



Affiliation, dominance and friendship among companion dogs

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Abstract

Dog social behaviour has been well studied, but little is known about affiliative relationships between dogs. We report a yearlong study of dominance and affiliation in 24 dogs at a dog daycare facility and provide additional details on dog relationships through long-term observations of pairs of dogs who lived together in the same household or met frequently for years. Companion dogs formed highly differentiated relationships with one another. At daycare, some dyads affiliated and displayed one-way submission (formal dominance), others affiliated without a dominance relationship (egalitarian), and the majority of dyads did not affiliate at all (agonistic or non-interactive). The dogs in household environments showed formal and egalitarian relationships, and two dyads exchanged two-way agonism without submission (unresolved). Sex influenced the types of relationships dogs formed, with mixed sex dyads more likely to affiliate and less likely to exhibit dominance than same-sex pairs. Dominance influenced the nature of affiliation in relationships; egalitarian dyads were more likely to play and showed more equitable gentle affiliation. Gentle affiliation was reciprocal in the group as a whole, but it was highly skewed in many dyads, especially those with dominance relationships. Gentle affiliation was usually, but not always, directed up the hierarchy. Certain dyads affiliated at much higher rates than others, indicating that the dogs formed friendships. Most friends were mixed sex and/or egalitarian pairs, but friendships occurred in all of the sex class/dominance combinations. Long-term observations demonstrated how dyadic relationships can change over time. Such highly differentiated relationships suggest significant social complexity in dogs.

Keywords

affiliation, play fighting, dominance, social bonds, friendship, dogs.

1. Introduction

The past 20 years have seen an explosion of research on how dogs interact with humans (summarized in Kaminski & Marshall-Pescini, 2014). From this research emerges a sense of dogs as skillful social creatures, highly sensitive to specific aspects of the social environment and capable of great flexibility in responding to varying circumstances (e.g., Hare & Tomasello, 2005; Miklósi & Topál, 2013). This picture of dogs is incomplete, however, without a better understanding of how they interact with each other. It is becoming increasingly clear that dogs' evolutionary niche has nearly always included interactions with both other dogs and humans (Smuts, 2010; Lord et al., 2013). Recent studies of free-ranging dogs in Italy show that they live in packs in which survival and reproduction depend on how they get along with each other (Bonanni et al., 2010a, b; Cafazzo et al., 2010, 2014). Such strong selection pressures must have operated on dogs' inherited intraspecific tendencies and modified them to meet new and ever-changing circumstances.

Since dogs evolved from wolves (Freedman et al., 2014), this raises the question: how do dogs' intraspecific relationships compare to those of wolves? Wolves live in packs that vigorously defend territories from neighbouring packs (Mech & Boitani, 2003; Cassidy et al., 2015). Within packs, however, interactions are usually peaceful. Within-pack relationships show the following features: wolves generally avoid injurious aggression by using ritualized dominance and submission to establish dominance relationships; formal, linear dominance relationships exist, but some pairs of wolves have frequent agonistic interactions while others rarely do; within-pack aggression is sometimes bi-directional; after conflicts occur, wolves tend to repair disruptions to friendly relationships through reconciliations and third party affiliation; friendly greetings involving friendly submission by subordinates help to maintain social bonds; adult wolves play; and some pairs form especially close, affiliative bonds (Schenkel, 1967; Zimen, 1981; Moran, 1982; Fentress et al., 1987; van Hooff & Wensing, 1987; Cordoni & Palagi, 2008, 2015; Cordoni, 2009; Palagi & Cordoni, 2009; Jenks, 2011; Baan et al., 2014). The work cited above, most of it published after Mech's (1970) book, indicates the aptness of his summation of wolves as animals who form close emotional bonds, who are averse to fighting, and whose personalities differ strikingly.

Research on free-ranging dogs indicates many similarities with wolves, including pack living, territorial defence, avoidance of serious fights through

ritualized interactions, formal linear dominance hierarchies, some bi-directional aggression, frequent friendly greetings initiated by subordinates, differentiated social relationships, and personality differences (Pal et al., 1998, 1999; Pal, 2005; Boitani et al., 2007; Bonanni & Cafazzo, 2014; Miklosi et al., 2014). Research on groups of companion dogs indicates the existence of formal dominance hierarchies mediated primarily by ritualized submissive behaviours and postures (Trisko & Smuts, 2015; van der Borg et al., 2015). However, knowledge about dogs' intraspecific friendly behaviour has not kept pace with studies of agonistic behaviour and dominance (Smuts, 2014). This study aims to address this imbalance, specifically for companion dogs.

There is a growing emphasis on the importance of differentiated social relationships in nonhuman animals and the challenges involved in measuring and describing them (Cords & Aureli, 2000; Mitani, 2009; Fraser & Bugnyar, 2010; Aureli et al., 2012; Silk et al., 2013; Bergman & Beehner, 2015). With some notable exceptions (e.g., ravens, Fraser & Bugnyar, 2010; bottlenose dolphins, Stanton & Mann, 2012; Blasi & Boitani, 2014; Connor & Krutzen, 2015), most of this research has involved nonhuman primates. In concluding a detailed review of animal social bonds, Dunbar & Shultz (2010) emphasized the need for detailed descriptions of the natural history of social relationships in a wider range of species (Dunbar & Shultz, 2010: p. 796). This study includes such detailed descriptions for dogs, with some dyads studied continuously for up to 9 years.

Research on affiliation in dogs has focused on mutual play-fighting behaviour, such as chasing, play biting, and tackling each other to the ground (reviewed in Smuts, 2014; Bradshaw et al., 2015), but dogs also display gentle affiliative behaviours, such as nose nudges, licks and head rubs (Handleman, 2008). In wolves, gentle affiliation is observed in the contexts of submission, friendly greetings, courtship, grooming and reconciliation (Zimen, 1981; van Hooff & Wensing, 1987; Baan et al., 2014), but very little is known about gentle affiliation among dogs (Smuts, 2014). As puppies, companion dogs exhibit preferences for certain play-fighting partners (Ward et al., 2008), but, until now, differentiated partner preferences among adult dogs have remained unexplored. Here, we investigate play-fighting, gentle affiliation and social bonds among companion dogs and how they are related to dominance.

