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Dominance relationships in a group of domestic dogs (*Canis lupus familiaris*)

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Abstract

We investigated the extent to which dominance relationships, as described for feral dogs and wolves, applied to a group of 24 neutered companion dogs at a dog daycare facility. Similar to other studies of dogs and wolves, we found significant linear dominance hierarchies based on highly unidirectional displays of submission and aggression. Submission was the most frequent, unidirectional and linear type of agonistic behaviour and, therefore, a better indicator of status than aggression or dominance displays. Aggression was low intensity, consisting mainly of ritualized threats with no physical contact, and conflicts involving physical contact were never injurious. Older dogs out-ranked younger dogs, but size was unrelated to dominance rank. Dominance relationships were more often expressed in same-sex dyads than between males and females. The coverage of dominance relationships in the daycare group was low compared to that reported for sexually intact dogs and wolves, which was probably a result of reduced competition due to neutering and other human influences. In many dyads dogs never exchanged agonistic behaviours, but bi-directional relationships were rare, and most dogs formed some dominance relationships with other dogs. Except for their low coverage, muzzle licks met the criteria for a formal display of submission. Our results suggest that dominance remains a robust component of domestic dog behaviour even when humans significantly reduce the potential for resource competition. The possible proximate benefits of dominance relationships for dogs are discussed.

Keywords

dominance, domestic dog, agonistic behaviour, submission, aggression, dominance hierarchy, formal dominance, social relationships.

1. Introduction

For decades, ethologists have used dominance to describe social relationships among group-living animals. In order for dominance to apply to a

particular relationship, outcomes of agonistic interactions should be unidirectional (i.e., occur in only one direction in a dyadic relationship); if a dominance hierarchy is a useful model for describing relationships within a social group, dominance relationships should also be linear (i.e., transitive rather than circular) and show high coverage (i.e., occur in a high proportion of relationships within the group) (Chase, 1974; Hinde, 1974; Rowell, 1974; van Hooff & Wensing, 1987; Drews, 1993; de Vries, 1995). In many species, measures of dominance based on communicative agonistic displays tend to be more consistent across contexts than do measures of competitive outcomes (de Waal & Luttrell, 1985; van Hooff & Wensing, 1987; Preuschoft et al., 1998; Vervaeke et al., 2000; Flack & de Waal, 2007; Lu et al., 2008). De Waal (1986) introduced the concept of formal dominance, or 'the unequivocal communication of status', to account for discrepancies between agonistic displays and competitive outcomes. In formal dominance relationships, dominants may occasionally allow subordinates to assert themselves in competitive encounters provided they consistently express their subordinate status through formal displays. Formal displays of submission can promote tolerance and resource sharing by the dominant. Thus, even when competitive outcomes are somewhat inconsistent, a formal dominance relationship can be present.

Formal dominance is most likely in societies characterized by high levels of both competition and cooperation/affiliation (de Waal, 1986, 1989; East et al., 1993; Vervaeke et al., 2000; Lu et al., 2008). To qualify as a formal indicator of status, a behaviour should: (1) be unidirectional, (2) show high coverage, (3) remain stable across different social contexts, (4) correlate, at least to some degree, with agonistic dominance relationships based on aggression and (5) communicate relative status rather than overt aggression or conditioned fear (i.e., it should occur in the absence of aggression) (de Waal & Luttrell, 1985; de Waal, 1986, 1989; Preuschoft, 1999; Vervaecke et al., 2000).

Dominance has traditionally been regarded as an important aspect of social relationships among domestic dogs (Scott & Fuller, 1965; Beach, 1970; Pal et al., 1998; Bauer & Smuts, 2007; Cafazzo et al., 2010, 2012; van der Borg et al., 2012; Schilder et al., 2014) and among dogs' ancestors, wolves (Schenkel, 1967; Zimen, 1978; Lockwood, 1979; van Hooff & Wensing, 1987; Derix et al., 1993; Peterson et al., 2002; Sands & Creel, 2004; Jenks, 2011). Recently, however, there has been a debate in the literature about

whether dominance applies to domestic dog behaviour particularly for sexually neutered companion dogs that live closely with humans (Bradshaw & Nott, 1995; Eaton, 2002; Shepherd, 2002; van Kerkhove, 2004; O'Heare, 2007; Bradshaw et al., 2009; Schilder et al., 2014; see Smuts, 2014, for a review). Unfortunately, quantitative data on dominance in neutered companion dogs is sparse (Bauer & Smuts, 2007; Bradshaw et al., 2009).

In this study, we tested the hypothesis that pet domestic dogs form dominance relationships similar to those reported for feral dogs (Cafazzo et al., 2010) and wolves (van Hooff & Wensing, 1987). We investigated dominance in a group of 24 neutered companion dogs that socialized regularly at a dog daycare facility by recording the frequency and direction of agonistic behaviours in the group. We addressed the following questions: (1) Are agonistic behaviours unidirectional and linear, and do they show high coverage? (2) What type of agonistic behaviour is the most appropriate for determining dominance relationships? (3) How are individual factors such as age, sex, and size related to dominance relationships? (4) Do any agonistic behaviours meet the criteria for formal status signals? (5) How do dominance relationships in the group compare with those reported for other groups of dogs and wolves? We also discuss proximate benefits that pet dogs may derive from dominance relationships.

2. Material and methods

2.1. Subjects and observations

The study was conducted at a dog daycare facility in Evanston, IL, USA and approved by the University Committee on Use and Care of Animals at the University of Michigan, approval No. 8988. Approximately 100 neutered companion dogs attended the facility on a regular basis (1–5 days per week) with approx. 40 dogs present on any given day, Monday through Friday, 7 a.m.–7 p.m. Dogs were housed in three separate groups of approx. 10–20 dogs in outdoor or indoor enclosures approx. 92.9–185.8 m^2 in size. Dogs arrived and left the facility at various times throughout the day, group membership fluctuated often, and new dogs were regularly introduced. Behavioural observations were recorded in one of the three groups several days per week on 90 days distributed over the course of one year for a total of 224.4 h of observations. We collected behavioural data for a total of 81 dogs. Because group membership fluctuated daily, each pair of dogs (dyad) was observed together for a different amount of time, and several dyads among

the total 81 dogs observed were never observed together. For this reason, 24 dogs (276 dyads) with the highest number of observation hours with one another were chosen for final analyses. The final 276 dyads were observed together for a minimum of 4 and maximum of 214 h on a minimum of 3 and maximum of 90 separate days. All 276 dyads had interacted on several occasions and were familiar with one another prior to the start of data collection. Data analysis included 12 males and 12 females of various pure and mixed breeds, ranging from 7 months to 11 years of age and 9–46 kg in weight (Table 1).

Table 1.
Summary of subject information.

