fewer fear-related behaviours when the partner was present (phase 1 and phase 3 versus phase 2: $P < 0.05$ for both species; see Supplementary Material for full results), wolves showed fearful behaviours for longer in the last phase than dogs (dog versus wolf: phase 3: estimate $\pm$ SE $= -1.47 \pm 0.36$, z-ratio $= -4.15$, $P < 0.001$; Fig. 4d).

The null–full model comparison for close to partner was not significant ($X^2_3 = 2.73$, $P = 0.44$), showing that neither the species nor the partner present influenced how much time the subjects spent close to their partner.

Puppies spent a different proportion of time close to the camera-person depending on the phase ($X^2_2 = 58.95$, $P < 0.001$). In particular, they spent more time close to the camera-person in phase 1 than in phase 2 (estimate $\pm$ SE $= 1.64 \pm 0.20$, z-value $= 8.34$, $P < 0.001$) and in phase 3 (estimate $\pm$ SE $= 0.66 \pm 0.18$, z-value $= 3.72$, $P < 0.001$), and more in phase 3 than in phase 2 (estimate $\pm$ SE $= 0.99 \pm 0.20$, z-value $= 4.94$, $P < 0.001$; Fig. 4e).

Exploration of the room depended on the phase of the experiment ($X^2_2 = 38.12$, $P < 0.001$). Puppies spent more time exploring in phase 1 and 2 than in phase 3 (phase 1 versus 3: estimate $\pm$ SE $= 1.32 \pm 0.23$, z-value $= 5.77$, $P < 0.001$; phase 2 versus 3: estimate $\pm$ SE $= 1.34 \pm 0.22$, z-value $= 6.05$, $P < 0.001$), while they spent similar amounts of time exploring in both phase 1 and 2 (phase 1 versus 2: estimate $\pm$ SE $= 0.02 \pm 0.19$, z-value $= 0.12$, $P = 0.90$; Fig. 4f).

Complete results can be found in the Supplementary Material. All significant results are summarized in Table 4.

DISCUSSION

We compared the supportive role played by social partners (either a human or a conspecific peer) in equally intensively socialized dog and wolf puppies, when facing different stressful situations (i.e. two neophobia tasks and an isolation-reunion-separation task) either alone or accompanied by a partner. Thereby, we aimed to test three main hypotheses: (1) given a similar preweaning development in the two species, we argued that conspecifics would act as stress buffers for both dogs and wolves to a similar extent; (2) assuming that a strong effect of domestication has facilitated dogs' use of humans as supportive social partners, we hypothesized that dogs would benefit more from the presence of a human than wolves, which instead would benefit more from the presence of a conspecific than a human; and finally, (3) if, however, domestication has a limited effect and mainly changed the amount of socialization necessary to use humans as social buffers similarly to conspecifics, we predicted that due to the equally intense socialization with humans in our population, both conspecifics and humans could have a similar supportive role without differences between the two species.

Overall, we found partial support for each of the three hypotheses, suggesting that both domestication and socialization have an impact on the potential stress buffering effects caused by social partners. In support of our first hypothesis, we found that wolves