We begin in Part 1 with a study of dyadic interactions among 24 dogs (276 dyads) at a dog daycare facility over the course of one year. In a previous study of this group of dogs (Trisko & Smuts, 2015), we found a significant linear dominance hierarchy based on highly unidirectional submissive behaviour. To deepen our understanding of dog social relationships, here we investigate affiliation and how it is related to dominance in the same group of dogs. We address the following questions:

- (1) How do affiliation and dominance overlap in dog–dog relationships? Do dyads form different types of relationships?
- (2) What dyadic characteristics (e.g., sex composition, age difference, size difference, time spent together) influence the type of relationships dyads form?
- (3) How are play-fighting and gentle affiliation distributed among the dyads, and how are they related to one another?
- (4) Does gentle affiliation tend to be equitable or skewed in dyads? Does it tend to be directed up the hierarchy?
- (5) Is there evidence that dogs show close, mutually affiliative bonds, or friendships?
- (6) How does dominance influence the nature of affiliation in relationships?

In Part 2 we provide detailed descriptions of 16 closely observed pairs associating in home environments, yards and dog parks for periods ranging from 6 months to 9 years. With descriptive analysis, we document intricate details of dominance, affiliation and friendship, illustrate complexity and variability in social relationships, and provide examples of how relationships change over time.

2. Part 1

2.1. Methods

2.1.1. Subjects and observations

Submissive and affiliative behaviours (Table 1) were recorded among 24 dogs who socialized regularly at a dog daycare facility in Evanston, IL, USA. Subjects included 12 males and 12 females of various pure and mixed

Table 1.

Ethogram of submissive and affiliative behaviours recorded in Part 1.

Submission (A, actor; R, recipient)	
Muzzle lick	A licks R's nose, lips, and/or chin.
Crouch	A lowers his head and body with bent legs and a rounded back. A's tail is down or tucked between the legs.
Belly up	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 quickly turns and moves away from R when R displays aggression or dominance.
Gentle affiliation	
Nose nudge	A uses the tip of her nose to gently nudge R's mouth, head, or body.
Coat lick	A licks anywhere on R's body other than the muzzle or ano-genital area.
Genital lick	A licks R's genitals and/or anus.
Head rub	A rubs or presses his face or head on R's body.
Body rub	A turns in a circle, gently rubbing his/her hip on R.
Nibble	A uses her front teeth to rapidly nibble on R's coat.
Mutual play-fighting	
Both dogs displayed relaxed body postures and facial expressions and exaggerated, bouncy locomotion and chased, mouthed, bit, pawed, jumped on, tackled, body slammed, nose punched and/or sat on the other.	

Adapted from van Hoof & Wensing (1987), Bauer & Smuts (2007), Handelman (2008).

breeds, ranging from 7 months to 11 years of age and 9–46 kg in weight. Dogs were housed in temporary groups of 10–20 individuals at a time in enclosed areas of approximately 70–90 m² and were observed by R.K.T. several days per week on 90 different days over the course of one year for a total of 224 observation hours (mean \pm SD h/individual = 99 \pm 64, range = 26–224).

In the daycare environment, all dogs were spayed/neutered and screened for non-aggressive behaviour, and human supervisors often used verbal interruptions and food rewards to stop and deter dogs from aggression. These factors almost certainly led to fewer aggressive interactions in the daycare dogs than in a random sample of dogs with less human involvement. However, such intervention likely characterizes the natural lives of many companion dogs. See Trisko & Smuts (2015) for additional information on the dog daycare facility, the study subjects, and the nature of human intervention during interactions.

2.1.2. *Dominance relationships*

In a previous study of dominance in this group of dogs, we found using all occurrence sampling that submission was the most frequent and unidirectional type of agonistic behaviour and resulted in a significant linear hierarchy in the group (Trisko & Smuts, 2015). Thus, the presence or absence of unidirectional (one-way) submission (Table 1) was used to determine whether or not a dyad exhibited dominance. Submissive behaviour included muzzle licking, which is also affiliative in nature. Given its unidirectionality and relevance to dominance, muzzle licking was classified as a submissive behaviour and was excluded from our consideration of gentle affiliation in all statistical analyses. See Trisko & Smuts (2015) for additional information about muzzle licking and other agonistic behaviours.

2.1.3. *Affiliation*

Affiliative behaviours were split into two categories, mutual play-fighting and gentle affiliation. Mutual play fighting occurred when both dogs displayed relaxed body postures and facial expressions and exaggerated, bouncy locomotion and chased, mouthed, bit, pawed, jumped on, tackled, body slammed, nose punched and/or sat on the other (Table 1). During bouts of play fighting between dogs, play behaviours are exchanged so rapidly that frame-by-frame video analysis is necessary to quantify each individual play fighting behaviour (Bauer & Smuts, 2007; Ward et al., 2008, 2009; Horowitz, 2009). Because observational data were collected in real-time, it was not possible to record each distinct play fighting behaviour. Instead, play fighting was recorded using one-zero sampling at 60 second intervals (Bernstein, 1991; Lehner, 1992). Gentle affiliation occurred when a dog initiated any of the following behaviours: nose nudges, coat licks, head rubs, body rubs, and nibbles (Table 1). Because gentle affiliation was not exhibited at a very rapid pace, it was possible to code each behaviour individually, so for every gentle affiliative behaviour, the actor and the recipient were recorded using all occurrence sampling (Bernstein, 1991; Lehner, 1992).

2.1.4. *Relationship types*

To identify how affiliation and dominance overlapped in relationships and to classify different types of relationships among the dogs, we assessed whether or not a dyad exhibited affiliation (play fighting or gentle affiliation) and/or one-way submission (i.e., exhibited dominance). Based on the presence or absence of affiliation and dominance, dyads fell into 4 categories. (1) Dyads

that affiliated and exhibited dominance were labelled ‘formal’ dominance relationships. (2) Dyads that affiliated and did not exhibit dominance were labelled ‘egalitarian’ relationships. (3) Dyads that exhibited dominance and did not affiliate were labelled ‘agonistic’ dominance relationships. (4) Dyads that did not affiliate or exhibit dominance were labelled ‘non-interactive’ relationships.

In a previous study muzzle licking emerged as the behaviour that best fit the criteria for a formal display of submission in this group (Trisko & Smuts, 2015). As mentioned above, muzzle licking, which is both submissive and affiliative in nature, was excluded from gentle affiliation in all statistical analyses to avoid confounding variables and to allow for comparisons of affiliation in dyads with or without dominance relationships. However, for the purposes of classifying dyads into the four relationship types, dyads that exhibited only one-way muzzle licking but no other gentle affiliative behaviours were labelled as having ‘formal’ relationships. Dyads with ‘agonistic’ relationships exhibited one-way submission other than muzzle licking (crouch, belly up, or retreat) and no muzzle licking nor gentle affiliative behaviours.