Rank[a]	Dog	Initials	Sex	Age (months)	Size (kg)	Breed	No. of Dom[b]	No. of Sub[c]
1	Bailey	BA	F	116	19.07	Basenji mix	10	0
2	Charlie	CH	F	71	38.14	Husky mix	9	0
3	Junebug	JB	F	94	10.90	Beagle	10	1
4	Cody	cd	M	76	33.60	Airedale	6	1
5	Happy	hp	M	140	13.17	Beagle mix	4	0
6	Wrigley	wr	M	37	31.78	Golden retriever	2	1
7	Wallaby	wa	M	39	28.60	Cattle dog mix	9	6
8	Lily H	LH	F	41	45.40	Scottish deerhound	9	3
9	Lily A	LA	F	43	26.79	Belgian Tervuren	5	3
10	Freedom	FR	F	65	19.52	Labrador mix	2	1
11	Taggart	tg	M	66	32.69	Vizsla	0	1
12	Maggie	MG	F	40	21.79	Boxer mix	3	7
13	Rex	rx	M	29	24.52	Portuguese water dog	3	4
14	Molly	ML	F	20	45.85	Newfoundland	2	2
15	Fielding	fd	M	45	11.35	Bichon mix	0	0
16	Sawyer	sy	M	41	36.32	Spinone Italiano	0	1
17	Buddy	bd	M	19	33.86	Golden retriever mix	1	2
18	Mason	ms	M	28	19.52	Vizsla	1	4
19	Lionel	li	M	42	39.95	Labrador retriever	2	3
20	Riley	RI	F	7	22.70	Boxer mix	0	3
21	Mindy	MD	F	38	9.54	Pug	2	5
22	Lizzy	LZ	F	40	31.78	Golden-doodle	2	5
23	Benny	bn	M	30	24.97	Golden-doodle	0	15
24	Sachi	SA	F	16	21.79	Vizsla	0	13

[a] Dominance rank based on matrix of submission using the I&SI method (de Vries, 1998).
[b] Number of dyadic relationships in which dog only receives submission.
[c] Number of dyadic relationships in which dog only emits submission.

Submissive, aggressive and dominant behaviours based on previous research in wolves and ethograms of canine behaviour (Van Hooff & Wensing, 1987; Abrantes, 1997; Handleman, 2008) were recorded among the dogs in the focal group. After spending many months becoming familiar with the dogs and their behaviours, the first author conducted all data collection in real time using the *ad libitum* method for all-occurrence sampling (Altmann, 1974). We employed this method because it was possible to observe every dog in the group at once, and agonistic behaviours were relatively rare and obvious. Submissive behaviours included muzzle licks, low posture, passive submission, and retreat, aggressive behaviours included threats and attacks, and dominant behaviours included muzzle bites, high posture, mounts and chin-overs (see Table 2 for detailed descriptions of all behaviours). 'Active submission' (Schenkel, 1967; Goodman et al., 2002) is a behaviour complex that combines muzzle licking and a low posture. If a dog displayed the full complex of active submission the behaviour and the posture were recorded separately (e.g., active submission was coded as a muzzle lick and a low-posture). We considered behaviours and postures separately because posture was sometimes difficult to determine due to morphological variation (e.g., floppy ears, a cropped tail, a bushy coat of fur, large discrepancies in size).

Since some agonistic behaviours can be displayed during play, we also recorded playful interactions (Table 2). If the actor displayed a submissive or dominant behaviour within one minute of a play behaviour, the agonistic behaviour was recorded as occurring in a playful context. Although play behaviours sometimes mimic aggressive behaviours (e.g., growling, baring teeth, biting), play was distinguished from actual aggression by the fluid body posture, relaxed facial expression and exaggerated bouncy movements of the actor. By definition, aggression (Table 2) was not accompanied by fluid body posture and bouncy movements and could not occur in a playful context. We distinguished passive submission from voluntary downs during play (Bauer & Smuts, 2007; Ward et al., 2008) as follows. For the behaviour to be recorded as passive submission during play the actor had to pause and remain still for at least one full second lying on his side or back while the recipient of the submission sniffed his underside. A voluntary down occurred when the actor dropped to the ground on her own initiative, but the belly was not necessarily exposed, the genitals were not sniffed and play did not pause.

Human supervisors at the dog daycare facility directly intervened in some of the dogs' social interactions. Most threats were immediately followed by

Table 2.
Ethogram of agonistic behaviours.

Behaviour	Description
Aggressive	
Threat	*A* directs a mild display of aggressive behaviour at *R*, that may include any of the following behaviours: barking, growling, staring, lip curling, and/or snapping, but *A* makes no body contact or bite contact with *R*.
Attack	*A* directs aggressive behaviour at *R* that may include any of the behaviours listed above for threat, and also includes one or more of the following behaviours: forceful body contact, open mouth jaw sparring, and/or closed mouth bite contact.
Dominant	
High posture	*A* stands close to *R* and raises himself to full height, with head and tail held high, back legs straight and stiff, body leaning slightly forward.
Muzzle bite	*A* hold's *R*'s nose between her jaws and holds it gently for one second or longer.
Mount	*A* places his forepaws around *R*'s torso. *A* can approach from the rear, side, or front, and may or may not thrust his pelvis.
Chin-over	*A* places her head on *R*'s back or shoulders for one second or longer.
Submissive	
Muzzle lick	*A* licks *R*'s nose, lips, and/or chin.
Low posture	*A* lowers his head and body with legs bent and a rounded back. *A*'s tail is down or tucked between the legs.
Passive submission	*A* lies on her side or back and remains still for at least one second, exposing her ano-genital region, belly, and/or chest for *R*'s inspection.
Retreat	*A* turns his head and body and moves away from *R* in response to an aggressive or dominant behaviour from *R*.
Play	*A* maintains a fluid body posture with a relaxed facial expression and exaggerated bouncy movements and displays one or more of the following play behaviours: play bow, paw, jump on, mouth, play bite, tackle, nose jab, chase. Mutual play is recorded if *R* also displays one or more play behaviour with a fluid body posture and relaxed facial expression.

A, actor; *R*, recipient. Adapted from Van Hooff & Wensing (1987); Handleman (2008).

a verbal interruption from the human supervisor unless the recipient immediately retreated before a verbal interruption was made; in this case, a retreat was recorded for the recipient of the threat. If a human interrupted the threat, no retreat was recorded. All aggression that included physical

contact was immediately interrupted with verbal or physical means (e.g., physically separating and/or restraining one or both dogs), and the dogs involved were separated from the other group members and confined to a crate for 3–5 min immediately afterwards. Pairs of dogs that had several aggressive interactions, as well as those that human supervisors considered likely to get into conflicts, were permanently placed in separate groups. In order to prevent threats and attacks, dogs who approached in a high-posture or mounted another dog were interrupted (the behaviour was subsequently recorded). Human supervisors also reinforced non-aggression. For example, if an active young dog accidentally bumped into an older dog who was resting, the human supervisor would interrupt and redirect the dogs by calling one or both over to sit for a piece of kibble, thereby preventing a potential agonistic interaction and possibly reducing the likelihood of aggressive behaviours in the future. Dogs who displayed aggression during an initial evaluation, frequently initiated aggression or caused an injury more severe than a few small scratches were excluded from the facility. In summary, the dogs were selected for non-aggression, aggressive behaviour was humanely punished (i.e., verbal interruption or temporary isolation from the group), and the absence of aggressive behaviour was rewarded. Therefore, the frequencies of threats, retreats, attacks, high-posture and mounts among the dogs were undoubtedly reduced by human interventions, but it is unlikely that the directionality of agonistic behaviours were altered. We will revisit the issue of human intervention in the discussion.

