Relationship quality affects social stress buffering in dogs and wolves

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Social relationships can be described by a series of components, all having putatively different functional roles in the lives of humans and other social species. For instance, certain relationship characteristics can strongly influence how individuals deal with stress, ultimately influencing their fitness. However, species vary highly in regard to which components of their relationships influence stress buffering and how. Variation in species’ social organization could explain such differences. Comparing closely related species subjected to different ecological constraints can be especially informative when investigating this hypothesis. Here, we compared whether relationship quality differently influences how grey wolves, Canis lupus, and domestic dogs, C. l. familiaris, react to a series of stressors. We tested the role of various relationship components (i.e. two affiliation indices and two aspects of dominance rank) in mediating stress reactivity, social support seeking and social referencing in dyads of pack-living animals. To do so, we conducted systematic long-term observations of the social interactions between animals and an experimental test battery exposing animal dyads to a series of stressors (e.g. novel environment exploration, separation from and consequent reunion with the partner, exposure to a novel object and a threatening human). We found that a large rank distance and high affiliation index based on the number of friendly behaviours exchanged during everyday life (but not dominance status or the affiliation index based on the time spent in body contact) were related to a dampened stress response in both species. These results suggest a functional role of these two relationship components in the stress buffering of both dogs and wolves.

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Reite, & Laudenslager, 1989; Aureli & Smucny, 2000). Also, behav-
ioral mechanisms such as physical presence or closeness of a
potential ally (leading to a reduction in cortisol levels, Hennessy,
Mendoza, Mason, & Moberg, 1995), receiving social support dur-
ing stressful events (e.g. intergroup conflicts, Bonanni, Valsecchi, &
Natali, 2010), obtaining valuable information from a more knowl-
edgeable partner (Merola, Prato-Previde, & Marshall-Pescini, 2012)
or behavioural coordination (partners acting together and thereby
better dealing with a stressor, such as a predator's presence,
Duranton & Gaunt, 2016) can ultimately lead to stress reduction.

Importantly, the presence of affiliative partners affects stress
levels differently in species with diverse social organizations (Hennessy,
Kaiser, & Sachser, 2009), even when the species are
closely related. For instance, social contact has positive effects in
monogamous but not in polygynous rodent species (Glasper
& DeVries, 2005), and stress reactivity is dampened by the presence
of a bonded mate in a New World monkey species characterized by
long-term pair bonding (titi monkeys, Callicebus moloch) but not in
another species (squirrel monkeys, Saimiri sciureus) characterized by
larger mixed-sex groups (Hennessy et al., 1995).

The dominance component of a relationship (described by the
asymmetric exchange of submissive and/or dominance signals,
Cafruzzo, Valsecchi, Bonanni, & Natali, 2010; De Waal & Luttrell, 1989)
between individuals living in the same group seems to be also
related to stress coping, wellbeing and fitness (Cree, 2005; Majolo,
Lehmann, de BortoliVizzioli, & Schino, 2012). For instance, the pres-
ence of a dominance hierarchy can help members of a group deal
with environmental stressors (Bonanni et al., 2017; Sárová et al.,
2013). Specifically, an age-graded hierarchy facilitates group coor-
dination, with more dominant (and older) individuals being better
informed and making decisions, and more subordinate individuals
benefiting from following the dominant’s decisions (Bonanni et al.,
2017; McComb et al., 2011; Sárová et al., 2013). However, whether
dominant or subordinate animals in a group have higher cortisol
levels (Sands & Cree, 2004; Sapolsky, 2005) depends on the type of
stressor, the species and what type of stress-coping strategies the
individuals adopt. For instance, in stressful situations, subordinate
individuals might actively look for social support or avoid dominant
individuals, depending on the species-specific dominance (i.e.
whether more or less despotic) and breeding style (e.g. whether
cooperative or not; see Cree, Dantzler, Goymann, & Rubenstein,
2013 for a review). Comparative studies investigating the potentially
different effects of relationship components such as affiliation and
dominance on stress buffering are still scarce (but see Koski, Koops,
& Sterck, 2007 for an example), even though they would help us
understand how different socioecologies shape the functions of such
relationship components (Cree et al., 2013; De Waal & Luttrell, 1989;
Thierry, 2000). Moreover, it remains to be investigated whether
stress buffering is different for individuals of different rank.

Here we set out to investigate whether affiliation and domi-
nance have a functional role in buffering environmental stress in
two canid species: the grey wolf, Canis lupus, and the domestic dog,
C. l. familiaris. We chose to compare these two species because
wolves and dogs are closely related and still interfertile (Lindblad-
Oh & Mendoza, 2007 for an example), even though they would help us
understand how different socioecologies shape the functions of such
relationship components (Boitani & Ciucci, 1995; Boitani, Ciucci,
& Ortolani, 2007; Van Kerkhove, 2004) and a general
absence of cooperative breeding (see Marshall-Pescini, Cafruzzo,
et al., 2017). For a breed of Canis lupus, the presence of pack mates
in certain conditions and often roam alone or in pairs, which is why
dogs have been described as facultatively social (Boitani & Ciucci,
1995), posing questions about the functional role of their sociality
and how this may differ from that of wolves. The lack of studies
specifically investigating the link between various relationship
components and factors strongly connected to fitness (e.g. stress
buffering) does not allow us to disentangle to what extent the
differences in the socioecologies of dogs and wolves shape the
functions of their social relationships.

Only one study has investigated comparatively how the pres-
cence of a specific pack mate influenced how wolves and dogs
behave when facing an environmental stressor (i.e. a novel object;
Moretti, Hentrup, Kotschal, & Range, 2015). This study found that
the presence of pack mates favoured object exploration, suggesting
social stress buffering. Some species differences have also emerged,
with rank distance influencing wolves’ (the smaller the rank dis-
tance, the longer the subjects investigated the object) but not dogs’
investigation of novel objects (Moretti et al., 2015). However, in this
study, animals were tested in a single context, the effect of only one
relationship component (i.e. ordinal rank in the pack) was inves-
tigated, and the behavioural analyses focused on interactions with
the novel object, rather than social behaviours directed towards the
partner. Therefore, the study provides a limited insight into the role
of social relationships in moderating dogs' and wolves’ reactions to
environmental stressors.

The aim of the present study was to investigate how the
dominance and affiliative components of a relationship may
modulate the behavioural and physiological response to potentially
stressful situations wolves and dogs may encounter in their daily
lives. To this aim, we conducted the present study on similarly
raised, captive dogs and wolves living in conspecific packs at the
Wolf Science Center near Vienna (Austria). Based on systematic
long-term observations of the social interactions between animals,
we first characterized the relationship between individuals in
terms of dominance and affiliation. We then experimentally tested
each dyad using a recently developed test battery (Cimarelli,
Marshall-Pescini, Range, & Viranyi, 2019) that includes a series of
components investigating the link between various relationship
components and factors strongly connected to fitness (e.g. stress
buffering) in the presence of a partner, being separated from (and being subsequently reunited with) the partner in a novel environment, encountering a novel object together, and together facing a potential conflict with an unfamiliar
subject. During the tests, we recorded to what extent individuals in the dyad showed a behavioural and physiological stress activation, sought social support (e.g. by staying near each other) and coordinated their behaviours (e.g. by looking towards one another). To evaluate the physiological stress response of the animals (using changes in salivary cortisol as a proxy), we collected saliva samples before and after the testing procedure.