2.1.5. Directionality and skew in gentle affiliation

For information about the directionality of gentle affiliation in the group as a whole, we calculated (1) the percentage of dyads that had completely uni-directional (one-way) gentle affiliation versus those that had bi-directional (two-way) gentle affiliation, and (2) for dyads with dominance relationships, the percentage of total gentle affiliation behaviours displayed by subordinates toward dominants. To identify particular dyads that displayed high degrees of skew in their exchange of gentle affiliation, we used the following method (Silk et al., 1999). Within each dyad, s is the number of gentle affiliative behaviours directed by the subordinate to the dominant, and d the number of gentle affiliative behaviours directed by the dominant toward the subordinate. The total number of events, N , is equal to $s + d$. We assigned ‘relative rank’ by comparing the dogs’ positions in the submission hierarchy from Trisko & Smuts (2015). We computed the cumulative binomial probability of the smaller of the two values (s or d) in a sample of N events. This value equaled the probability, for each dyad, of obtaining the smaller of the two observed values under the null assumption that each member of the dyad was equally likely to show gentle affiliation. Dyads in which the cumu-

lative probability of s was less than or equal to 0.1 were considered ‘highly skewed’.

2.1.6. Friendship

We defined mutual friendships as particularly close relationships based on mutual play and gentle affiliation partner preferences. We first calculated partner preferences by dividing each dyad’s number of play-fighting minutes and gentle affiliative behaviours by the amount of time the dyad spent together, controlling for the opportunity the dyad had to interact. Next, we adapted a method used by Johnson et al. (2014) to determine dogs’ primary affiliation partners. We determined each dog’s top three play-fighting partners and top three gentle affiliation partners and limited the friendships to those in which both dogs had the other listed in his/her top three play or gentle affiliation partners (or both). Play fighting was mutual by definition, but gentle affiliation was unidirectional. Therefore, if both dogs had the other in his/her top three gentle affiliation partners but neither had the other in his/her top three play partners, dyads with one-way or highly skewed gentle affiliation were excluded. This method ensured that affiliation (either play, gentle affiliation or both) was mutual in dyads labelled as friends.

2.1.7. Statistical analyses

2.1.7.1. Kendall’s rowwise matrix correlations. To examine the relationship between play and gentle affiliation, test for reciprocity in gentle affiliation, and assess whether gentle affiliation was directed up or down the hierarchy, we performed K_r matrix correlations. K_r matrix correlations are robust tests for data in which there are large individual differences in behaviour or large variation in the frequencies of behaviours (Hemelrijk, 1990). To examine the relationship between play fighting and gentle affiliation, we performed a K_r matrix correlation between play fighting and gentle affiliation. The matrix of gentle affiliation was arranged with actors in the rows and recipients in the columns. Play fighting was mutual by definition and produced a symmetrical matrix. To test for reciprocity in gentle affiliation, we performed a K_r matrix correlation between gentle affiliation given (actors in the rows, recipients in the columns) and its transposition (recipients in the rows, actors in the columns). To assess whether gentle affiliation was directed up or down the hierarchy, we created a binary matrix of ‘relative rank’. If the actor was lower-ranking than the recipient the cell contained a 1, and if the actor was higher-ranking than the recipient the cell contained a 0. We performed a K_r matrix correlation between gentle affiliation displayed and the

matrix of relative rank. In both matrices, actors were represented in the rows and recipients were represented in the columns. All K_r tests were run with 5000 permutations to obtain significance values using MatMan 1.1 (Noldus).

2.1.7.2. Generalized linear mixed models. To assess the factors that influenced affiliation, dominance, skew, and friendship, we conducted generalized linear mixed models (GLMMs) using the ‘lme4’ package (Bates et al., 2015) in R (version 3.2.2) (R Core Team, 2015).

To assess the influence of dyadic characteristics on relationship type, we ran a series of binomial distribution GLMMs with the following binary responses: (1) whether or not a dyad interacted, (2) if they interacted, whether or not they affiliated, and (3) if they affiliated, whether or not they exhibited dominance. Dyadic observation time, sex composition, age difference, and size difference were included as fixed effects and identity of each of the dogs within the dyad were included as random effects.

To assess the influence of dominance on play fighting, gentle affiliation, gentle affiliation skew and friendship, we ran a second series of binomial GLMMs with the following binary responses: (4) whether or not the dyad engaged in mutual play fighting, (5) whether or not the dyad exhibited gentle affiliation, (6) whether or not the dyad had highly skewed gentle affiliation, and (7) whether or not the dyad was labelled friends. The second series of binomial GLMMs was conducted only on dyads that affiliated. The presence of one-way submission was the fixed effect and identities of the dogs within the dyad were included as random effects.

In all the models, the first outcome mentioned above is considered ‘positive’ and the second outcome is considered ‘negative’ (e.g., in the first GLMM described above, positive means the dyad did interact and negative means they did not interact). To assess model fit, we used the classification function (calculated by the ‘caret’ package in R; Kuhn, 2015). We report model accuracy (percent of dyads classified correctly), sensitivity ($a/(a+b)$, where a is the number of positive dyads correctly identified and b the number of positive dyads incorrectly identified) and specificity ($c/(c+d)$, where c is number of negative dyads correctly identified and d the number of negative dyads incorrectly identified). In other words, high sensitivity implies a low type-II error rate (low false negatives), and a high specificity implies a low type-I error rate (low false positives). The R code and related files are available as supplementary material in the online edition of this journal,

which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1568539x>.

2.2. *Results*

2.2.1. *Relationship types*

Based on the presence or absence of affiliation and/or dominance in each dyad, 22% affiliated and had a dominance relationship (formal relationships), 21% affiliated but did not exhibit dominance (egalitarian relationships), 7% had a dominance relationship but never affiliated (agonistic relationships) and 50% never interacted (non-interactive relationships) (Table 2). Each dog formed several different types of relationships with different dogs.

2.2.2. *Predictors of relationship type*

Sex class predicted non-interactive relationships; male–male dyads were less likely to interact than female–female dyads ($Z = 2.029, \beta = 1.38 \pm 0.68, p = 0.043$) and mixed sex dyads ($Z = 2.293, \beta = 1.01 \pm 0.44, p = 0.022$). Age difference, size difference, and hours observed together did not predict interaction/non-interaction. The model accurately predicted whether or not dogs interacted for 74.6% of dyads with high sensitivity (0.745) and high specificity (0.748) ($N = 276$ total dyads).