2.2. Statistical analyses

In order to investigate agonistic dominance relationships, frequencies of aggressive, dominant, and submissive dyadic interactions were used to construct three matrices with actors on the vertical axis and recipients on the horizontal axis. The matrices of submission and dominant behaviours in playful and non-playful contexts were significantly correlated with one another (submission: $\tau_{rw,av} = 0.411$, $p = 0.001$, dominant behaviours: $\tau_{rw,av} = 0.456$, $p = 0.001$). Therefore, to increase sample size, agonistic behaviours occurring in playful and non-playful contexts were combined for analyses of unidirectionality, linearity, coverage, and for comparing different agonistic behaviours. For analyses, all matrices of submissive behaviour were transposed, moving recipients to the vertical axis and actors to the horizontal axis, allowing us to compare aggression or dominance emitted with submission

received. All matrix analyses were performed using MatMan 1.1 (Noldus Information Technology). For each behavioural matrix, linearity of dominance relationships was assessed using de Vries (1995) improved version of Landau's index of linearity (h) (Landau, 1951), which accounts for blank and tied relationships (h'). The linearity index (h') accounts for the presence of circular relationships in the group, but blank relationships can also lower the value of h' even when no circular relationships exist (Klass & Cords, 2011); perfect linearity ($h' = 1$) occurs when there are no circular and no blank relationships. The statistical significance of h' was tested by means of a 2-step randomization test with 10 000 randomizations (de Vries, 1995). If significant linearity was found, we applied the procedure proposed by de Vries (1998) to reorder the dogs in the dominance rank order most consistent with a linear hierarchy for each matrix. The directional consistency index (DCI) of each matrix was calculated as the total number of times a behaviour was performed in the direction of the higher frequency within each dyad (H) minus the total number of times the behaviour occurred in the direction of the lower frequency within each dyad (L), divided by the total number of times the behaviour was performed by all individuals: $\mathrm{DCI} = (H - L)/(H + L)$ (van Hooff & Wensing, 1987; Cafazzo et al., 2010). To assess the coverage of a behaviour or a behavioural category, we subtracted the number of bidirectional and blank relationships from the total number of dyads to calculate the percentage of unidirectional (1-way relationships). As an additional measure of coverage, we calculated the percentage of dogs in the study group that performed each behaviour at least once.

We calculated three types of correlations. For correlations between agonistic rank orders or between rank order and age (in months) and between rank and size (in pounds) we calculated Kendall τ correlations. To test correlations between matrices, we calculated rowwise matrix correlations, which use row totals to control for individual differences in behaviour (Hemelrijk, 1990; de Vries, 1993). For correlations between behavioural matrices with continuous variables we present Kendall's $\tau_{\mathrm{rw,av}}$ statistics. To compare dominance relationships in same-sex versus cross-sex relationships, we constructed a matrix of 'sameness of sex' (1 = same-sex, 0 = cross-sex) and compared this to the behavioural matrices. Because group membership fluctuated daily, each dyad was observed together for a different number of hours (range = 4-214, average = 42). Because there was such large variation in the amount of time each of the 276 dyads were observed with one another, it is

possible that a blank relationship for a given dyad was due to the lack of sufficient observation time. We therefore investigated the relationship between two matrices: dyadic observation time and the presence or absence of submission in each dyad (1 = unidirectional or bidirectional submission, 0 = no submission). For correlations that include at least one binomial matrix (i.e., only 1s and 0s) we present K_r test statistics.

In order to investigate behavioural signals of formal dominance in dogs, separate matrices were constructed using the frequencies of each agonistic behaviour. Directional consistency (DCI) and the number and proportion of 1-way relationships were calculated for each agonistic behaviour matrix. The dogs were never observed in competitive situations, so in order to determine whether the behaviour was multi-contextual, we recorded the proportion of each behaviour in playful and non-playful contexts. Overall, 37% of agonistic behaviours (excluding threats, retreats and conflicts) occurred during play; percentages for each behaviour are shown in Table 5. We then performed rank order correlations to determine if each submissive or dominant behaviour correlated with the aggressive rank order and could therefore be considered 'agonistic' (Table 5). Finally, we calculated the percentage of times that each submissive behaviour was triggered by aggression to determine whether a behaviour communicated formal status rather than aggression or fear. Counter-aggression was defined as threats and attacks triggered by aggression.

For all statistical analyses, two-tailed probabilities are reported. Results were considered statistically significant at probabilities less than or equal to 0.05.

3. Results

3.1. Linearity, directional consistency and coverage of dominance relationships

Submissive displays were the most frequent type of agonistic behaviour and were highly unidirectional ($N = 609$; DCI = 0.974). Dominance displays and aggression were less frequent and showed slightly lower levels of directional consistency (Table 3). The matrix of total submission (Table 4) resulted in low but significant linearity ($h' = 0.258$, $p = 0.017$). The hierarchy based on aggression was also significantly linear ($h' = 0.236$, $p = 0.036$), but dominance displays did not result in significant linearity ($h' = 0.135$,

$p = 0.770$). Aggressive behaviours among the dogs were of low intensity; the majority of aggressive behaviour consisted of threats with no physical contact (88%) and attacks never resulted in injury. Counter aggression was rare for threats (2%) but common for attacks; 13 attacks were initiated and 6 (46%) of these involved counter aggression.

The three types of agonistic behaviours were all correlated with one another (aggression and submission received, $\tau_{\mathrm{rw,av}} = 0.4$, $p = 0.0001$; dominance and submission received, $\tau_{\mathrm{rw,av}} = 0.51$, $p = 0.0001$; dominance and aggression, $\tau_{\mathrm{rw,av}} = 0.36$, $p = 0.0001$). All three types of agonistic behaviours showed low coverage indicated by 1-way relationships in less than one third of dyads. There were high percentages of blank relationships, but bidirectional relationships and tied relationships were rare, especially for submission (Table 4). Submission had higher coverage than aggression or dominance displays, with 29% 1-way relationships. In order to determine whether the high percentage of blank relationships was a result of insufficient observation time, we calculated the correlation between the presence of a unidirectional dominance relationship and the number of hours that each dyad was observed in the group together. The presence of a submissive relationship was not significantly correlated with dyadic observation hours ($K_{\mathrm{r}} = 414$, $p = 0.210$), suggesting that blank relationships were due to a real lack of agonistic interactions in these dyads rather than sampling limitations.

Total submission was significantly linear and showed the highest level of linearity, directional consistency, and coverage of the three types of agonistic behaviours (Table 3). Therefore, we chose the matrix of submissive behaviour (Table 4) to apply the inconsistencies and strength of inconsistencies (I&SI) method proposed by de Vries (1998) to arrange the dogs in the rank order most consistent with a linear hierarchy. We applied the I&SI procedure 20 times, consistently resulting in the same rank order. We used this rank order to correlate dominance rank with age and size.

3.2. Age, size, sex and individual differences

Dominance rank was significantly correlated with age ($\tau = 0.514$, $p < 0.001$) with older dogs outranking younger dogs. The rank order did not perfectly coincide with age (Table 1), but the older dog was dominant in 74 (91%) of the 81 known dominance relationships. In all relationships in which the younger dog was dominant, the dogs' ages differed by 18 months or less.

Table 3.
Linearity, unidirectionality and coverage of the 3 types of agonistic behaviour.

	N	Linearity (h')	Probability (2-tailed)	DCI	Blank relationships	1-way relationships	2-way relationships	Tied relationships
Submission	609	0.258	0.014	0.974	191 (69.2%)	81 (29.35%)	4 (1.45%)	1 (0.36%)
Aggression	160	0.236	0.036	0.825	197 (71.38%)	71 (25.72%)	8 (2.9%)	5 (1.81%)
Dominance	219	0.135	0.770	0.790	243 (88.04%)	27 (9.78%)	6 (2.17%)	0 (0.0%)

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Table 4.
Matrix of total submission.