Given the results from previous studies in which affiliation seems to play a similar role in dogs and wolves, positively modulating synchrony and communication in stressful situations (e.g. territorial defence, Bonanni, Valsecchi, & Natoli, 2010; Cassidy, MacNulty, Stahler, Smith, & Mech, 2015), we predicted that in both species, affiliation would promote separation distress (Mazzini et al., 2013) but dampen stress reactivity to other stressors (both behaviourally and physiologically, Rault, 2012) while being together with the partner. This may occur, for instance, by means of social support seeking (measured as proximity seeking and body contact in a potentially stressful situation, Bonanni, Valsecchi, & Natoli, 2010; Dale et al., 2017; Marshall-Pescini, Schwarz, et al., 2017), social information seeking for coordination (measured as gaze duration and gaze alternation between the partner and a novel stimulus, Merola et al., 2012) and movement coordination during exposure to the stressor (Duranton & Gaunet, 2016). However, given wolves’ higher dependence on pack mates (i.e. for hunting, high-risk territorial defence and puppy rearing, (Marshall-Pescini, Cafazzo, et al., 2017), we expected such stress-mediating effects to be stronger in wolves than in dogs (Glasper & DeVries, 2005; Hennessy et al., 1995).

Regarding dominance, we predicted that in both dogs and wolves, subordinate individuals would be more stressed and actively look for social support more from the dominant partner than vice versa (Essler et al., 2017; Mazzini et al., 2013; McLeod, Moger, Ryon, Gadbois, & Fentress, 1996). Thus, subordinates should follow and seek proximity with their dominant partners (Ákos, Beck, Nagy, Vísek, & Kubinyi, 2014; Bonanni, Cafazzo, et al., 2010; Peterson et al., 2002) and carry out more social referencing (i.e. by looking longer and alternating the gaze more often between novel stimuli and their partner) towards the dominant partner than vice versa (assuming that the more dominant partner is seen as better informed, Peterson et al., 2002; Bonanni, Cafazzo, et al., 2010). However, considering that dogs might form more despotic social groups than wolves (Range, Ritter, & Virányi, 2015), we also expected subordinate dogs to be generally more stressed than subordinate wolves.

Further, since previous studies have shown that wolves closer in rank distance are more likely to coordinate with each other, but no or an opposite effect was found in dogs (Moretti et al., 2015; Marshall-Pescini, Schwarz, et al., 2017), we expected that rank distance would also affect stress mediation differently in the two species. As such, the smaller the rank distance the higher the stress-buffering effect of a partner (hence, the lower the cortisol response) and the more time spent in proximity in wolves, with the opposite in dogs.

METHODS

Ethical Note

The experimental procedures were approved in accordance with Good Scientific Practice guidelines and national legislation by the Ethical Committee for the use of animals in experiments at the University of Veterinary Medicine Vienna (Ref: 19/04/97/2014).

Subjects

All subjects tested in the present project were raised and lived in packs at the Wolf Science Center, Austria (www.wolfscience.at). Eleven grey wolves, all originating from captive populations living in game parks in Austria, the United States and Canada, participated in the study. The dogs originated from shelters in Hungary (N = 8) or were bred at the Wolf Science Center from two females and external, mixed-breed males (N = 6, 2014 generation). Subjects were hand-raised in peer groups from the age of 10 days on or, in case of the dogs born in 2014, spent at least 4 h per day with humans and other puppies (without the mother). After 5 months, all animals started to live full-time in their packs in large 2000–8000 m² enclosures, but they continued to take part in daily training and various behavioural experiments and were walked regularly by their trainers with whom the animals had a close and trustful relationship (see Range et al., 2015 for more details). Pack composition had been stable for at least 1 year when pairs of animals living in the same pack participated in the current study. We tested dogs belonging to four different packs (three formed by three individuals and one formed by six individuals), while wolves belonged to three different packs (two formed by three individuals and one formed by five individuals). Fourteen dogs in 15 dyads (nine males, five females; mean age ± SD = 31.93 ± 17.49 months) and 11 wolves in 14 dyads (seven males, five females; mean age ± SD = 53.68 ± 20.13 months) participated. Five dog dyads were composed of siblings and three wolf dyads of siblings or cousins. See Table 1 for a complete list of the dyads tested.

Observations

Packs were regularly observed using 10 min focal observations (Pocket Observer program, 3.2 Software) and data were then imported into the Observer XT 10.5 program (both from Noldus Information Technology, Wageningen, The Netherlands). Agonistic and affiliative interactions were recorded using an ‘all occurrence method’ (Altmann, 1974) when all individuals of the pack were present. Data were then analysed to identify the dominance and affiliative relationships between all individuals in the pack.

Table 1

| Dyad (Individuals) | Species | Sex | Related | Pack |
|--------------------|---------|-----|---------|------|
| Geronimo–Amakor   | Wolf    | M–M| No      | Geronimo|
| Amakor–Kenai      | Wolf    | M–M| No      | Geronimo|
| Geronimo–Kenai    | Wolf    | M–M| No      | Geronone|
| Chitto–Aragorn    | Wolf    | M–M| No      | Kaspar|
| Aragorn–Shima     | Wolf    | M–F| Yes     | Kaspar|
| Kaspar–Aragorn    | Wolf    | M–M| Yes     | Kaspar|
| Aragorn–Tala      | Wolf    | F–M| No      | Kaspar|
| Chitto–Shima      | Wolf    | M–F| No      | Kaspar|
| Kaspar–Shima      | Wolf    | M–F| Yes     | Kaspar|
| Tala–Shima        | Wolf    | F–F| No      | Kaspar|
| Kaspar–Tala       | Wolf    | M–F| No      | Kaspar|
| Nanuk–Una         | Wolf    | M–F| No      | Nanuk |
| Nanuk–Yukon       | Wolf    | M–F| No      | Nanuk |
| Una–Yukon         | Wolf    | F–F| No      | Nanuk |
| Banza–Asali       | Dog     | M–M| No      | Asali |
| Bora–Asali        | Dog     | F–M| No      | Asali |
| Banza–Bora        | Dog     | M–F| No      | Asali |
| Hiari–Meru        | Dog     | M–M| No      | Meru  |
| Hiari–Imara       | Dog     | M–F| Yes     | Meru  |
| Meru–Imara        | Dog     | M–F| No      | Meru  |
| Enzi–Zuri         | Dog     | F–M| No      | Nuru  |
| Enzi–Panya        | Dog     | F–M| Yes     | Nuru  |
| Layla–Nuru        | Dog     | F–F| No      | Nuru  |
| Layla–Zuri        | Dog     | F–F| No      | Nuru  |
| Panya–Pepeo       | Dog     | F–M| Yes     | Nuru  |
| Panya–Zuri        | Dog     | F–F| No      | Nuru  |
| Pepeo–Zuri        | Dog     | M–F| No      | Nuru  |
| Nuru–Zuri         | Dog     | M–F| Yes     | Nuru  |
| Sahibu–Gombo      | Dog     | M–M| Yes     | Nia   |