Of the dyads that interacted, sex class predicted whether dogs affiliated or not, with mixed-sex dyads more likely to affiliate than female–female dyads, who were more likely to have agonistic relationships ($Z = 2.23, \beta = 1.41 \pm 0.63, p = 0.026$). No differences were found between other sex classes, and no other dyadic characteristics were strong predictors of whether or not a dyad affiliated. The model accurately predicted whether or not dogs affiliated for 86.3% of dyads, but it produced a high rate of false negatives (sensitivity = 0.10, specificity = 0.992; $N = 139$ total dyads).

Table 2.

Types of social relationships formed among the daycare dogs based the presence or absence of affiliation and dominance.

Relationship type		Number of dyads
Formal:	affiliation + one-way submission	61 (22%)
Egalitarian:	affiliation + two-way or no submission	58 (21%)
Agonistic:	no affiliation + one-way submission	20 (7%)
Non-interactive:	no affiliation + no submission	137 (50%)

Of dyads that affiliated, mixed sex dyads were less likely to exhibit dominance relationships (i.e., more likely to have egalitarian relationships) than female–female dyads ($Z = -2.73$, $\beta = -2.67 \pm 0.98$, $p = 0.006$). No differences were found between other sex classes, and no other dyadic characteristics were strong predictors of dominance in affiliative dyads. The model accurately predicted whether or not dogs had dominance for 86.5% of dyads (sensitivity = 0.81, specificity = 0.92; $N = 119$ total dyads).

2.2.3. Play fighting, gentle affiliation and friendship

There was a significant positive correlation between play fighting and gentle affiliation ($K_r = 1001$, $p < 0.001$). However, the scatter plot of play vs. gentle affiliation revealed that although a small number of dyads displayed high rates of both types of affiliation, many others displayed only one type or the other or low rates of both (Figure 1).

Play fighting and gentle affiliation were not distributed equally among the dyads. Even when we excluded the dyads that did not affiliate at all, most dyads only rarely played or exhibited gentle affiliation, with a smaller number of dyads forming considerably stronger social bonds based on play or gentle affiliation (Figure 2).

Twenty-nine dyads (11%) were considered to have mutual friendships based on mutual partner preferences. The majority of friendships occurred

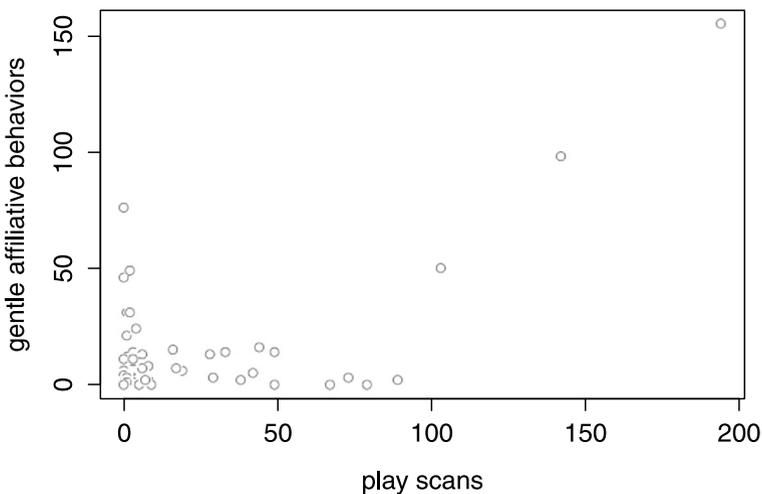


Figure 1. Scatter plot of gentle affiliative behaviours and play fighting scans.

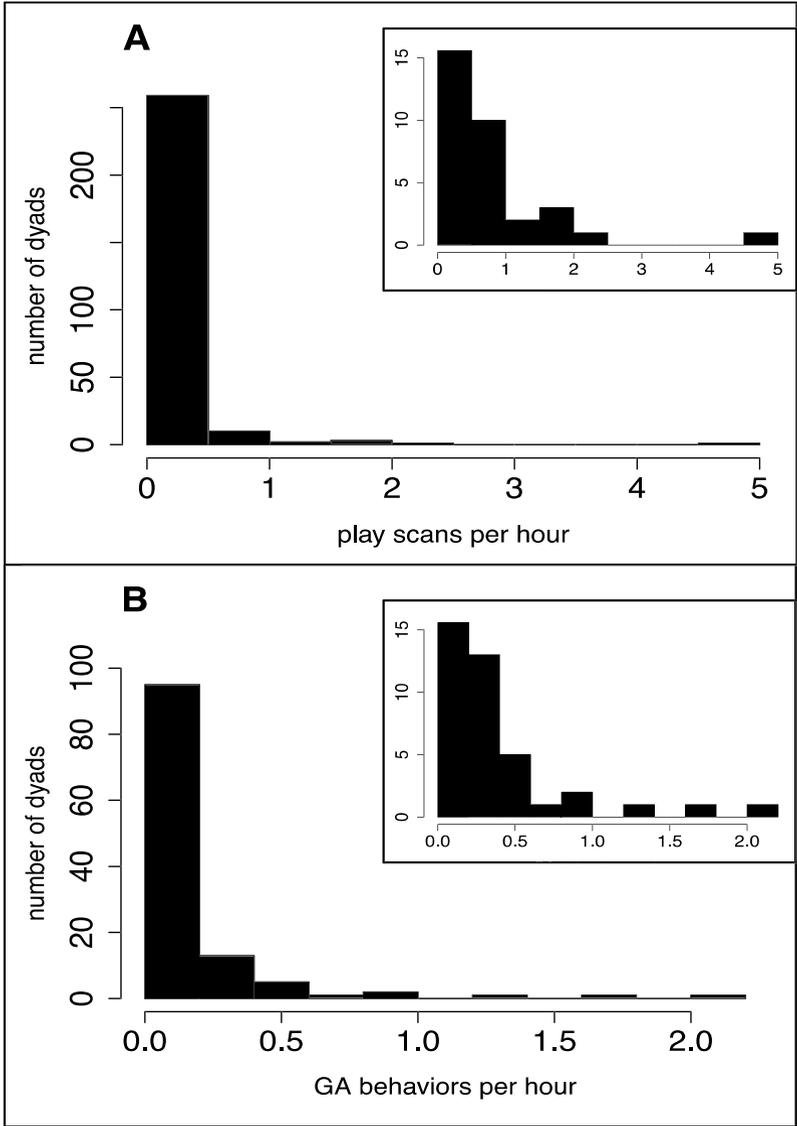


Figure 2. Histograms of play fighting and gentle affiliation: (A) Histogram of play scans per hour. (B) Histogram of gentle affiliative behaviours. Insets zoom on the tail.

Table 3.