Actor	Recipient																							
	BA	CH	JB	cd	hp	wr	wa	LH	LA	FR	tg	MG	rx	ML	fd	sy	bd	ms	li	RI	MD	LZ	bn	SA	Total
BA	–																								0
CH		–																							0
JB	1		–																						1
cd	2			–																					2
hp					–																				0
wr			1			–																			1
wa	2	1	6	157	4	1	–	1*																	172
LH		19	1	1			2*	–																	23
LA	2	1	1						–																4
FR		2								–											4*				6
tg			1								–														1
MG	4	1	1	6			10	1	1			–													24
rx							2	1	1			1	–												5

Table 4.
(Continued.)

Actor	Recipient																							
	BA	CH	JB	cd	hp	wr	wa	LH	LA	FR	tg	MG	rx	ML	fd	sy	bd	ms	li	RI	MD	LZ	bn	SA	Total
ML			1										1	–											2
fd															–										0
sy													1			–									1
bd							1	1									–								2
ms		1		2			7	4										–				2*			16
li					1			1	2										–						4
RI	2		2				1													–					5
MD	2	1					6	3		4*				1							–				17
LZ	5				1		32	2		6								4*				–			50
bn	1	109	5	5	6	4	2	22	7	12		2						3	1		1	4	–	1*	184
SA	5	30	3	1			8	20	1			3	10	1			1				1	1	3*	–	89
Total	26	165	22	172	12	5	71	56	12	22	0	6	12	2	0	0	1	7	1	0	6	7	3	1	609

Lower case, males; upper case, females.
* 2-way relationships.

Dominance rank was not correlated with weight ($\tau = 0.029$, $p = 0.862$). Aggression ($K_r = 187$, $p = 0.039$) and 1-way submissive relationships ($K_r = 264$, $p = 0.022$) were significantly more frequent in same-sex than in cross-sex dyads. We found large individual variation in the number of known dominance relationships that each dog formed; one dog had zero known relationships; nine dogs had between one and four known relationships; ten dogs had between five and ten, and five dogs had between 11 and 15 (Table 1).

3.3. Formal dominance

Muzzle licks ($N = 364$) occurred more often than any other agonistic behaviour and were performed in the highest proportion of relationships (18%) and by the highest proportion of dogs (58%). Bi-directional muzzle licking occurred in only 4 dyads (1%). Except for low coverage they met the criteria for a formal display of submission (i.e., unidirectional, multi-contextual, correlated with aggressive relationships, not induced by aggression) (Table 5). Muzzle licks were highly unidirectional (DCI = 0.961) and were consistent in both playful (23%) and non-playful contexts (77%). The muzzle lick rank order was significantly correlated with the rank order based on aggression ($\tau = 0.77$, $p < 0.0001$). The muzzle lick matrix was significantly correlated with the matrix of aggression ($\tau_{rw,av} = 0.31$, $p = 0.001$), but muzzle licks were never induced by aggression, suggesting that they are not a conditioned fear response.

Low posture, passive submission, and retreats were perfectly unidirectional, but they had lower coverage than muzzle licks and were sometimes induced by aggression. Muzzle bites and high posture had low coverage but met the other criteria for a formal status signal (i.e., unidirectional, multi-contextual, correlated with aggressive relationships, not induced by aggression). Chin-overs had low directional consistency (DCI = 0.698). Mounts were perfectly unidirectional and showed relatively high coverage. However, the directionalities of mounts and chin-overs were not correlated with those of aggression or submission, and therefore these behaviours were not good indicators of status in dogs (see Table 5 for all results). Threats ($N = 142$) showed high directional consistency (DCI = 0.905), relatively high coverage (26.8%) and produced a rank order that was significantly correlated with the submissive rank order ($\tau = 0.49$, $p = 0.0009$).

Table 5.
Analysis of behaviours as formal displays of status.

	N	DCI	Performed in playful contexts	1-way relationships	2-way relationships	Dogs that performed the behaviour	Correlation with aggression ($\tau_{rw,av}$)	Induced by aggression
Muzzle lick	364	0.961	83 (22.8%)	50 (18.1%)	4 (1.5%)	14 (58.3%)	0.31*	0 (0.0%)
Low posture	193	1	57 (29.5%)	29 (10.5%)	0 (0.0%)	6 (25%)	0.39*	18 (9.3%)
Passive submission	18	1	8 (44.4%)	10 (3.6%)	0 (0.0%)	8 (33.3%)	0.22*	3 (16.7%)
Retreat	34	1	0 (0.0%)	27 (9.8%)	0 (0.0%)	14 (58.3%)	0.58*	34 (100%)
High posture	6	1	2 (33.3%)	4 (1.5%)	0 (0.0%)	3 (12.5%)	0.39*	0 (0.0%)
Muzzle bites	70	1	59 (84.3%)	8 (2.9%)	0 (0.0%)	7 (29.2%)	0.34*	0 (0.0%)
Mount	90	1	43 (47.8%)	18 (6.5%)	0 (0.0%)	13 (54.2%)	0.01	0 (0.0%)
Chin over	53	0.698	41 (77.4%)	11 (4%)	3 (1.1%)	7 (29.2%)	0.04	0 (0.0%)
Threat	141	0.905	N/A	74 (26.8%)	6 (2.2%)	18 (75%)	N/A	3 (2.2%)
Attack	19	0.368	N/A	6 (2.2%)	4 (1.5%)	6 (25%)	N/A	6 (46.2%)

* Statistically significant; two-tailed p-value < 0.05.

4. Discussion

4.1. Linearity, directional consistency and coverage of dominance relationship

Dominance relationships based on submission and aggression among the dogs in this study were highly unidirectional and significantly linear. An age-based linear dominance hierarchy applied to the group as a whole with submissive behaviour being the best indicator of dominance relationships. This 'submission' hierarchy showed significant linearity, very few bidirectional relationships and no circular relationships (Tables 3 and 4). The coverage of dominance relationships in the daycare group, however, was low, with unidirectional submissive relationships observed in only 29% of the dyads (Table 3). Aggression in the daycare group was significantly linear, correlated with the receipt of submission, and showed fairly high directional consistency, but it was not as unidirectional as submission (Table 3). Dominant behaviour did not result in significant linearity.

Similar data exist on the directional consistency, linearity and coverage of agonistic behaviour for a captive wolf pack (Van Hooff & Wensing, 1987), a group of free-living dogs on the outskirts of Rome (Cafazzo et al., 2010), and a semi-permanent group of sexually intact companion dogs that were temporarily housed together in an outdoor enclosure (van der Borg et al., 2012). These three studies, like this one, found that submission was the most unidirectional, linear, and frequent agonistic behaviour and therefore served as a better indicator of dominance relationships than dominance displays or aggression (Van Hooff & Wensing, 1987; Cafazzo et al., 2010; van der Borg et al., 2012). Although submission was highly unidirectional and significantly linear in all 4 groups, linearity (h') for submission was lower in this study than it was in the other three (Table 6). Because submission was highly unidirectional with very few non-transitive relationships (Table 4), the lower value of h' in our study likely reflects the high percentage of blank relationships (Table 3). Coverage of submission was highest in the wolf pack with 1-way submissive relationships evident in 85% of dyads, slightly lower in the groups of feral and intact companion dogs with 1-way relationships documented in 72–75% of dyads, and lowest in the daycare group of neutered dogs with 1-way relationships in 29% of dyads (Table 6).