M: male; F: female.
The frequency of agonistic interactions (formal signals of dominance and submission as in Dale et al., 2017; Essler et al., 2017; see Table 2) were used to calculate each individual’s David’s score, (Gammell, de Vries, Jennings, Carlin, & Hayden, 2003). David’s scores were calculated based on the behavioural matrix that showed the best coverage, linearity and directional consistency index (i.e. frequency of submissive or dominant behaviours, and in some cases both frequencies combined, Gammell et al., 2003). Based on the David’s score we assessed for each dyad which was the dominant partner (dominance status) and calculated the absolute rank distance between the two individuals (i.e. the absolute value of the difference between individual A’s and B’s David’s score, as a measure of disparity between the respective dominance positions, De Waal, 1991). We used both measures, since dominance status can provide information at a dyadic level about who is dominant over whom, while rank distance also quantitatively takes the relative ‘strength’ of each individual in relation to its partner into account while also considering their relationships to all other pack members (more directly linked to competition, Marshall-Pescini, Schwarz, et al., 2017).

The frequency and/or duration of affiliative behaviours (number of times in which the two individuals were seen in body contact, time spent in body contact, number of times an individual approached the partner in a friendly way, number of times an individual lay down or stood in a friendly manner close to a partner, time spent grooming the partner; see Table 2) were first normalized per dyadic observation time and then used to calculate dyadic affiliation scores by conducting a principal component analysis (PCA, Silk et al., 2013).

Procedure

Testing took place in unfamiliar outdoor enclosures at the Wolf Science Center (average size = 3000 m²). In each test, we tested a dyad, and each subject was tested at least twice with two different partners, in two different enclosures to avoid habituation. The experiment included 20% of the videos to assess interrater reliability (depending on the variable, agreement was good or excellent; intraclass correlation coefficient ranging between 0.60 and 1.00, all P < 0.05).

After the first saliva collection (see below), the animals were walked by the animal trainers to the testing area using collar and leash. Upon arrival, both animals were simultaneously released in the testing area which they could freely explore (exploration). After 3 min, the trainers called the animals by name directing them into two smaller enclosures that were at least 10 m apart and physically and visually separated from each other (separation). After 3 min, the animals were again released into the main testing area and could reunite (reunion). After 3 min, both animals were again called by the trainers and directed to enter into a smaller area, thereby allowing the experimenter to place, unseen, the novel object (e.g. a child’s plastic castle) in the main testing area. Then the animals were again released into this area and could explore the novel object freely (novel object). The novel object was moved up and down by an experimenter present outside the testing enclosure by means of a rope attached to it. After 3 min, the animals were called into a separate smaller area for the social threat test. Here, the experimenter approached them wearing a costume that covered her face and her whole body. The experimenter and the animals were separated by a fence to avoid direct contact. The experimenter showed up about 10 m away from the fence and approached the dyad making weird movements such as jumping and agitating the arms. She walked until 2 m away from the fence, moved up and down with threatening movements for about 10 s and then went back to the starting position. The test ended when the experimenter was no longer in sight of the subjects. For more detailed description of the experimental procedure see Cimarelli et al. (2019). During the test, the trainers remained near the testing area but did not interact with the animals (except when they needed to move them from one area to the other as the test required).

Behavioural Analysis

The experiment was video recorded using two hand-held cameras and then coded offline using SolomonCoder Beta 15.01.13 (Andrés Péter, http://solomoncoder.com). A second coder, blind to the relationships of the animals and the hypotheses of the study, analysed 20% of the videos to assess interrater reliability (depending on the variable, agreement was good or excellent; intraclass correlation coefficient ranging between 0.60 and 1.00, all P < 0.05).

Table 2

| Category | Behaviour | Definition | Type |
|----------|-----------|------------|------|
| Dominant | Stand tall | Straightening up to full height, with a rigid posture and tail. It may include raised hackles, ears erect and tail perpendicular or above the back | Count |
|          | Stand over | Standing over another's body, with all four paws on the ground with tail held high. The receiver may have either the whole body or just the forepaws under the actor’s belly/side | Count |
|          | Paw on | Placing one or both forepaws on the other’s back | Count |
|          | Ride up | Mounting another one from behind or from the side, exhibiting a thrusting motion | Count |
|          | Head on | Approaching another’s shoulder/back and putting the head on it | Count |
|          | Muzzle bite | Grabbing the muzzle of another subject either softly or with enough pressure to make the other whimper | Count |
| Submissive | Crouch | Lowering the head, sometimes bending the legs, arching the back, lowering the tail between the hindlegs, and avoiding eye contact | Count |
| Affiliative | Withdraw | Moving away slowly in the opposite direction, displaying a submissive posture | Count and duration |
|          | Grooming | Nipping, licking or scratching another’s fur or skin | Count and duration |
|          | Body contact | Staying (for at least 10 s) with at least a part of the body in contact with the other subject, in a relaxed position | Count and duration |
|          | Approach friendly | Approaching another subject within one body length and remaining within that distance for at least 5 s. The approach is characterized by the subject holding the tail perpendicular to or below the plane of the back and wagging it | Count |
|          | Lie/stand friendly | Lying on the back, wagging the tail, maybe kicking with the foreleg against another subject sometimes with open mouth. Standing with tail perpendicular to or below the plane of the back, wagging it, ears pointed forward, while another is approaching it or orienting looking towards the subject | Count |
We coded stress-related behaviours, fear-related behaviours during the novel object test and the social threat, escape attempts during the separation phase and the social threat, proximity between the two partners, active proximity seeking, attempts to stay in body contact with the partner during the social threat, attempts to hide behind the partner during the social threat, gaze towards the partner, alternation of gaze between the partner and the novel object or between the partner and the masked experimenter and synchronized movements. See Table 3 for definitions of all coded variables.

Cortisol Analysis

Before the experiment, while the animals were still in their home enclosures, a saliva sample was taken orally using Salivette (Sarstedt, Ges.mbH, Wr. Neudorf, Austria). Food (e.g. cheese) was given to the subjects to increase salivation and acceptance of the swab in the mouth. A second and third saliva samples were taken immediately after the test and also 15 min later. All saliva samples were stored at −20 °C until analysis. A cortisol enzyme immunoassay (for details including cross-reactivity of the antibody see Palme & Möstl, 1997) was used to analyse cortisol levels. The assay was validated and successfully utilized in a series of previous studies conducted on canines (e.g. Haubenhofer and Kirchengast, 2007; Glenk et al., 2013, 2014; Affenzeller, Palme, & Zulch, 2017).

Statistical Analysis

A PCA on the affiliative behaviours shown by the subjects in their home enclosure during everyday life (body contact, grooming, lying down or standing in a friendly manner, approaching in a friendly manner) was conducted using an Oblimin rotation method. Two affiliation components emerged ('BC (body contact) affiliation' and 'FB (friendly behaviour) affiliation', see below) and were used as predictors in the models.