Frequency, coverage and directionality of submission and affiliation among the daycare dogs.

	<i>N</i>	Dogs that displayed behaviour	Dyads that exchanged behaviour	One-way relationships	Two-way relationships
Submission	609	20 (83%)	85 (31%)	81 (95%)	4 (5%)
Gentle affiliation	873	23 (96%)	87 (33%)	56 (64%)	31 (36%)
Play fighting	1215	23 (96%)	57 (21%)	0 (0%)	57 (100%)

in mixed sex ($N = 20$; 69%) and egalitarian dyads ($N = 20$; 69%), but some friendships occurred in all sex class/dominance combinations.

2.2.4. Reciprocity and directionality of gentle affiliation

Gentle affiliation was significantly reciprocal in the group ($K_r = 1124$, $p = 0.001$). Nevertheless, gentle affiliation was completely unidirectional in most (64%) of dyads in which it occurred (Table 3). There was a significant correlation between gentle affiliation given and relative rank, showing that gentle affiliation was directed up the hierarchy ($K_r = 313$, $p = 0.002$). In dyads with dominance relationships, 80% of gentle affiliation was directed from subordinate to dominant.

2.2.5. The effects of dominance on play, gentle affiliation, skew and friendship

There was a trend for egalitarian dyads to be more likely to engage in mutual play fighting than formal dyads ($Z = -1.72$, $\beta = -0.78 \pm 0.46$, $p = 0.086$). The model fit the data well and accurately predicted whether or not a dyad played for 79.8% of dyads, (sensitivity = 0.89, specificity = 0.69; $N = 119$ total dyads).

One-way submission did not predict whether or not a dyad exhibited gentle affiliation ($Z = -1.48$, $\beta = -0.86 \pm 0.58$, $p = 0.14$). The model accurately predicted whether or not dyads exchanged gentle affiliation 78.2% of the time, but sensitivity was low (0.22), indicating a high false negative rate, although specificity was high (0.98) ($N = 119$ dyads).

Based on binomial probabilities, we classified twenty-four dyads (28%) as having highly skewed gentle affiliation. Formal dyads were more likely than egalitarian dyads to show high degrees of skew in their exchange of gentle affiliation ($Z = 2.19$, $\beta = 2.30 \pm 1.05$, $p = 0.028$). The model fit the data

well (accuracy = 89.7%, sensitivity = 0.94, specificity = 0.79; $N = 119$ dyads).

Egalitarian dyads appeared to be more likely to be friends ($Z = -2.446$, $\beta = -1.11 \pm 0.45$, $p = 0.014$), but the model did not predict friendship any better than chance (accuracy = 75.6%, sensitivity = 1.0, specificity = 0.0; $N = 119$ dyads).

2.3. Summary

The daycare dogs formed highly differentiated relationships with one another. Some dyads affiliated with dominance (formal), others affiliated without dominance (egalitarian), and the majority of dyads did not affiliate at all (agonistic and non-interactive). Each dog formed several different types of relationships, suggesting the capacity for high degrees of social flexibility. The sex composition of the dyad influenced the types of relationships the dogs formed; male–male dyads were the most likely sex class to have non-interactive relationships, female–female dyads were the most likely sex class to have agonistic relationships, (non-affiliative dominance relationships), and mixed sex dyads were the most likely sex class to have egalitarian relationship (affiliative relationships without dominance). Certain dyads affiliated at much higher rates than others, providing evidence that the dogs formed friendships. Gentle affiliation was reciprocal in the group as a whole, but it was highly skewed in 28% of the dyads that displayed it. It was mainly directed up the hierarchy, but dominants sometimes displayed gentle affiliative behaviours toward subordinates, as well. Dominance influenced the nature of affiliation in relationships; egalitarian dyads were more likely to engage in play fighting and less likely to have highly skewed gentle affiliation. Most friends were of mixed sex and egalitarian, but friendships occurred in all of the sex class/dominance combinations.

3. Part 2

3.1. Methods

3.1.1. Subjects and observations

From 1991–2015, 11 dogs were observed for periods ranging from four months to 14.5 years (Table 4). Four of these dogs belonged to BS, three others lived in her home for varying periods of time, three visited BS's home and yard most days of the week during their observation period, and one dog

Table 4.
Subjects in Part 2.

Dog	Sex	Ages when observed (years)	Household or visiting	Breed	Weight (kg)
Bear	M	3	V	German shepherd	41
Bentley	M	0.15–3	H	Mixed	7–23
Kobi	F	1–5	V	Mixed	29
Lela*	F	0.25–3	H	German shepherd	14–32
Osa	M	1–2	V	Mixed	23
Osa	M	6	H	Mixed	29
Safi*	F	1–14	H	German shepherd	32–36
Tasha	F	7	H	Mixed	23
Tex*	M	0.5–10	H	Mixed	23–27
Tuna	F	2–3	H	German shepherd	32
Violet	F	1–8	V	German shepherd	34–41

Dogs belonging to BS are marked with an asterisk. Osa was observed at two different times, 3 years apart. Males were neutered, except for Tex and Bear, before 2 years; females were spayed, except for Lela, before 8 months. When only one year is shown, rather than a range of years, the dog was observed for 4–6 months. H, household: dogs living in the same home; V, visiting: dogs present in the house and yard for several hours on most days during the period of observation.

(Osa) initially visited but later briefly lived in the household. The dogs were medium to large in size, and they were studied over a range of ages. All of the studied dogs were spayed or neutered, except for Bear (who interacted only with Safi), Tex before the age of 2, and Lela under 8 months.

Based on when they overlapped in time, these 11 dogs comprised 16 dyads. Eight of the pairs were mixed sex and 7 were female–female. There was only one male–male dyad because only one of BS’s dogs was male, and he co-existed with only one other male. Since all of the dyads involved 1–2 of BS’s 4 dogs, the same dogs appear in multiple dyads.

With the agreement of the dog’s owners, human intervention in dog–dog interactions was minimized. Although a human was often present, after introductory supervision the dogs frequently socialized on their own, especially in the yard. Typically, mild threats and dominance displays were not interrupted. Snarling or growling occasionally occurred, but most of these conflicts ended so quickly that intervention was not possible. Thus, interactions among these dogs were interrupted less frequently than interactions among the daycare dogs in Part 1.

With the exception of the Safi/Bear dyad, interactions among all dogs present were videotaped several days a week from 1995–2015 (except for occasional vacation breaks). Videotaping focused opportunistically on dog–dog play because, when they occurred in isolation, agonistic and affiliative events usually did not last long enough to capture on tape. However, during play, many such interactions were recorded. Some of these data have been analysed and published (Bauer & Smuts, 2007; Byosiere et al., data not shown), and many hours of videotape have been coded. However, since data analysis is incomplete, qualitative descriptions, in all cases supported by videotaped observations (except for Safi/Bear), are reported here.