The lower coverage of dominance relationships in the daycare group compared to the other groups of dogs and wolves was most likely a result of

Table 6.
Directional consistency, linearity and coverage of submission in four groups of canines.

	Directional consistency (DCI)	Linearity (h')	Coverage (% 1-way relationships)
Neutered companion dogs[a] (current study)	0.97	0.26	29%
Intact companion dogs[b] (van der Borg et al., 2012)	0.97	0.94	75%
Feral dogs, mostly intact[a] (Cafazzo et al., 2010)	0.96	0.63	72%
Captive wolves[c] (van Hooff & Wensing, 1987)	0.98	0.92	85%

[a] Based on all submission combined.
[b] Based on 'low posture' only.
[c] Based on 'low posture' only (data from 1978 only).

reduced competition due to neutering and other human influences. The study dogs were neutered and fed meals outside of the group setting, eliminating the need to compete for mates or food; they socialized at the daycare facility regularly, but group membership was constantly changing and the group did not live together on a full-time basis. Competition for some resources (e.g., space, social partners, small pieces of kibble, etc.) did still occur in the dog daycare setting, but if there is little need for two dogs to compete with one another for meals and mates, it may sometimes be advantageous for them to avoid social interactions and peacefully co-exist without establishing a dominance relationship. Indeed, about half of the dyads in this group were not observed engaging in any social interactions at all other than occasional sniffing. In other dyads with blank agonistic relationships, however, the dogs affiliated regularly and engaged in social play without exchanging agonistic behaviour or establishing a dominance relationship (unpublished data), suggesting that true 'egalitarian' relationships, which appear to be rare in most social mammals (Hand, 1986), may be common in neutered companion dogs and are worthy of further study. Human supervisors also interrupted and/or humanely punished aggression (e.g., temporary isolation), reinforced non-aggression (e.g., praise, kibble), and excluded more aggressive dogs from the environment, undoubtedly reducing the frequency of agonistic interactions in this study, particularly aggression and dominance displays. Another

potential reason for low coverage in this study is that some agonistic displays, particularly high or low postures, were sometimes difficult to detect due to floppy ears, cropped tails, bushy coats and large size discrepancies between many of the daycare dogs. The observer probably recognized postural displays less often in the daycare group than researchers did in other studies in which the animals showed less variation in size and coat (Van Hooff & Wensing, 1987; Cafazzo et al., 2010; van der Borg et al., 2012). An intriguing but as yet unstudied question is whether the dogs themselves find it more difficult to identify displays of high or low posture when interacting with morphologically variable conspecifics.

The four studies reviewed here suggest that even without direct human influence the coverage of dominance relationships may be lower for dogs than for wolves (Table 6). The companion dogs studied by van der Borg et al. (2012) were sexually intact and the observers did not intervene directly in the dogs' interactions. The dogs in the feral group studied by Cafazzo et al. (2010) were intact, and they ranged freely, competed for food and mates, and rarely, if ever, interacted with humans (Bonanni et al., 2010; Cafazzo et al., 2010). Coverage of dominance relationships in these groups was higher than in our daycare group, but still lower than in the captive wolf pack (Table 6). A closer examination of the feral group reveals that about half of the female–female dyads had blank agonistic relationships (Cafazzo et al., 2010), suggesting that blank relationships may be relatively common in groups of domestic dogs. This apparent reduced coverage of dominance relationships in dogs compared to wolves may be related to competitive pressures and may have a genetic component due to the effects of domestication. Since dogs split from wolves their group structures have become more variable and fluid, and cooperative hunting and communal pup care seem to be less common in feral dogs than they are in wolves (Pal, 2003; Boitani et al., 2007; Miklosi, 2007; Cafazzo et al., 2014; Viryáni & Range, 2014). Dominance rank continues to correlate with reproductive success in free-living dogs now (Cafazzo et al., in press) and probably did throughout the course of domestication (Smuts, 2010), but it may be less critical to reproductive success in groups of dogs than in wolf packs, which typically contain only one dominant, breeding pair (Peterson et al., 2002; Mech & Boitani, 2003; Sands & Creel, 2004; Vonholdt et al., 2008). In general, due to their association with humans, the range of social environments has become much more variable for dogs than for wolves (Boitani et al., 2007; Miklosi, 2007).

Perhaps what has been selected for in dogs since their split with wolves is greater social flexibility, or the capacity to develop several different types of social relationships (e.g., dominant/subordinate, egalitarian, non-interactive) with different individuals (canine and human) depending on the particular social environment.

Before concluding that domestication has reduced the tendency for dogs to engage in agonistic interactions, however, one should consider Mech's (1999) argument that dominance relationships may be more relaxed in wild wolf packs compared to captive packs whose members cannot disperse as they might in the wild. It is possible that coverage tends to be lower in wild wolves than reported for van Hooff & Wensing's (1987) captive pack and may be more similar to the coverage reported for the groups of intact dogs. To our knowledge, no studies of directional consistency, linearity and coverage in a wild wolf pack have been published, and further studies are needed to resolve this issue.

Our results conflict with those reported by Bradshaw et al. (2009) for a different group of neutered companion dogs. Bradshaw et al. (2009) reported some asymmetrical agonistic relationships but no linear hierarchy in a group of 19 neutered male shelter dogs, and concluded that dominance is not a useful construct for describing social relationships among domestic dogs. The different conclusions about dominance in our study and the study by Bradshaw et al. (2009) are likely due to differences in methodology. Bradshaw et al. (2009) calculated David's scores (Gammell et al., 2003) based on a combination of aggressive, dominant, and submissive behaviour, but they did not conduct statistical tests of linearity, directional consistency, or coverage. Further, submission was found to be the most unidirectional and linear type of agonistic behaviour in this study and other dog studies (Cafazzo et al., 2010; van der Borg et al., 2012), but Bradshaw et al. (2009) combined submission with aggressive and dominant behaviours to calculate David's scores and did not consider it on its own.

In contrast to the view that domestication has generally reduced aggressive behaviour in dogs compared to wolves (Lindsey, 2001; Tópal et al., 2009), Viryáni & Range (2014) hypothesize that dogs show less ritualized aggression toward within-group conspecifics and have steeper hierarchies than do wolves. The steepness of a hierarchy refers to the degree to which individuals differ in their likelihood of winning a dominance encounter (de Vries et al., 2006). In line with this hypothesis, Frank & Frank (1982) and

Fedderson-Peterson (1991, 2004) report higher levels of aggression among juveniles in some breeds of dogs than among wolves of the same age raised in the same manner, and Ritter et al. (2012) report that dogs are less tolerant and less likely to share food in pair-wise feeding competitions than are wolves. On the other hand, Beckoff (1974) found the development of play and aggression in dog and wolf litters to be very similar, with dog and wolf pups playing more and fighting less than coyote pups of the same age. Also, despite many hours of observations of large numbers of dogs interacting in four different open areas (reviewed by Smuts, 2014) injurious aggression was never seen (Bradshaw & Lea, 1992; Shyan et al., 2003; Capra et al., 2011; Carrier et al., 2013). Further, the vast majority of within group aggression among feral dogs in India and Italy was highly ritualized and did not cause injury (Pal et al., 1998; S. Cafazzo, personal communication). Aggression among the daycare dogs was also highly ritualized; 88% of the aggressive interactions were threats and attacks involving physical contact were never injurious. Due to the above-mentioned human influences on aggressive behaviour among the daycare dogs, however, our data are not ideal for direct comparisons with wolves. In addition, Fedderson-Peterson's findings on agonism in dogs versus wolves, which are the most extensive available, indicate striking breed differences, which complicate any inter-specific comparison. More research on within-group aggression and competitive dominance in various contexts in different breeds of dogs and in wolves is needed to gain a thorough understanding of how the intensity of aggression and the steepness of hierarchies may differ in these two species.