To investigate whether the behaviours shown during the test or the cortisol levels were influenced by the affiliative and dominance relationships of the subjects and/or the species, we fitted general (LMMs) or generalized linear mixed models (GLMMs, Baayen, 2008), depending on the distribution of the response variable. Considering the imbalance of related versus nonrelated dyads (8 versus 21) we did not investigate whether this variable influenced the response variable of interest, but we included the predictor ‘relatedness’ (yes versus no) in all models to control for it. Similarly, we included sex (male versus female) or dyadic sex combination (male–male, female–female, male–female) and pack type (whether small (N = 3) or big (N = 4–6 individuals)) in all models to control for them, but we did not consider their significance.

For variables coded in more than one test, we fitted LMMs or GLMMs (depending on the distribution of the response variable) with the identity of the subject and partner, the dyad and the pack

![Figure 1. Experimental task. The experimental task conducted in the present study comprised five tests: (a) exploration of the unfamiliar enclosure; (b) separation from the partner; (c) reunion with the partner; (d) a novel object test; (f) a social threat from a human. Photo credits: Robert Bayer.](image)

| Table 3 | List and definitions of the behavioural variables coded for the experimental procedure |
| --- | --- |
| Category | Behaviour | Definition | Type | Test |
| Behavioural stress | Stress | The subject shows yawning, body shaking, self-grooming, lips or nose licking, scratching | Occurrence | All |
| | Fear | The subject shows a crouched body position, tail tucked between the legs or jumps away from the object | Occurrence | Novel Object, Social Threat |
| Social support seeking | Proximity | The subjects are positioned within two body lengths from each other | Count | Separation, Social Threat |
| | Proximity seeking | The subject actively moves towards the partner until both individuals are within two body lengths from each other | Count | Exploration, Reunion, Novel Object |
| | Start body contact | The subject actively moves towards the partner until body contact between the two individuals occurs | Count | Social Threat |
| Reference/Coordination | Hide behind the partner | The subject positions herself behind the partner | Count | Social Threat |
| | Gaze to partner | The subject orients the head towards the partner | Count | Exploration, Reunion, Novel Object |
| | Alternation of gaze | The subject’s head orientation towards the partner is followed/preceded by looking towards the object/experimenter within 1 s | Count | Novel Object, Social Threat |
| | Synchronization | The subject moves in the same direction as the partner within 2 s and within 2 m (i.e. active locomotion, sniffing on the ground, vocalizing) | Count | Exploration, Reunion, Novel Object, Social Threat |
as random intercept effects plus all theoretically identifiable random slopes (Barr, Levy, Scheepers, & Tily, 2013; Schielzeth & Forstmeier, 2009). The occurrence (GLMMs with binomial error distribution and logit link function, McCullagh & Nelder, 1989), relative duration (LMMs) or count of the behaviours (GLMMs with Poisson error distribution and log link function) shown during the experimental task were included as dependent variables. Explanatory variables included in the model were the two affiliation components (‘BC affiliation’ and ‘FB affiliation’, see below), rank distance, dominance status, species, test, sex and relatedness as well as the following three-way interactions: BC affiliation*species*test, FB affiliation*species*test, rank distance*species*test, dominance status*species*test (and all lower order terms these encompass). For the variable proximity (bidirectional), we conducted an LMM with the proportion of time spent in proximity as the response variable (only one value per dyad) and the same random and fixed effects as the other models (but using sex combination instead of sex), but without including dominance status (and relative interactions).

For variables coded only during the social threat test (‘hiding behind the partner’ and ‘start body contact’), we fitted GLMMs (with binomial error distribution) with the identity of the subject and partner, the dyad and the pack as random effects (including all

Table 4
Pattern matrix

| Variable name | Component: ‘FB affiliation’ | Component: ‘BC affiliation’ |
|---------------|-----------------------------|-----------------------------|
| Grooming (count) | 0.89 | –0.07 |
| Grooming (duration) | 0.87 | –0.16 |
| Lie down or stand friendly (count) | 0.83 | –0.02 |
| Approach friendly (count) | 0.74 | 0.19 |
| Body contact (count) | 0.00 | 0.99 |
| Body contact (duration) | –0.02 | 0.98 |

Loadings on each component are represented in bold.

Table 5
Summary of significant results

| Category | Dependent variable | Test | FB affiliation | BC affiliation | Dominance status | Rank distance |
|----------|--------------------|------|----------------|----------------|-----------------|--------------|
| Stress reactivity (behavioural and physiological stress) | | All | | | | |
| Stress | | *Test: | NS | NS | NS |
| | | ↓ S | | | |
| | | ↑ ST | | | |
| Fear | NO, ST | NA | NA | NA | NA |
| Escape | S, ST | NS | ↑ | NS | ↑ |
| Delta cortisol (second – first sample) | / | NS | NS | NS | ↑ |
| Delta cortisol (third – second sample) | / | ↓ | NS | NS | ↑ |
| Proximity | E, R, NO | NS | NS | NS | ↓ |
| Social support seeking | | *Test*Species: | | | | |
| | | D: ↓ E, ↑ R, ↑ NO | | | |
| | | W: ↓ R | | | |
| Proximity seeking | E, R, NO | NS | NS | NS | NS |
| Start body contact | ST | NS | ↑ | NS | ↑ |
| Reference/Coordination | Hide behind the partner | ST | NS | NS | NS |
| Gaze to partner | E, R, NO | NS | NS | NS | NS |
| Alternation of gaze | NO, ST | NS | NS | NS | NS |
| Synchronization | E, R, NO, ST | *Test: | NS | NS | NS |
| | | ↓ E, NO | | | |
| W: wolves; D: dogs; E: exploration; S: separation; R: reunion; NO: novel object; ST: social threat; NA: not available. Asterisks indicate interactions.

Figure 2. Delta cortisol (third – second sample). Cortisol difference between the third and the second post-test samples according to (a) rank distance and (b) friendly behaviour (FB) affiliation. Regression lines are represented by dashed lines.
Theoretically identifiable random slopes). Explanatory variables included in the model were the two affiliation components, rank distance, dominance status, species, sex and relatedness as well as the following two-way interactions: BC affiliation*species, FB affiliation*species, rank distance*species, dominance status*species and all main effects these encompass.

For cortisol levels, we calculated the delta cortisol between the log-transformed values of the second and the first sample (as a proxy of the stress reactivity to the first four tests) and between the third and the second sample (as a proxy for the stress reactivity to the social threat test). We then conducted LMMs built with the same predictors as the other models (the two affiliation components, rank distance, dominance status, species, sex and relatedness as well as the following two-way interactions: BC affiliation*species, FB affiliation*species, rank distance*species, dominance status*species and all main effects these encompass) with the raw cortisol pretest levels (log transformed) and the delta cortisol between the two samples as response variables.