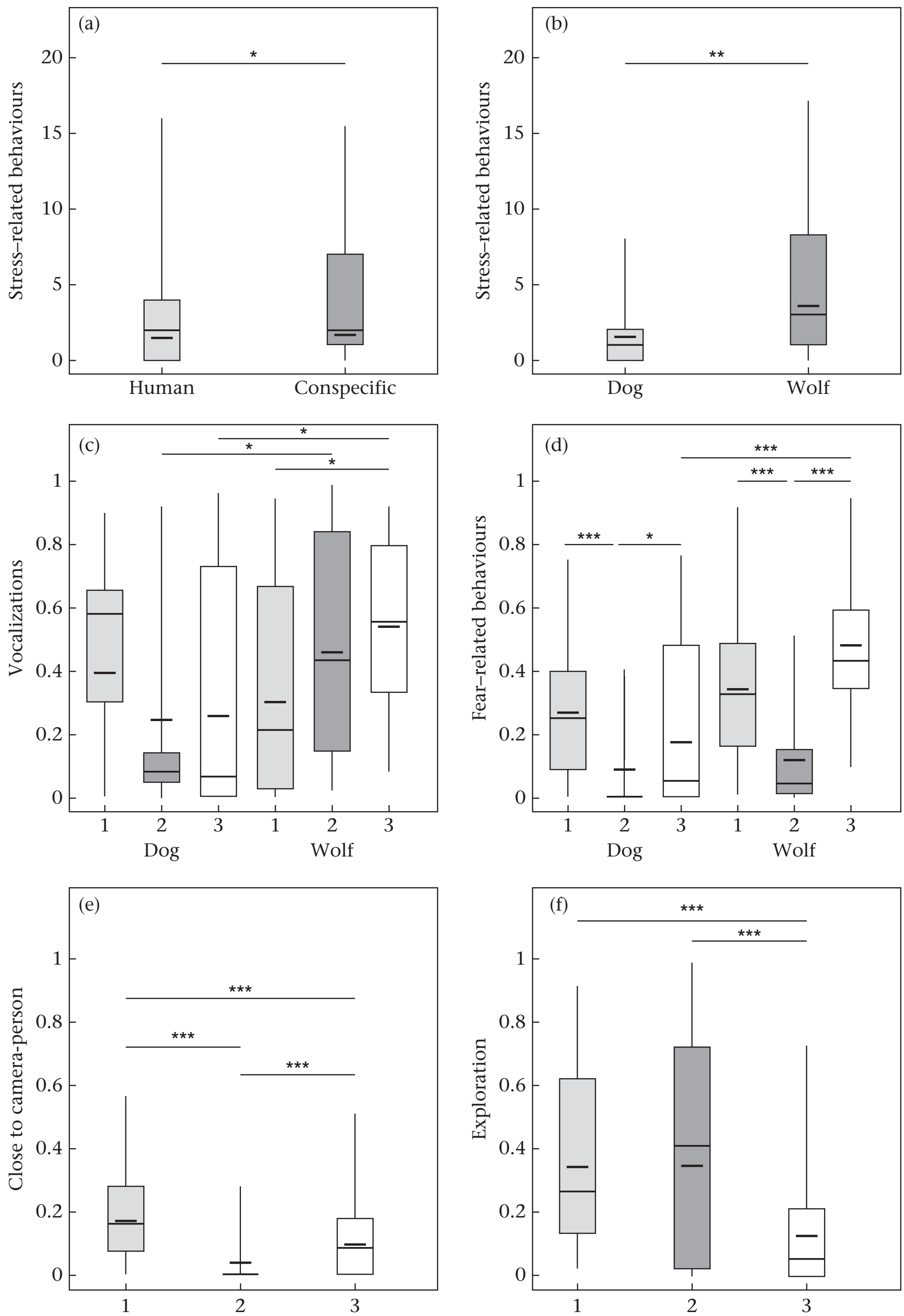

Figure 4. Results of the isolation-reunion-separation test: number of stress-related behaviours across (a) conditions and (b) species; (c) proportion of time spent vocalizing across species and phases; (d) proportion of time spent showing fearful posture/escape attempts across species and phases; (e) proportion of time spent close to the camera-person across phases; and (f) proportion of time spent exploring across phases. Median (thin horizontal line) and interquartile range (IQR; represented by the box), 25th percentile + 1.5 IQR, and 75th percentile − 1.5 IQR (represented by the lower and the upper whiskers, respectively). Fitted values extracted from the model are represented by the thick, short horizontal lines. $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

and dogs did not differ significantly in their behaviours when accompanied by a conspecific partner, and that a young conspecific can act as a stress buffer for puppies of both species facing a novel environment. In fact, when a peer was present, individuals showed fewer fear-related behaviours and escape attempts from the experimental room than when alone. Moreover, they spent more time close to the camera-person and exploring when the partner was present than when they were alone. Such results are not surprising, considering that both dog and wolf puppies spend the first weeks of their lives in and around dens with their littermates, which are their main social partners when left alone by the adult members of the pack (Mech, 1970; Pal, 2015); their presence can be decisive for their survival (Scott, 1967; Scott & Fuller, 1965; Sidorovich et al., 2017). These results also suggest that domestication did not change whether and to what extent dogs and wolves rely on their littermates, in line with previous studies showing that young dogs (Pettijohn et al., 1977) and both adult wolves and dogs (Cimarelli et al., 2019; Cimarelli, Marshall-Pescini, et al., 2021; Jean-Joseph et al., 2020; Kortekaas & Kotrschal, 2020; Moretti et al., 2015; Pettijohn et al., 1977) benefit from the presence of a conspecific when dealing with potential stressors. Interestingly, the present results differ from those of a recent study comparing domestic chickens to their wild ancestor in a similar paradigm, where the domestic form has been shown to benefit less from the presence of a conspecific than the wild form (Gjøen et al., 2023). This difference might be due to the different domestication histories in the two species (thus, different selection pressures), speaking against a possible general reduction of reliance on conspecifics resulting from domestication.

When it comes to the supportive role of humans, we had mixed results. On the one hand, we found evidence that both dog and wolf puppies showed fewer stress- and fear-related behaviours in the presence of a human partner than when alone. This supports our hypothesis and previous results that, with intensive socialization, wolves can also form strong bonds with humans and use them as social supporters (Hall et al., 2015; Hansen Wheat et al., 2022; Lenkei et al., 2020). However, the results regarding the stress-related behaviours need to be interpreted with care. In fact, while in the Ball task the puppies of both species showed more stress-related behaviours when alone than when with the human partner, the opposite was true in the Clock task. Although the function of behaviours such as lip-licking, scratching and yawning is yet to be fully understood, it is accepted that these are shown at increasing stress levels (Pedretti et al., 2023). Still, it is unclear whether the present apparently contradictory results could be because the clock was more stressful than the ball and the animals showed more stress-related behaviours with a communicative function (Kaminski et al., 2017) when the partner was present in the Clock task.