4.2. Age, sex, size and individual variation

Rank was significantly correlated with age in the daycare group. The older dog was dominant to the younger dog in 91% of known dominance relationships, and in six of the seven relationships in which the younger dog was dominant, the dogs' ages differed by 18 months or less (Table 1). Dominance relationships were not related to size; older/smaller dogs commonly outranked younger/bigger dogs. Age-graded dominance hierarchies have been reported in several other studies of dogs (Bradsaw & Nott, 1995; Bonanni et al., 2010; Cafazzo et al., 2010) and wolves (Zimen, 1978; Lockwood, 1979; van Hooff & Wensing, 1987; Mech, 1999). In wolves, the top ranking male and female are typically the parents of the other pack members and usually the only animals that breed (Mech, 1999; Mech & Boitani, 2003;

Sands & Creel, 2004; Vonholdt et al., 2008). These two older animals take the lead during hunts, travel and territorial defence, but the cooperation of other pack members (usually their offspring) is crucial for successful group hunts and pup care (Peterson et al., 2002; Mech & Boitani, 2003; Packard, 2003; MacNulty et al., 2011). While, as mentioned above, dogs may be less likely than wolves to cooperatively hunt and care for pups, a tendency to submit to older dogs may still be important for survival and reproductive success for many free-living dogs. For example, Bonanni et al. (2010) found that groups of feral dogs competed for territories and food resources, and group members tended to follow the lead of a few high-ranking/older dogs. In free-living canine groups, many young animals might not survive without the assistance and tolerance of older animals, and established dominance relationships may facilitate cooperation, allowing more cooperative groups to successfully compete with other groups. Therefore, deference to older animals is likely adaptive for wolves and feral dogs, and companion dogs appear to retain this behavioural tendency, even when they have little need to compete for food or mates.

Although dominance relationships did occur between males and females, they were significantly more common in same-sex pairs. Aggression was also more frequent in same-sex pairs than between males and females. Similar to reports in wolves (Zimen, 1978; van Hooff & Wensing, 1987; Derix et al., 1993; Packard, 2003), it appears that even for neutered dogs, competition is greater and dominance relationships are more defined within sex than between the sexes. Unlike in the studies of wolves and feral dogs, however, we did not find a tendency for males to out-rank females: the top three dogs in the hierarchy were females. Neutered male dogs sometimes outranked neutered females of similar age, however, and further studies are needed to assess the effects of neutering on inter-sexual dominance relationships in dogs.

The daycare dogs showed a large amount of individual variation in agonistic behaviour. Most dogs formed some dominance relationships with other dogs, but some dogs had a stronger tendency to form dominance relationships than others (Table 1). Other studies of feral and companion dogs have also reported considerable individual variation in agonistic behaviour (Goddard & Beilharz, 1985; Pal et al., 1998). As a species, dogs appear to engage in nearly all of the social behaviours observed in wolves (Abrantes, 1997; Handelman, 2008), but large variation occurs in the behavioural repertoires

of individual dogs. Some dogs perform almost all of the social behaviours observed in wolves, while others perform only a few (Goodwin et al., 1997; Bradshaw et al., 2009; current data). Goodwin et al. (1997) proposed that breed influences the tendency for dogs to display agonistic behaviour. Our sample size was not large enough to assess breed differences in behaviour, but we did observe one vizsla (a Hungarian hunting dog breed) with 13 known dominance relationships and another dog of the same breed with only one, suggesting that differences between individuals may sometimes be greater than differences between breeds. Personality is likely to play a part, but rather than the personality dimension ranging from dominant to submissive as some researchers have proposed (Jones & Gosling, 2005), the dimension may range from 'concerned with status' to 'unconcerned with status'. The term 'concerned with status' does not necessarily imply conscious awareness of dominance relationships but might simply involve greater or lesser tendencies to engage in agonistic interactions.

4.3. Formal dominance

Muzzle licks were the best candidate for a display of formal submission in the daycare dogs (Table 5). Muzzle licks had very high directional consistency, and they (and all other submissive behaviours) remained unidirectional in both playful and non-playful contexts (Table 5). Muzzle licks corresponded with dominance rank based on aggression but were never triggered by aggression and are therefore not likely to be an expression of fear. Despite the low coverage in the group as a whole (18% 1-way), muzzle licks were the most commonly displayed submissive behaviour, and the majority of dogs in the group (58%) displayed them at least once. Muzzle licks were often accompanied by low posture; these behaviours taken together constitute a submissive display (termed 'active submission' in wolves and 'affiliative submission' in feral dogs) that has been proposed by others to be a formal display of submission in dogs and wolves (Schenkel, 1967; Van Hooff & Wensing, 1987; Cafazzo et al., 2010).

Interestingly, mounts and chin-overs did not correspond to any of the other agonistic behaviours measured in this study, although they are traditionally considered to be displays of dominance in wolves and dogs (Abrantes, 1997; Handelman, 2008; Lindsey, 2001). Similar to our findings, however, van Hooff & Wensing (1987) found mounts and 'head-ons' (equivalent to chin-overs) were more closely related to affiliative behaviours (i.e., play, courtship

and grooming) than to behaviours related to status communication. In summary, data suggest that mounts and chin-overs may sometimes be related to dominance, but they are not indicators of status in dogs and wolves. Their relationship to affiliative behaviours is worthy of further study.

4.4. Possible proximate benefits of dominance relationships

Although dominance relationships in neutered companion dogs are no longer adaptive in terms of securing mating opportunities, formal dominance relationships may provide short-term benefits by reducing aggression and promoting tolerance and sharing by dominants (de Waal, 1986; Drews, 1993). Schenkel (1967) defines submission in wolves as 'the effort of the inferior to attain friendly or harmonic social integration' (p. 319). The affiliative nature of submissive displays in dogs seems consistent with this definition (Smuts, 2014). Dominant dogs often tolerate muzzle-licking, but not infrequently they act as if being licked is annoying or even aversive, as indicated by turning the muzzle away or even growling/snapping at the muzzle licker (pers. observ.). Such variable responses to muzzle-licking are expected if this behaviour functions to test the dominant's attitude toward the muzzle-licker (Zahavi, 1977). Zahavi (1977) argued that in order to obtain accurate information about another animal's willingness to form a bond, the individual seeking this information must exhibit a behaviour that is potentially costly to the recipient, at least until a trusting relationship develops. In other species, actions that make the recipient (and sometimes also the actor) vulnerable to potential injury have been hypothesized to be bond-testing behaviours, including kissing in humans (Zahavi, 1977), scrotum handling by male baboons (Smuts & Watanabe, 1990) and sticking a finger up another animal's nostril or using a finger to poke another in the eye in white-faced capuchins (Perry & Manson, 2008). Muzzle-licking in dogs, which makes both animals vulnerable to having the mouth bitten, may serve a similar function. In the daycare dogs, recipients of muzzle licks who were relatively unfamiliar with the licker seemed more likely to show an aggressive reaction, but over time responses became more tolerant, as one would expect if affiliative relationships eventually developed.