For all variables, we compared the respective full model with a null model (Forstmeier & Schielzeth, 2011) containing the same random effects and the control variables (sex or sex combination, relatedness, pack type) as the respective full model, and we used a likelihood ratio test (Dobson, 2002) for the full-null model comparison. We used a likelihood ratio test also 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. Considering the high complexity of the models given the small sample size, we decided to investigate individual effects in all cases in which the null-full model comparison revealed a P value lower than 0.1. However, we still considered an individual effect to be significant at the P value threshold of 0.05. Normality and homoscedasticity of residuals of LMMs were ascertained via residual distribution plots. For GLMMs with Poisson distribution,
we also assessed overdispersion, which was acceptable. Model stability was determined by removing individual cases one at a time and comparing model estimates obtained from each subset to those obtained for the full data set. Confidence intervals were determined based on parametric bootstrapping (N = 1000 bootstraps; function bootMer of the package lme4, Bates, Mächler, Bolker, & Walker, 2015). The analyses were conducted using the package lme4 (version 1.1–21, Bates et al., 2015) in R (version 3.6.2, R Core Team, 2019). All models including complete random-effects structure, sample size confidence intervals and stability are reported in the Supplementary Material.

RESULTS

Affiliation Scores

The PCA (Kaiser–Meyer–Olkin, KMO: 0.56, Bartlett’s sphericity test: $R^2_{15} = 203.175, P = 0.00$) conducted on the affiliative behaviours recorded during regular observations of spontaneous interactions revealed two components: one based on frequency and time spent in body contact (‘BC affiliation’) and one based on grooming and other friendly behaviours (‘FB affiliation’), explaining 48.66% and 31.30% of the total variance, respectively (see Table 4 for the variable loadings to each component). The two components were not correlated with one another (Pearson $r = -0.10$).

Variables Analysed during the Behavioural Test

We report here the results from the variables for which the null–full model comparison revealed a significant result. Complete results can be found in the Supplementary Material. All significant results are summarized in Table 5.

Stress reactivity

The experimental task activated a stress response, since most of the tested animals showed an increase in cortisol in the post-test samples in comparison to the pretest ones (79.31%). In both dogs and wolves, increasing FB affiliation (LMM: $X^2_1 = 5.02, P = 0.03$; Fig. 2) and rank distance (LMM: $X^2_1 = 4.07, P = 0.03$; Fig. 2) were significantly associated with a smaller difference in cortisol between the two post-test samples.

Similarly, both dogs and wolves were less likely to show stress-related behaviours when separated from a partner with whom they had higher FB affiliation scores but also more likely to show stress-related behaviours during the social threat test when with a partner with whom they had higher FB affiliation scores (interaction between FB Affiliation and test: GLMM: $X^2_4 = 9.92, P = 0.04$; Fig. 3). Similarly, both dogs and wolves tried to escape more often during the separation and the social threat test if they were tested with a partner with whom they had higher scores of BC affiliation (GLMM: $X^2_1 = 8.25, P = 0.004$; Fig. 4) and who were further away in the hierarchy (GLMM: $X^2_1 = 6.15, P = 0.01$; Fig. 4). Generally, wolves showed more stress-related behaviours (GLMM: $X^2_1 = 5.16, P = 0.02$) and tried to escape more often than dogs (GLMM: $X^2_1 = 13.12, P = 0.0003$), but the two species did not differ in how the various relationship components affected the likelihood of showing stress-related behaviours or the number of escape attempts (all interactions including species with $P > 0.05$). Overall, both dogs and wolves tried to escape more during the separation than during the social threat test (GLMM: $X^2_1 = 8.92, P = 0.003$).

Social support seeking

Social support seeking was differently modulated by relationship quality in dogs and wolves. In fact, for dogs, the lower the rank distance, the more time was spent in proximity during the exploration phase while the effect was the opposite during the reunion and the novel object tests. In contrast, for wolves the lower the rank distance, the less time was spent in proximity during the reunion phase (interaction between rank distance, species and test: LMM: $X^2_2 = 7.12, P = 0.03$; Fig. 5). During the social threat test, we found that the likelihood that dogs started to be in body contact with the partner increased with rank distance, whereas the opposite was true for wolves (interaction between rank distance and species: GLMM: $X^2_1 = 4.56, P = 0.03$; Fig. 6). However, in both dogs and...
wolves the higher the BC affiliation score, the more attempts were made to initiate body contact during the social threat test (GLMM: $X^2_1 = 10.03, P = 0.002$; Fig. 7).

Reference/Coordination

Both dogs and wolves synchronized their movements more often when tested with a highly affiliative partner especially in the exploration phase (interaction between FB affiliation and test: GLMM: $X^2_3 = 9.31, P = 0.03$; Fig. 8). Generally, dogs synchronized their movements with those of their partners more than wolves (GLMM: $X^2_1 = 8.45, P = 0.004$) but the two species did not differ in how the various relationship components affected how often they synchronized (all interactions including species with $P > 0.05$).

DISCUSSION

The aim of the present study was to investigate the role of affiliative and dominance relationship components in shaping wolves’ and dogs’ reaction to stressful situations. Overall, our results provide evidence that affiliation and rank distance influence the behavioural and physiological responses of dog and wolf dyads facing stressful stimuli, with few differences between the two species. Our results help shed light on the function of these relationship components (and relationships in general) in canines.

While previous studies on dogs and wolves have calculated affiliation using a single measure (e.g. Bonanni, Valsecchi, & Natoli, 2010; Essler et al., 2017; Marshall-Pescini, Schwarz, et al., 2017), in our sample two uncorrelated components emerged: one based on grooming and other friendly behaviours and one based on body contact. Also for other species, affiliative bonds have been described along different components, which do not always correlate with each other (e.g. proximity remains distinct from other affiliative behaviours such as grooming, Massen et al., 2010). Considering that in the present study these two components mediated different behaviours, we hypothesize that they reflect different animals’ motivations and have different functional roles.
As predicted, the affiliation component based on friendly behaviours such as grooming was mostly involved in stress regulation, being associated with reduced cortisol level responses and with more frequent synchronized movements. These results suggest that this component might be linked to a stress-management strategy, in which animals coordinate their actions to deal with an environmental stressor together (at least during the exploration and the novel object test). In fact, we could show that both dogs and wolves tested with a partner scoring higher on this component showed a lower stress reactivity (i.e., lower cortisol increase) than subjects tested with a less affiliative partner. Considering that this affiliation component was also associated with movement synchronization, we suggest that synchronized movements might have mediated the effect of affiliation on stress buffering (Cimarelli et al., 2019; Duranton & Gaunet, 2016). These results are in line with previous evidence showing that close affiliative partners are more likely to act together when dealing with external threats (e.g., when defending the territory from intruders, Bonanni, Valsecchi, & Natoli, 2010), suggesting a functional role of affiliative relationships during group defence in both dogs and wolves. These results are also in agreement with previous studies conducted on a variety of species confirming the role of affiliation in mediating stress buffering (see Rault, 2012 for a review).

Differently to our predictions (and to previous studies, e.g., Mazzini et al., 2013) we also found that higher scores of affiliation were associated with a lower likelihood of showing stress-related behaviours during the separation phase and with a higher likelihood of showing stress-related behaviours during the social threat test. A higher likelihood of producing stress signals when accompanied by a closer affiliative partner would seem to be contrary to the stress-buffering hypothesis of affiliation (Kiyokawa & Hennessy, 2018). However, this apparent incongruence might be explained by the fact that some stress-related behaviours (e.g., lip licking) might have gained a communicative function, in addition to expressing a negatively aroused internal state (as also suggested by Kaminski, Hynds, Morris, & Waller, 2017). In line with this, considering previous evidence that partners with a stronger affiliative bond are more likely to cooperate in a defensive context (Bonanni, Valsecchi, & Natoli, 2010), and the other associations we found between affiliation and movement synchronization, it is possible that during the social threat test the function of these behaviours was to better coordinate with a closely bonded affiliative partner.