The present results also show that conspecifics were not better social supporters than human partners in the isolation-reunion-separation test, as most of the behaviours were expressed similarly with both partners. One could argue that the conspecific partner (another young animal of the same age) might have been as stressed as the subject during testing (or at least, more stressed than a human experimenter), amplifying the potential stress perceived by the subject (Rault, 2012; Wu, 2021), potentially through the mechanism of emotional contagion (Nakahashi & Ohtsuki, 2015). However, if the two partners had not calmed one another, but, to the contrary, had mutually amplified their stress responses, we would have detected even greater differences between them. Still, the absence of a difference between the supportive role of conspecifics and humans does not support the second hypothesis predicting that conspecifics should be less supportive than humans with dogs but would rather support the idea that intense socialization can overshadow potential domestication effects (Jean-Joseph et al., 2020).

Still, a few differences between wolf and dog pups emerged, supporting the hypothesis that domestication has affected how humans and conspecifics can act as supportive partners in dogs. Dogs spent more time than wolves in proximity to the human in both neophobia tasks, suggesting that dogs rely more on humans in a novel environment than wolves. Similarly, dog puppies spent more time than wolves exploring when alone in the Clock test than when with the human partner. Taken together with the fact that in the Ball test, dog puppies also showed more fearful behaviours when alone than when with the human partner and in the Clock test they vocalized more when alone than in the human condition (while this was not true for wolves), we can interpret a higher level of exploration when alone as a sign of looking for the partner. In fact, if a higher exploratory activity had been shown when the partner was present, we would have interpreted it as a sign of security in the presence of a partner (i.e. secure base effect: Cimarelli, Schindlbauer, et al., 2021; Horn et al., 2013). All in all, these differences would suggest that dogs are more reliant on the presence of a human partner in stressful situations than wolves, indicating a domestication effect in this regard.

Another difference that emerged between the two species is that wolf puppies spent more time close to the camera-person than dogs when the human partner was present. One could argue that this difference might speak for a less clear differentiation between human partners in wolves than in dogs (Topál et al., 1998). Given that the camera-person was also closely familiar to the subjects, such a phenomenon could be explained by the fact that in a wolf pack, all adult members of the group help raising the young (allo-parental care, Marshall-Pescini et al., 2017); hence, it would be advantageous for wolf puppies at that developmental stage to differentiate less between different (but similarly familiar) social partners. In contrast, dog puppies are predominantly taken care of by their mothers, with involvement of other adult members of the pack as an exception (Marshall-Pescini et al., 2017). Thus, dog puppies might have kept using the human closer and more available to them (the experimenter), rather than switching between the two familiar humans. Although the presence of a camera-person allowed us to highlight an additional difference between the two species, it could also be seen as a potential limitation, as a human was present also during the alone conditions and phases. Although the camera-person was not reachable, puppies could see them and they indeed spent some time close to them. Future studies could use a surveillance camera system in which no additional human is present, to ensure that the isolation is indeed such.

To conclude, both wolf and dog puppies benefit from the presence of a young conspecific partner, which is in line with the developmental process they go through when living in the wild (e.g. in a pack in the case of village dogs). However, it is less clear to what extent the domestication process has modified dogs' reliance on humans as social support in comparison to wolves. On the one hand, our present results suggest that the ability to benefit from the presence of a human is present in both dogs and wolves, as puppies of both species showed decreased stress- and fear-related behaviour in the presence of a human partner when facing our experimental stressors. Still, a few differences between the two species suggest that dog puppies might rely more on humans as social supporters than wolves, suggesting that despite the intensive socialization of the wolves, dogs' way of relying on humans as social buffers might differ from that of wolves. Future studies are needed to address whether such differences might be explained by a different way of behaviourally expressing stress and fear in the two species (especially in a social setting) and/or by a differential effect given by socialization on the animal–human relationship quality (e.g. dogs might become overly reliant on an individual social partner when this is a human, while wolves might be more flexible in using various partners as social supporters). Although challenging from the practical perspective, we suggest that to fully disentangle the effects of domestication and intensive socialization, one would need to vary the levels of socialization applied to raise both dogs and wolves and compare differently socialized groups of both species.

Author Contributions

Conceptualization: M.G., F.R., Z.V., K.K.; Data curation: K.H., G.C.; Formal analysis: G.C.; Funding acquisition: G.C., Z.V., F.R., K.K.; Investigation: K.H., Z.V., F.R.; Methodology: G.C., K.H., M.G., F.R., Z.V., K.K.; Project administration: G.C., Z.V., F.R.; Visualization: G.C.; Writing–Original draft: G.C.; Writing–Review & editing: G.C., K.H., M.G., F.R., Z.V., K.K. All co-authors revised and approved the manuscript.

Data Availability

The full data set is available as Supplementary Material.

Declaration of Interest

The authors declare no conflicts of interest.

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Supplementary Material

Supplementary material associated with this article is available in the online version at https://doi.org/10.1016/j.anbehav.2024.01.001.

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