4.5. Conclusions

The dogs in this study associated in semi-permanent groups, all were neutered, and they did not compete for food. Humans actively prevented

competitive encounters, humanely punished aggression, rewarded tolerance and excluded more aggressive dogs from the social environment. Yet, despite these multiple mitigating factors, agonistic relationships were highly unidirectional, significantly linear, and similar in nature to those reported for other groups of dogs and wolves. This indicates that dominance is a robust component of neutered companion dog social behaviour. On the other hand, many dyads in the study did not show detectable dominance relationships (there was low coverage), suggesting that human involvement can reduce the tendency for neutered companion dogs to engage in agonistic encounters and form dominance relationships. Overall, dominance appears to be applicable to some, but not all, relationships among neutered companion dogs. When dominance relationships are present among dogs (neutered, intact, and/or feral), they tend to be expressed primarily though affiliative displays of submission on the part of the subordinate rather than dominant displays of aggression on the part of the dominant.

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References

Abrantes, R. (1997). Dog language. — Wakan Tanka, Naperville, IL.

Altmann, J. (1974). Observational study of behaviour: sampling methods. — Behaviour 49: 227-267.

Bauer, E.B. & Smuts, B.B. (2007). Cooperation and competition during dyadic play in domestic dogs. — Anim. Behav. 73: 489-499.

Beach, F.A. (1970). Coital behaviour in dogs: VIII. Social affinity, dominance and sexual preference in the bitch. — Behaviour 36: 131-148.

Bekoff, M. (1974). Social play in coyotes, wolves and dogs. — Bioscience 24: 225-230.

Boitani, L., Ciucci, P. & Ortolani, A. (2007). Behaviour and social ecology of free-ranging dogs. — In: The behavioral biology of dogs (Jensen, P., ed.). CAB International, Wallingford, p. 47-165.

Bonanni, R., Cafazzo, S., Valsecchi, P. & Natoli, E. (2010). Effect of affiliative and agonistic relationships on leadership behavior in free-ranging dogs. — Anim. Behav. 79: 981-991.

Bradshaw, J.W.S. & Lea, A.M. (1992). Dyadic interactions between domestic dogs. — Anthrozoos 5: 245-253.

Bradshaw, J.W.S. & Nott, H.M.R. (1995). Social and communication behavior of companion dogs. — In: The domestic dog: its evolution, behavior and interactions with people (Serpell, J., ed.). Cambridge University Press, New York, NY, p. 115-130.

Bradshaw, J.W.S., Blackwell, E.J. & Casey, R.A. (2009). Dominance in dogs: useful construct or bad habit? — J. Vet. Behav. 3: 176-177.

Cafazzo, S., Bonanni, R., Valseechi, P. & Natoli, E. (2014). Social variables affecting mate preferences, compulation and reproductive outcome in a pack of free-ranging dogs. — PLoS ONE 9: e98594, DOI:10.1371/journal.pone.0098594.

Cafazzo, S., Natoli, E. & Valsecchi, P. (2012). Scent-marking behaviour in a pack of free-ranging domestic dogs. — Ethology 118: 955-966.

Cafazzo, S., Valsecchi, P., Bonanni, R. & Natoli, E. (2010). Dominance in relation to age, sex, and competitive contexts in a group of free-ranging domestic dogs. — Behav. Ecol. 21: 443-455.

Capra, A., Barnard, S. & Valesecchi, A.C. (2011). Flight, foe, fight! Aggressive interactions between dogs. — J. Vet. Behav. 6: 62.

Carrier, L.O., Cyr, A., Anderson, R.E. & Walsh, C. (2013). Exploring the dog park: relationships between social behaviours, personality and cortisol in companion animals. — Appl. Anim. Behav. Sci. 146: 96-106.

Chase, I.D. (1974). Models of hierarchy formation in animal society. — Behav. Sci. 19: 374-382.

de Vries, H. (1993). The rowwise correlation between two proximity matrices and the partial rowwise correlation. — Psychometrika 58: 53-69.

de Vries, H. (1995). An improved test of linearity in dominance hierarchies containing unknown or tied relationships. — Anim. Behav. 50: 1375-1389.

de Vries, H. (1998). Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. — Anim. Behav. 55: 827-843.

de Vries, H., Stevens, J.M.G. & Vervaecke, H. (2006). Measuring and testing the steepness of dominance hierarchies. — Anim. Behav. 71: 585-592.

de Waal, F.B.M. (1986). The integration of dominance and social bonding in primates. — Q. Rev. Biol. 61: 459-479.

de Waal, F.B.M. & Luttrell, L. (1985). The formal hierarchy of rhesus monkeys: an investigation of the bared-teeth display. — Am. J. Primatol. 9: 73-85.

Derix, R., van Hooff, J., de Vries, H. & Wensing, J. (1993). Male and female mating competition in wolves: female suppression vs. male intervention. — Behaviour 127: 141-174.

Drews, C. (1993). The concept and definition of dominance. — Anim. Behav. 125: 283-313.

East, M.L., Hofer, H. & Wickler, W. (1993). The erect 'penis' is a flag of submission in a female-dominated society: greetings in Serengeti spotted hyenas. — Behav. Ecol. Sociobiol. 33: 355-370.

Eaton, B. (2002). Dominance: fact or fiction? — Dogwise, Wanatchee, WA.

Fedderson-Peterson, D. (1991). The ontogeny of social play and agonistic behavior in selected canine species. — Bonner Zool. Beitr. 42: 97-114.

Fedderson-Peterson, D. (2004). Hundepsychologie: Sozialverhalten und Wesen, Emotionen und Individualität. — Kosmos, Stuttgart.

Flack, J.C. & de Waal, F.B.M. (2007). Context modulates signal meaning in primate communication. — Proc. Natl. Acad. Sci. USA 104: 1581-1586.

Frank, H. & Frank, M.G. (1982). On the effects of domestication on the development of canine social-development and behavior. — Appl. Anim. Ethol. 8: 507-525.

Gammell, 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. — Anim. Behav. 66: 601-605.

Goddard, M.E. & Beilharz, R.G. (1985). Individual variation in agonistic behavior in dogs. — Anim. Behav. 125: 283-313.

Goodman, P.A., Klinghammer, E. & Willard, J. (2002). Wolf ethogram. — Eckhard H. Hess Institute of Ethology, Battle Ground, IN.

Goodwin, D., Bradshaw, J.W.S. & Wickens, S.M. (1997). Paedomorphosis affects agonistic visual signals of domestic dogs. — Anim. Behav. 53: 297-304.

Hand, J.L. (1986). Resolution of social conflicts: dominance, egalitarianism, spheres of dominance, and game theory. — Q. Rev. Biol. 61: 201-220.

Handleman, B. (2008). Canine behavior: a photo illustrated handbook. — Dogwise, Wanatchee, WA.

Hemelrijk, C.K. (1990). Models of, and tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. — Anim. Behav. 39: 1013-1029.

Hinde, R. (1974). The biological basis of human social behavior. — McGraw-Hill, New York, NY.

Jenks, S.M. (2011). A longitudinal study of the sociosexual dynamics in a captive family group of wolves: The University of Connecticut wolf project. — Behav. Genet. 41: 810-829.