Based on the idea that wolves, which are cooperative hunters and cooperative breeders, might benefit more from the presence of an affiliative partner than dogs, which are mostly scavengers and mostly do not engage in cooperative breeding (Marshall-Pescini, Cafazzo, et al., 2017), we expected a stronger association between affiliation and stress buffering in wolves than in dogs. Nevertheless, there was no difference between the two species and stress reactivity was dampened in both. These results support previous evidence showing that both dogs and wolves cooperate to defend their

![Figure 6](image-url)  
**Figure 6.** Body contact. Number of attempts to be in body contact with the partner during the social threat test according to rank distance and species: (a) dogs; (b) wolves. Regression lines are represented by dashed lines.

![Figure 7](image-url)  
**Figure 7.** Body contact. Number of attempts to be in body contact during the social threat test according to body contact (BC) affiliation. Regression lines are represented by dashed lines.
territory and they coordinate their movements to deal with potential threats (e.g. intruders: Bonanni, Valsecchi, & Natoli, 2010; Cassidy et al., 2015; Pal, 2015), and that affiliative bonds with the individuals present affect dogs’ choice to engage in or retreat from an intergroup conflict (Bonanni, Valsecchi, & Natoli, 2010). Hence, we suggest that the function of affiliative relationships in such ‘defensive’ contexts (i.e. when a potential danger may be present, as in the social threat test) might be conserved across social canid species, and might not have changed in dogs during the process of domestication.

Rank distance was also confirmed to play a role in stress buffering: the bigger the distance to the partner in the dominance hierarchy, the more tempered the physiological stress reaction was in both species. Closeness of rank between individuals might carry uncertainty (less clear who is dominant over whom, De Waal, 1991), thereby reducing the stress-buffering effect of a social partner or even adding to the stress created by the situation. Different to previous studies where rank distance mediated coordinated activities in dogs and wolves differently (with wolves closer in rank being more likely to coordinate and vice versa in dogs, Marshall-Pescini, Schwarz, et al., 2017; Moretti et al., 2015), we did not find that rank distance modulated stress reactivity differently in the two species. However, we found that rank distance potentially affects the link between proximity and stress buffering in opposite ways in dogs and wolves, reflecting different stress-coping strategies, both leading to stress reduction. In dogs, individuals further apart in the hierarchy spent more time in proximity (especially during the reunion and novel object test) and were more likely to look for body contact during the social threat test. This suggests that physical proximity with individuals more distant in rank may help to mitigate stress in dogs. Instead, in wolves, we found that individuals closer in rank were more likely to spend time in proximity during the reunion phase and seek body contact during the social threat test than those more distant in rank. These results seem to contradict the finding that being tested with a partner closer in rank resulted in a higher increase in cortisol, suggesting that the link between rank distance and proximity might not be necessarily related to stress buffering in wolves.

Figure 8. Synchronization. Number of synchronized movements according to friendly behaviour (FB) affiliation during the tests: (a) exploration; (b) reunion; (c) novel object; (d) social threat. Regression lines are represented by dashed lines.
In fact, wolves closer in rank were more likely to be in proximity than individuals further away in the hierarchy both in potentially stressful contexts (as in the present study and in Moretti et al., 2015) and in a cooperative task involving food (Marshall-Pescini, Schwarz, et al., 2017). Hence, rank distance in wolves might promote physical proximity in different contexts and, possibly, more generally reflect a form of social monitoring (McNelis et al., 1998), rather than of social support seeking. Therefore, the stress-buffering effect of partners with distant rank is likely to be mediated by mechanisms other than physical closeness. Future studies are needed to clarify the connection between rank distance and physical proximity in wolves, but also to investigate the role of rank distance depending on the individual’s dominance status (that is, whether rank distance has a differential effect in subordinate or dominant individuals). The other affiliation component identified here, based on the time spent in body contact during everyday life, was mostly associated with behaviours related to physical proximity during the test: in fact, this component positively influenced the number of escape attempts (especially during the separation test) and body contact seeking during the social threat test. However, we found no clear evidence that this relationship component affected coping with stress. Therefore, the finding that the animals tried to escape their partner more often when tested with partners with whom they had high body contact affiliation scores may reflect their attempts to follow their usual patterns of body contact with their different partners rather than a stress-coping strategy. Future studies will be needed to better comprehend the reasons behind the variation between dyads along this component and its functions.

We found no evidence that dominance status affected social stress buffering. We predicted such an effect based on previous studies conducted in the wild showing that subordinate dogs and wolves follow their dominant partners’ movement initiations (in relatively relaxed contexts) more than vice versa (Bonanni, Cafazzo, et al., 2012; Shepherd et al., 2006), an effect of affiliation or dominance that makes it impossible to draw a conclusion and calls for further investigations.

One could argue that the fact that the single tests were carried out one after the other might have led to a potential accumulation effect (animals being more and more stressed throughout the experiment) which might have overshadowed the effect of the other variables. However, including the variable test in the models allowed us to control for this element. Only one variable, ‘escape attempts’, was affected by test, and interestingly more escape attempts occurred during the separation test than the last, social threat test. Thus, a stress accumulation effect seems unlikely. Still, further studies are required to investigate whether a longer delay between the single tests would influence the animals’ behaviours.

We recommend caution in generalizing the results of the present study to other dog and wolf populations, since both dogs and wolves involved in the present study deal with the same environmental challenges (i.e. same captive setting) and because of the limited sample size. Further studies will need to confirm whether affiliation and dominance similarly regulate how free-ranging animals deal with stressful situations that occur in their natural environment.

Conclusions

Both dogs and wolves’ social relationships can be described in terms of formal dominance and affiliation. Importantly, affiliation appears to be represented by two uncorrelated components, one based on friendly behaviours and the other on body contact. Although the two species have different social ecologies, their affiliation components similarly regulate the way in which they deal with stressful situations. We showed a positive link between affiliative relationship components and stress buffering, as well as social support seeking in both species, and a similar regulatory role of rank distance in stress reactivity and social support seeking. Still, a few differences also emerged, suggesting that the rank distance between two individuals regulates social support seeking in dogs and wolves differently: dogs were more likely to look for social support from a partner far away in rank, while the opposite was true in wolves. Taken together, these results suggest that the different social organizations of the two species do not seem to influence how affiliation and dominance affect how the animals cope with stressful situations.

Author Contributions

G.C., S.M.P., F.R. and Z.V. designed the study; G.C. and Z.V. collected the data; G.C. and A.B. analysed the data; all authors interpreted the data. G.C. wrote the first draft of the paper; S.M.P., F.R., A.B. and Z.V. critically revised the manuscript. All authors gave final approval for publication and agree to be held accountable for the work described therein.

Declaration of Interest

The authors declare no competing interests.