3.2. *Results and discussion*

3.2.1. *Unusual events and significant changes in relationships*

Observations of the 16 dyads demonstrated that, in general, relationships among dogs were quite stable over the long-term. However, we begin this section by describing exceptions to this general trend.

3.2.1.1. Safi and Osa. When these dogs met (Table 5, Safi/Osa 1), Safi was older than Osa and outweighed him by 16 kg. They played every time they met, sometimes very roughly. For example, Osa launched flying attacks that knocked Safi to the ground, which she never objected to. Their relationship was considered formal because Osa occasionally showed friendly submission, but in most respects, it was egalitarian. Two years later, Osa moved away, and then, after a 3-year gap, he joined BS's household for 2 months (Table 5, Safi/Osa 2). By this time, Osa was in his prime and had gained weight, whereas Safi was elderly and had lost weight, so they were close in size. Their videotaped reunion was friendly but casual. It was clear that they knew each other since, within 10 min, they resumed a game that Safi played only with Osa. Osa also had friendly interactions with two 'new' dogs: Bahati, Safi's housemate, and Kobi, a frequent visitor.

About a week after Osa arrived, BS videotaped a pivotal event. Safi, Osa, Bahati and Kobi were walking off leash when they encountered an unfamiliar human/dog pair. Before their separation, Osa expressed his arousal when meeting a new dog by pouncing on Safi, which she tolerated. This time, Osa pounced on Safi, and she fell, scraping her chin on the ground. Clearly, Safi was no longer strong enough to tolerate this behaviour, but before BS could intervene, Osa pounced again. Safi immediately charged Osa, but when she tried to bite his neck, he instead bit her neck, forcing her to the ground.

Table 5.
Dyadic social relationships of the dogs in Part 2.

1. Dog 1/dog 2	2. Dog 1 age (years)	3. Dog 2 age (years)	4. Age diff. (years)	5. Observation period (years)	6. Higher ranking dog	7. Type of relationship	8. Submission	9. Dominance	10. Aggression	11. Play fighting	12. Affiliation	13. Friends?
Mixed sex dyads												
1. Safi*/Bear (v)	3	3	0	0.5	None	E	None	None	None	R, SP	GA, PX	Y
2. Safi*/Osa 1 (v)	6	1	5	2	Safi/Older	F	FS, LP	None	None	R, SP	GA, PX, R	Y
2. Safi*/Osa ^a 2	11	6	5	0.4	Safi/Older	UR > NI ^c	FS	None	F	None	None	N
3. Bahati*/Tex	5	0.5	4.5	9.5	None	E	None	None	MT	SP, CP	GA, PX, CF, R	Y
4. Tex*/Tasha	1	6	5	0.5	None	E	None	None	None	SP	GA, PX, R	Y
5. Tex*/Tuna	4	2	2	1	Tex/older	F > E ^c	FS, LP	DP	DT	R, SP	GA, R	Y
6. Bahati*/Bentley	10	0	10	3	Bahati/Older	F	FS, LP	DP	DT	CP	GA, PX, R	Y
7. Tex*/Lela*	7	0	7	3+	Tex/Older	F	FS, N, LP	DP	DT	SP	GA, R	Y
8. Bentley/Lela*	2	0	2	1	Bentley/Older	F > E ^c	FS, N	DP	DT	AP > SP, CP	GA, PX, R	Y
Female-female dyads												
1. Safi*/Violele ^b (v)	1	1	0	7	Safi/Same	E > F ^c	FS	None > DM	None > F, DT	SP	GA	N
2. Safi*/Bahati	9	0.5	8.5	5.5	Safi/Older	F	FS, N, LP	DP	DT	AP, CP	GA, R	Y
3. Safi*/Kobi	10	1	9	4	Safi/Older	F	FS, LP	DP	None	AP	GA	Y
4. Bahati*/Kobi (v)	2	1	1	4	Bahati/Same	F	FS, LP	DP, SO	DT	SP	GA, PX, R	Y
5. Bahati*/Tasha	7	7	0	0.5	None	UR	None	MDP	MT	None	None	N
6. Bahati*/Tuna	9	2	7	1	Bahati/Older	F	FS, N, LP	DP, SO	DT	None	GA, R	N
7. Bahati*/Lela*	12	0	12	2	Bahati/Older	F	FS, N, LP	DP	DT	AP, CP	GA, R	N

Table 5.
(Continued.)

1. Dog 1/dog 2	2. Dog 1 age (years)	3. Dog 2 age (years)	4. Age diff. (years)	5. Observation period (years)	6. Higher ranking dog	7. Type of relationship	8. Submission	9. Dominance	10. Aggression	11. Play fighting	12. Affiliation	13. Friends?
Male-male dyad												
1. Tex*/Bentley	5	0	5	3	Tex/Older	F	FS, N, LP	DP, SS	MT	SP	GA, R	Y

^a Information in columns 7–13 is based on the Safi/Osa dyad after changes described in the text.

^b Information after the arrow in columns 8, 10 and 11 refers to Safi/Violet dyad after the change described in the text.

^c An arrow followed by a behaviour code indicates a change in the relationship over time.

1. Dog 1/dog 2. Dyads are listed in chronological order. Dogs belonging to BS are marked with an asterisk. V. dyads involving a visiting dog.

2. Dog 1 age, Dog 1's age when the dyad was first observed.

3. Dog 2 age, Dog 2's age when the dyad was first observed.

4. Observation period, total time that the dyad was observed.

5. Higher ranking dog, rank was based on the direction of consistent one-way submission (Table 1). After the name of the higher-ranking dog, his/her relative age is shown.

6. Type of relationship: E, egalitarian (dogs affiliated but did not show one-way submission); F, formal (dogs affiliated and showed one-way submission); NI, non-interactive (dogs did not interact at all); UR, unresolved (the dogs showed only bi-directional dominance interactions). An arrow followed by a different relationship type indicates that the relationship changed from one type to the other over time (see text for details).

7. Mutual play fighting (see Table 1): R, rough play; play characterized by mutual loud growling and/or barking and by tackles and pounces that sometimes knock the partner to the ground; AP, asymmetric play: one member of the dyad showed the vast majority of offense behaviours (e.g., chasing, tackling, forcing partner down); SP, symmetric play: both members of the dyad adopted the offensive role (Bauer & Smuts, 2007); AP → SP, the dyad shifted from asymmetric play to symmetric play as the younger dog matured; CP, courtship play: courtship play was characterized by nudges/nuzzles to the neck, head and genital regions; presenting the rear end, spinning, quick darts at the partner, placing a chin over the back of the neck, placing a paw on a flank, and wide open-mouth play faces.