Jones, A.C. & Gosling, S.D. (2005). Temperament and personality in dogs (*Canis familiaris*): a review and evaluation of past research. — Appl. Anim. Behav. Sci. 95: 1-53.

Klass, K. & Cords, M. (2011). Effect of unknown relationships on linearity, steepness and rank ordering of dominance hierarchies: simulation studies based on data from wild monkeys. — Behav. Proc. 88: 168-176.

Landau, H.G. (1951). On dominance relations and the structure of animal society. — Bull. Math. Biol. 13: 1-19.

Lindsey, S. (2001). Handbook of applied dog behavior and training. — Iowa University Press, Ames, IO.

Lockwood, R. (1979). Dominance in wolves: useful construct or bad habit? — In: The behavior and ecology of wolves (Klinghammer, E., ed.). Garland STPM Press, New York, NY, p. 225-245.

Lu, A., Koenig, A. & Borries, C. (2008). Formal submission, tolerance and socioecological models: a test with female Hanuman langurs. — Anim. Behav. 76: 415-428.

MacNulty, D.R., Smith, D.W., Mech, L.D., Vucetich, J.A. & Packer, C. (2011). Nonlinear effects of group size on the success of wolves hunting elk. — Behav. Ecol. 23: 75-82.

Mech, L.D. (1999). Alpha status, dominance, and division of labor in wolf packs. — Can. J. Zool. 77: 1196-1203.

Mech, L.D. & Boitani, L. (2003). Wolves: behavior, ecology, and conservation. — The University of Chicago Press, Chicago, IL.

Miklosi, A. (2007). Dog behavior, evolution and cognition. — Oxford University Press, New York, NY.

O'Heare, J.J. (2007). Social dominance: useful construct or quagmire? — J. Comp. Anim. Behav. 1: 56-83.

Packard, J.M. (2003). Wolf behavior: reproductive, social and intelligent. — In: Wolves: behavior, ecology, and conservation (Mech, L.D. & Boitani, L., eds). University of Chicago Press, Chicago, IL, p. 35-65.

Pal, S.K. (2003). Reproductive behavior of free-ranging rural dogs (*Canis familiaris*) in relations to mating strategy, season, and litter production. — Appl. Anim. Behav. Sci. 59: 331-348.

Pal, S.K., Ghosh, B. & Roy, S. (1998). Agonistic behavior of free-ranging dogs (*Canis familiaris*) in relation to season, sex and age. — Acta Theriol. 48: 271-281.

Perry, S. & Manson, J.H. (2008). Manipulative monkeys: the capuchins of Lomas Barbudal. — Harvard University Press, Cambridge, MA.

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*. — Can. J. Zool. 80: 1405-1412.

Preuschoft, S. (1999). Are primates behaviorists? Formal dominance, cognition and free-floating rationales. — J. Comp. Psychol. 113: 91-95.

Preuschoft, S., Paul, A. & Kuester, J. (1998). Dominance styles of female and male barbary macaques (*Macaca sylvanus*). — Behaviour 135: 731-755.

Ritter, C., Viryáni, Z. & Range, F. (2012). Who is more tolerant? Cofeeding in pairs of pack-living dogs (*Canis familiaris*) and wolves (*Canis lupus*). — Paper presented at the 3rd Canine Science Forum Barcelona, Spain. Available online at http://dogspies.com/Dog_Spies/Science!_files/CSF%202012%20Abstracts.pdf.

Rowell, T.E. (1974). Concept of social dominance. — Behav. Biol. 11: 131-154.

Sands, J. & Creel, S. (2004). Social dominance, aggression and faecal glucocorticoid levels in a wild population of wolves, *Canis lupus*. — Anim. Behav. 67: 387-396.

Schenkel, R. (1967). Submission: its features and functions in wolf and dog. — Am. Zool. 7: 319-329.

Schilder, M.B.H., Vinke, C.M. & van der Borg, J.A.M. (2014). Dominance in domestic dogs revisited: useful habit and useful construct? — J. Vet. Behav. 9: 184-191.

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

Shepherd, K. (2002). Development of behaviour, social behaviour and communication in dogs. — In: BSAVA manual of canine and feline behavioural medicine (Horwitz, D.F., Mills, D.S. & Heath, S., eds). British Small Animal Veterinary Association (BSAVA), Gloucester, p. 8-20.

Shyan, M.R., Fortune, K.A. & King, C. (2003). "Bark Parks." A study of interdog aggression in a limited-control environment. — J. Appl. Anim. Welfare Sci. 6: 25-32.

Smuts, B.B. (2010). Domestic dogs. — In: Encyclopedia of animal behavior (Breed, M.D. & Moore, J., eds). Elsevier, New York, p. 562-567.

Smuts, B.B. (2014). Social behavior in companion dogs with an emphasis on play. — In: The social dog: behavior and cogcition (Kaminski, J. & Marshall-Pescini, S., eds). Elsevier, New York, NY, p. 105-130.

Smuts, B.B. & Watanabe, J.M. (1990). Social relationships and ritualized greetings in adult male baboons (*Papio cynocephalus anubis*). — Int. J. Primatol. 11: 147-172.

Topál, J., Miklósi, A., Gácsi, M., Dóka, A., Pongracz, P., Kubinyi, E., Viryáni, Z. & Csányi, V. (2009). The dog as a model for understanding human social behavior. — Adv. Stud. Behav. 39: 71-116.

van der Borg, J.A.M., Schilder, M.B.H. & Vinke, C. (2012). Dominance and its behavioural measures in a pack of domestic dogs. — Paper presented at the 3rd Canine Science Forum Barcelona, Spain. Available online at http://dogspies.com/Dog_Spies/Science!_files/CSF%202012%20Abstracts.pdf.

van Hooff, J.A.R.A.M. & Wensing, J.A.B. (1987). Dominance and its behavioral measures in a captive wolf pack. — In: Man and wolf: advances, issues, and problems in captive wolf research (Frank, H., ed.). Dr. W. Junk, Dordrecht, p. 219-252.

van Kerkhove, W. (2004). A fresh look at the wolf-pack theory of companion-animal dog social behavior. — J. Appl. Anim. Welfare Sci. 7: 279-285.

Vervaecke, H., de Vries, H. & van Elsacker, L. (2000). Dominance and its behavioral measures in a captive group of bonobos (*Pan paniscus*). — Int. J. Primatol. 21: 47-68.

Viryáni, Z. & Range, F. (2014). On the way to a better understanding of dog domestication: aggression and cooperativeness in dogs and wolves. — In: The social dog: behaviour and cognition (Kaminski, J. & Marshall-Pescini, S., eds). Elsevier, New York, NY, p. 35-62.

Vonholdt, B.M., Stahler, D.R., Smith, D.W., Earl, D.A., Pollinger, J.P. & Wayne, R.K. (2008). The geneology and genetic viability of reintroduced Yellowstone grey wolves. — Mol. Ecol. 17: 252-274.

Ward, C., Bauer, E.B. & Smuts, B.B. (2008). Partner preferences and asymmetries in social play among domestic dog, *Canis lupus familiaris*, littermates. — Anim. Behav. 76: 1187-1199.

Zahavi, A. (1977). The testing of a bond. — Anim. Behav. 25: 246-247.

Zimen, E. (1978). The wolf. — Delacorte Press, New York, NY.