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Supplementary Material

Supplementary material associated with this article can be found online at https://doi.org/10.1016/j.anbehav.2021.06.008.

References

Afzenzeller, N., Palme, R., & Zulch, H. (2017). Playful activity post-learning improves training performance in Labrador Retriever dogs (Canis lupus familiaris). Physiology & Behavior, 168, 62–73. https://doi.org/10.1016/j.physbeh.2016.10.014
Altmann, J. (1974). Observational study of behavior: Sampling methods. Behaviour, 49(3/4), 227–267. Retrieved from https://www.jstor.org/stable/4533591, Aureli, F., & Smucny, D. (2000). The role of emotion in conflict and conflict resolution. In F. Aureli, & F. de Waal (Eds.), Natural conflict resolution (pp. 199–224). Berkeley, CA: University of California Press.
Baayen, R. (2008). Analyzing Linguistic Data: A Practical Introduction to Statistics. Cambridge, UK: 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. (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67(1). https://doi.org/10.18637/jss.v067.i01
Boccia, M. L., Retie, M., & Laundenslager, M. (1989). On the physiology of grooming in a pigtail macaque. Physiology & Behavior, 45(3), 667–670. https://doi.org/10.1016/0031-9384(89)90089-9
Boitani, L., & Ciucci, P. (1995). Comparative social ecology of feral dogs and wolves. Behavioral Ecology, 28, 10.1016/0031-9384(89)90089-9
Boitani, L., Ciucci, P., & Ortolani, A. (2007). Behaviour and social ecology of free-ranging dogs. Behavioral Ecology and Sociobiology, 71(7), 107. https://doi.org/10.1007/s00265-017-2339-8
Boitani, L. F. de Waal, M. L. (1995). Comparative social ecology of feral dogs and wolves. Behavioral Ecology, 28, 10.1016/0031-9384(89)90089-9
De Waal, F. B. M. (1991). Rank distance as a central feature of rhesus monkey social organization: A sociometric analysis. Animal Behaviour, 41(3), 383–395. https://doi.org/10.1016/0003-3170(91)90057-8
De Waal, F. B. M., & Luttrell, L. M. (1989). Toward a comparative sociology of the genus Macaca: Different dominance styles in rhesus and stump-tailed monkeys. American Journal of Primatology, 19(2), 83–109. https://doi.org/10.1002/ajp.1300190201
Dobson, A. (2002). An Introduction to Generalized Linear Models. London, UK: Chapman & Hall/CRC.
Duranton, C., & Gaument, F. (2016). Behavioral synchronisation from an ethological perspective: Overview of its adaptive value. Adaptive Behavior, 24(3), 181–191. https://doi.org/10.1177/1059712316649466
Essler, J. L., Marshall-Pescini, S., Range, F., Walker, S., Kubinyi, E., & Ciani, V. (2017). Domestication does not explain the presence of inequity aversion in dogs. Current Biology, 26, 601–605. https://doi.org/10.7120/09627286.2017.1360
Forstmeier, W., & Schielzeth, H. (2013). 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/s00265-010-1035-4
Gammel, M. P., de Vries, H., Jennings, D. J., Carlin, C. M., & Hayden, T. J. (2003). David’s score: A more appropriate dominance ranking method than Clutton-Brock et al.’s index. Animal Behaviour, 66(3), 601–605. https://doi.org/10.1016/S0003-3170(02)00126-3
Glaser, E. R., & DeVries, A. C. (2005). Social structure influences effects of pair-housing on wound healing. Brain, Behavior, and Immunity, 19(1), 61–68. https://doi.org/10.1016/j.bbi.2004.03.002
Glenk, L., Rothgassner, O., Stetina, B., Palme, R., Keppling, B., & Baran, H. (2013). The dogs’ salivary cortisol profile varies during animal-assisted interventions. Animal Welfare, 22, 369–378. https://doi.org/10.7120/09627286.22.3.369
Glenk, L. M., Rothgassner, O., Stetina, B. U., Palme, R., Keppling, B., & Baran, H. (2016). Anandulatory cortisol behavior in therapy dogs during animal-assisted interventions: A pilot study. Journal of Veterinary Behavior, 9, 98–106. https://doi.org/10.1016/j.jvbeh.2014.02.005
Haubenhofer, D. K., & Kirchengast, S. (2007). “Dog Handlers” and Dogs’ emotional and cortisol secretion responses associated with animal-assisted therapy sessions. Society and Animals, 15, 127–150. https://doi.org/10.1007/s12682-003-2226-3
Kiyokawa, Y., & Hennessy, M. B. (2018). Comparative studies of social buffering: A consideration of approaches, terminology, and pitfalls. Neuroscience & Biobehavioral Reviews, 86(December 2017), 131–141. https://doi.org/10.1016/j.neubiorev.2017.12.005
Koski, S. E., Koops, K., & Sterck, E. H. M. (2007). Reconciliation, relationship quality, and postconflict anxiety: Testing the integrated hypothesis in captive chimpanzees. American Journal of Primatology, 69(2), 158–172. https://doi.org/10.1002/ajp.20368
Lindblad-Toh, K., Wade, C. M., Mikkelsen, T. S., Karlsson, E. K., Jaffe, D. B., Kamal, M., et al. (2005). Genome sequence, comparative analysis and haplotype structure of the domestic dog. Nature, 438(7069), 803–819. https://doi.org/10.1038/nature04336
Lord, D. C., Melenberg, M., Steinbusch, H. W. M., & Coan, J. (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.2012.09.009
MacNulty, D. R., Tallian, A., Stahler, D. R., & Smith, D. W. (2014). Influence of group size on the success of wolves hunting Bison. PLoS One, 9(11), Article e101884. https://doi.org/10.1371/journal.pone.0101884
Madsen, J. M., Sterck, E. H. M., & de Vos, H. (2010). Close social associations in animals and humans: Functions and mechanisms of friendship. Behaviour, 147(11), 1397–1412. https://doi.org/10.1163/156853710X13077204
Mazzini, F., Townsend, S. W., Viranyi, Z., & Range, F. (2013). Importance of a species’ socioecology: Wolves outperform dogs in a conspecific compromise task. Proceedings of the National Academy of Sciences, 110(44), 11793–11798. https://doi.org/10.1073/pnas.1310027114
McComb, K., Shannon, C., Fagen, J. R., & Packer, C. (2011). Leadership in elephants: The adaptive value of age. Proceedings of the Royal Society B: Biological Sciences, 278(1722), 3270–3276. https://doi.org/10.1098/rspb.2011.0168
McNulty, D. R., Shannon, C., Cifelli, R., & Skotak, R. (2013). Characterization of food sharing in wolves and dogs. Behavioral Ecology and Sociobiology, 71(7), 107. https://doi.org/10.1007/s00265-017-2339-8
Mikat, S. E., & Sterck, E. H. M. (2007). The adaptive value of age. Proceedings of the Royal Society B: Biological Sciences, 278(1722), 3270–3276. https://doi.org/10.1098/rspb.2011.0168
McCullagh, P., & Nelder, J. (1989). Generalized Linear Models. Boca Raton, FL: CRC Press.