8. Gentle affiliation (see Table 1): PX, proximity: dogs sometimes rested in very close proximity or touching; CF, co-fed, meaning that the pair sometimes licked a greasy pan or dish at the same time without conflict; R, reconciliations: dogs showed GA within one minute after a conflict (most conflicts occurred during too-rough play).

9. Submission: FS, friendly submission: subordinate showed frequent friendly greetings toward the partner, involving muzzle flicks, ears back and rapid tail wagging, which the dominant partner tolerated; N = nervous greetings: subordinate showed crouch (Table 1) or muzzle-licking with tail tucked, or both; LP, low posture: the subordinate sometimes lowered his or her posture when in the vicinity of the dominant dog.

10. Dominance: DP, dominance posture: dominant member of the pair stood near subordinate with distinct high posture (standing tall, ears forward and tail erect); MDP, mutual dominance posture: both members of the dyad approached each other with high posture, frequently resulting in slow, tense circling; neither dog showed submission; SO, stand over: adopting a dominance posture, dominant stands over a prone subordinate and, for at least a few seconds, keeps subordinate from standing up; DM = dominance mount: in a non-play context, the dominant dog mounts subordinate from behind, side or front, sometimes from more than one angle in rapid succession.

11. Aggression: DT, dominant threatened subordinate by barking, growling or snapping but made no body or bite contact. MTH = mutual threat: both dogs occasionally threatened the other (not necessarily at the same time); SS = subordinate dog occasionally snapped/snarled at dominant dog; F = fight involving contact but no injuries (Safi/Osa 2 fought once; Safi/Violet fought twice).

12. Friends?: Y, the dyad consistently played together and/or that showed mutual gentle affiliation such that the overall tenor of the relationship was friendly and relaxed with only occasional agonism or no agonism; N, no.

Safi rose, facing Osa, and they briefly fenced with open mouths. Osa ran away, with Safi, Bahati and Kobi all chasing him. Osa moved off for 10 s. When he wandered back, Safi approached with a neutral posture, as if to initiate a reconciliation, a phenomenon documented in both dogs (Cools et al., 2008) and wolves (Cordoni & Palagi, 2008; Baan et al., 2014). However, Osa avoided her gaze and walked away.

These were the last interactions Safi and Osa had. Although Osa lived with Safi and Bahati for another 7 weeks, both dogs ignored him, as did Kobi when she visited. Osa did not try to interact with them, although he was still friendly with people in the home.

These events and their aftermath are noteworthy for three reasons. First, they suggest the importance of reconciling — or failing to reconcile — after a conflict. Second, they show that in dogs, as in humans, one event can end a close relationship. Third, apparently dogs can join forces to ostracize another dog.

3.2.1.2. Safi and Violet. These two female German shepherds began interacting as subadults. Neither showed submission, so their relationship was classified as egalitarian. They played frequently and vigorously. Both fetched in Safi's yard, but Violet passively gave way to Safi over the ball. However, when they were two, Violet grew larger than Safi and began to compete for the ball. In that context they had two brief, non-injurious fights. Right after the second fight — and from then on — Violet submitted to Safi, so their relationship shifted from egalitarian to formal.

The morning after the second fight, Safi mounted Violet for the first time. Remarkably, until we moved away 6 years later, Safi continued to mount Violet several times a week. Violet was the only familiar dog who ever challenged Safi, and Violet was the only dog Safi ever mounted.

Just as for Safi and Osa, the dramatic shift in the Safi/Violet relationship was triggered by singular events, in this instance, two fights that led to a permanent change in their dominance relationship. Both cases resemble decisive conflicts in captive wolves that produced permanent shifts in dyadic relationships, including ostracism and changes in dominance, although in wolves, in contrast to the dogs, the precipitating fights were often severe and produced injuries (Zimen, 1981).

Other relationship changes in these dogs were less dramatic. In two female/male dyads, Tex/Tuna and Bentley/Lela, the younger, subordinate female gradually stopped showing one-way submission, so that the dyad

shifted from a formal to an egalitarian relationship. In two dyads that initially involved Tex with a puppy, Tex/Bentley and Tex/Lela, Tex consistently asserted dominance and rarely played until Bentley and Lela reached the age of 1 year. At that point, virtually overnight, Tex began to play symmetrically with the younger dog and his dominance displays disappeared, except when Lela was particularly rough during play. Surprisingly, Bentley even began to threaten Tex when he was on a bed and Tex approached him. Tex always ignored Bentley's threats, which therefore seemed to express his emotional resistance to sharing the bed rather than a desire to change the balance of power in their relationship.

3.2.2. *Types of relationships*

None of the dyads had an agonistic relationship characterized by one-way submission and no affiliation. A majority showed both one-way submission and affiliation and therefore had formal relationships. In all formal dyads except Bahati and Kobi, who were the same age, the older dog was dominant. Interestingly, even toward the end of Safi's life, when she was very frail, Bahati and Kobi continued to spontaneously offer her active submission, and they never challenged her.

Of the 5 dyads that did not initially exhibit formal dominance, three were mixed-sex dyads with egalitarian relationships (Safi/Bear, Bahati/Tex and Tex/Tasha). Two other mixed-sex dyads with formal relationships later shifted to egalitarian ones (Tex/Tuna and Bentley/Lela), so that 5 of the 8 mixed sex dyads ended up egalitarian. None of the 7 same-sex dyads ended up with an egalitarian relationship. This pattern is consistent with the finding that mixed sex dyads were most likely to have egalitarian relationships (Part 1).

Two dyads had unresolved relationships involving dominance displays or aggression from both dogs but no submission. (Unresolved relationships were not documented in the daycare dyads because human supervisors chose to keep such pairs apart to prevent conflicts, but such relationships did occasionally occur in the daycare environment.) One, Safi and Osa, was described above. The other involved two females, Bahati ('Ba') and Tasha. Ba and Tasha were the same age and weight. They never exchanged friendly behaviours and almost never interacted except when Tasha and Tex played. In that context, Ba often interfered by approaching Tasha with a high posture, ears forward and tail raised. Tasha would stop playing with Tex and adopt the same posture. Then they would circle, eyeing each other warily, sometimes

for over 30 seconds. Ba usually walked away first, and then Tasha resumed playing with Tex. Remarkably, Ba and Tasha never growled or snapped at each other and never fought. They clearly illustrate dogs' abilities to use mutual, ritualized aggression to express hostile attitudes without coming to blows.