McLeod, P. J., Moger, W. H., Ryon, J., Gaddis, S., & Fentress, J. C. (1996). The relation between urinary cortical levels and social behavior in captive timber wolves. Canadian Journal of Zoology, 74(2), 209–216. https://doi.org/10.1139/z96-026

McNeil, N. L., & Boatright-Horowitz, S. L. (1998). Social monitoring in a primate group: The relationship between visual attention and hierarchical ranks. Animal Cognition, 1(1), 65–69. https://doi.org/10.1007/s100710050008

Mech, L. D. (1999). Alpha status, dominance, and division of labor in wolf packs. Canadian Journal of Zoology, 77(8), 1196–1203. https://doi.org/10.1139/z99-099

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

Merola, L., Prato-Previde, E., & Marshall-Pescini, S. (2012). Social referencing in dog-owner dyads? Animal Cognition, 15(2), 175–185. https://doi.org/10.1007/s10071-011-0443-0

Micheletta, J., & Waller, B. M. (2012). Friendships affect gaze following in a tolerant species of macaque, Macaca nigra. Animal Behaviour, 83, 459–467. https://doi.org/10.1016/j.anbehav.2011.11.018

Moretti, L., Hentrup, M., Kotrschal, K., & Range, F. (2015). The influence of relationships on neophobia and exploration in wolves and dogs. Animal Behaviour, 107, 159–173. https://doi.org/10.1016/j.anbehav.2015.06.008

Pal, S. K. (2015). Factors influencing intergroup agonistic behaviour in free-ranging domestic dogs (Canis familiaris). Acta Ethologica, 18(2), 209–220. https://doi.org/10.1007/s10442-014-0208-2

Palme, R., & Mostl, E. (1997). Measurement of cortisol metabolites in faeces of sheep as a parameter of cortisol concentration in blood. International Journal of Mammanlian Biology, 62(1), 192–197. https://doi.org/10.1023/a:1024695616125

Peterson, R. O., Jacobs, A. K., Drummer, T. D., Mech, L. D., & Smith, D. W. (2002). Leadership behavior in relation to dominance and reproductive status in gray wolves, Canis lupus. Canadian Journal of Zoology, 80(8), 1405–1412. https://doi.org/10.1139/z01-124

Range, F., & Virányi, Z. (2011). Development of Gaze Following Abilities in Wolves (Canis lupus). PLoS One, Article e16888. https://doi.org/10.1371/journal.pone.0016888

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

Rauf, J. L. (2012). Friends with benefits: Social support and its relevance for farm animal welfare. Applied Animal Behaviour Science, 136(1), 1–14. https://doi.org/10.1016/j.applanim.2011.10.002

Rauth, J. L. (2018). Be kind to others: Prosocial behaviours and their implications for animal welfare. Applied Animal Behaviour Science, 210(1), 113–123. https://doi.org/10.1016/j.applanim.2018.10.015

Romero, T., Ito, M., Saito, A., & Hasegawa, T. (2014). Social modulation of contagious yawning in wolves. PLoS One, 9(8), Article e105963. https://doi.org/10.1371/journal.pone.0105963

R Core Team. (2019). R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org/

Sand, J., & Creel, S. (2004). Social dominance, aggression and faecal glucocorticoid levels in a wild population of wolves, Canis lupus. Animal Behaviour, 67(3), 387–396. https://doi.org/10.1016/j.anbehav.2003.03.019

Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. Science, 308(5722), 648–652. https://doi.org/10.1126/science.1106477

Sárova, R., Spinka, M., Stěhálová, I., Ceccero, F., Šimečková, M., & Kotrba, R. (2013). Pay respect to the elders: Age, more than body mass, determines dominance in female beef cattle. Animal Behaviour, 86(6), 1315–1323. https://doi.org/10.1016/j.anbehav.2013.10.002

Schenkel, R. (1967). Submission: Its features and function in the wolf and dog. American Zoologist, 7(2), 319–329. https://doi.org/10.1093/axr/7.2.319

Schleizh, H. (2010). Simple methods to improve the interpretability of regression coefficients. Methods in Ecology and Evolution, 1(2), 103–113. https://doi.org/10.1111/j.2041-210X.2010.00102.x

Schleizh, H., & Forstmeier, W. (2009). Conclusions beyond support: Overconfident estimates in mixed models. Behavioral Ecology, 20(2), 416–420. https://doi.org/10.1093/beheco/arq145

Shepherd, S. V., Deane, R. O., & Platt, M. L. (2006). Social states and social attention in monkeys. Current Biology, 16, R119–R120. https://doi.org/10.1016/j.cub.2006.02.013

Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 362, 539–559. https://doi.org/10.1098/rstb.2006.1994

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., et al. (2010). Strong and consistent social bonds enhance the longevity of female baboons. Current Biology, 20, 1359–1361. https://doi.org/10.1016/j.cub.2010.05.067

Silk, J., Cheney, D., & Seyfarth, R. (2013). A practical guide to the study of social relationships. Evolutionary Anthropology, 22(5), 213–225. https://doi.org/10.1002/evan.21367

Thierry, B. (2000). Covariation of conflict management patterns across macaque species. In F. Aureli, & F. B. M. de Waal (Eds.), Evolutionary Anthropology, 22(3), 106–125. Berkeley, CA: University of California Press.

Trisko, R. K., Sandel, A. A., & Smuts, B. (2016). Affiliation, dominance and friendship among companion dogs. Behaviour, 153(6–7), 693–725. https://doi.org/10.1163/1568539X-00003522

Udell, M. A. R., & Wynne, C. D. L. (2010). Ontogeny and phylogeny: Both are essential to human-sensitive behaviour in the genus Canis. Animal Behaviour, 79(2), e9–e14. https://doi.org/10.1016/j.anbehav.2009.11.033

van der Borg, J. A. M., Schilder, M. B. H., Vinke, C. M., & de Vries, H. (2015). Dominance in domestic dogs: A quantitative analysis of its behavioural measures. PLoS One, 10(8), Article e0139378. https://doi.org/10.1371/journal.pone.0139378

van Kerkhove, W. (2004). A fresh look at the wolf-pack theory of companion-animal dog social behavior. Journal of Applied Animal Welfare Science, 7(4), 279–285. https://doi.org/10.1086/427167

Wang, G.-D., Zhai, W., Yang, H.-C., Wang, L., Zhong, L., Liu, Y.-H., et al. (2016). Out of southern east asia: The natural history of domestic dogs across the world. Cell Research, 26(1), 21–33. https://doi.org/10.1038/cr.2015.14

Werhahn, G., Virányi, Z., Herrera, G., Sommese, A., & Range, F. (2016). Wolves (Canis lupus) and dogs (Canis familiaris) differ in following human gaze into distant space but respond similar to their packmates’ gaze. Journal of Comparative Psychology, 130, 288–298. https://doi.org/10.1037/cpr0000036

Wittig, R. M., Crockford, C., Weltring, A., Langergraber, K. E., Deschner, T., & Zuberbühler, K. (2016). Social support reduces stress hormone levels in wild chimpanzees across stressful events and everyday affiliations. Nature Communications, 7(1), 13361. https://doi.org/10.1038/ncomms13361