3.2.3. *Agonistic behaviours*

By definition, all of the dyads classified as formal showed one-way submission, but this could involve friendly greetings in which the subordinate dog rapidly wagged the tail or nervous greetings involving a tucked tail, or both. Subordinates could also exhibit submission by adopting a low posture (van der Borg et al., 2015) when in the vicinity of the dominant dog. In about half of the formal dyads, the subordinate showed nervous submission, but this was restricted to dyads with at least a five-year age difference and/or dyads involving a puppy. In these dyads, nervous submission decreased and friendly submission increased as the younger dog grew up, suggesting that nervous submission characterizes younger dogs, especially early in relationships. All of the subordinate dogs, both visitors and household dogs, showed friendly submission toward the dominant dog, which is not always the case in other dog populations. Some daycare dyads (Trisko & Smuts, 2015) and some feral dog pairs (Cafazzo et al., 2010) exhibited only nervous submission.

Dominance posturing did not occur in mixed-sex dyads, with the exception of dyads in which the younger dog was a puppy when they met. As the younger dog matured, dominance posturing became rare to non-existent, and this was also the case for the single male–male dyad, Tex/Bentley. This decrease in dominance displays matched the decrease in nervous greetings mentioned above. In three of the female–female dyads, Safi/Bahati, Safi/Kobi and Bahati/Lela, dominance posturing was maintained, although it occurred rarely, but in two others, Bahati/Kobi and Bahati/Tuna, it occurred more often, accompanied by standing over. In both relationships, Bahati displayed dominance primarily in one context: when attempting to interrupt play involving a favorite partner and a third dog (Kobi with any other dog, or Tex with Tuna). Recall from the description of the Bahati/Tasha relationship that Bahati also displayed dominance to try to disrupt play between Tasha and Tex. Similar attempts to interfere with others' affiliative relationships were observed in the daycare dogs (Trisko, 2011), captive chimpanzees

(de Waal, 1982), stumptail macaques (Mondragón-Ceballos, 2001), horses (Schneider & Krueger, 2012) and ravens (Massen et al., 2014).

Serious aggression was very rare in household and visitor dyads. Only three fights were seen: two between Safi and Violet and one between Safi and Osa, as described above. Otherwise, all aggression involved threats, such as staring, growling, snarling or snapping. Such threats were shown by the dominant dog at least occasionally in all formal dyads, but subordinates also threatened dominants on rare occasions, as described above for Tex/Bentley. Threats by the dominant dog were often mild protests in response to friendly and sometimes persistent submission from a subordinate. Threats were absent in three mixed-sex dyads. Two of these were egalitarian (Safi/Bear and Tex/Tasha) and the other, Safi/Osa 1, described above, tended toward an egalitarian relationship. In the remaining egalitarian mixed-sex dyad, Tex/Bahati, threats went in both directions, usually when play escalated.

3.2.4. *Affiliative behaviour*

All dyads played except for the two with unresolved relationships and one with a formal relationship (Bahati/Tuna, a female–female dyad). Particularly rough play occurred in 3 mixed-sex dyads. Seven of the 8 mixed-sex dyads played symmetrically, and the eighth (Bentley/Lela) shifted to symmetric roles after Lela matured (see Table 4, Key to columns, number 7, for definitions of symmetric and asymmetric play). The single male–male dyad also played symmetrically. Of the 5 formal female–female dyads that played, the three with a large age difference (Safi/Bahati, Safi/Kobi, Bahati/Lela) played asymmetrically. In contrast, the two formal female–female dyads with little or no age difference, Bahati/Kobi and Safi/Violet, played symmetrically. Thus, of the 13 dyads that played, 10 ended up playing symmetrically, including 4 formal dyads, suggesting a tendency toward symmetric play in dyads who spent a great deal of time together. This contrasts with a significant tendency for asymmetric play roles in formal dyads composed mostly of dogs meeting at a dog park (Bauer & Smuts, 2007).

Only the two dyads with unresolved relationships failed to exhibit gentle affiliation and reconciliation, indicating that most pairs of dogs who spend a lot of time together will exchange friendly gestures and affiliate soon after conflict, even if, like Bahati and Tuna, they never play. Close proximity or touching while resting was not very common, but three of the four dyads that showed such behaviour were of mixed-sex. The ubiquity of gentle affiliation is consistent with the presence in all the interacting dyads of friendly

submission. Remarkably, one long-lasting mixed-sex dyad, Tex/Bahati, grew comfortable enough to jointly lick a coveted greasy pan without conflict.

Two other affiliative behaviours were not observed frequently enough to be included in Table 5 but are worth mentioning. First, dogs were observed providing agonistic support to a dog they lived with when an unfamiliar dog threatened the housemate. In addition, on several occasions, one dog 'notified' BS when a household member escaped or was accidentally locked out of the yard.

Based on the criteria in Part 1, we consider most of the dyads in Table 5 to be friends. In particular, with the exception of Safi/Osa after the change in their relationship, all mixed-sex dyads were friends. In contrast to the daycare dogs in Part 1, who could choose their favourite affiliative partners, most of the friend dyads involved dogs who shared a household because BS put them together (Safi/Osa and Bahati/Kobi were exceptions, since they initially favoured each other as play partners at a dog park and subsequently Osa and Kobi became frequent visitors). Possibly, dogs who must live together sometimes bond because they prefer friendship to conflict or unresolved relationships. The fact that aggression was so rare and affiliation so common indicates that companion dogs who do not compete for food or mates are exceptionally skilled at getting along. In particular, in this sample, mixed-sex dyads were more likely to form egalitarian relationships and less likely to show dominance displays, congruent with findings from Part 1. In addition, these mixed sex dyads were more likely to play symmetrically and more likely to become friends; in Part 1, mixed-sex dyads were the most likely sex class to affiliate, and the majority of friendships occurred in mixed sex dyads. Thus, although patterns in this sample of 16 dogs could not be tested statistically, they showed a number of trends consistent with findings in Part 1.

4. General discussion

4.1. Overall findings

Our study produced two main findings. First, dogs' conspecific relationships exhibited great social complexity. Second, their relationships tended to be peaceful and allowed them to avoid serious conflicts.

Our combination of quantitative and qualitative analyses demonstrated a complex interplay between affiliation and dominance that allowed us to

identify 5 relationship types: formal dominance, egalitarian, agonistic, non-interactive, and unresolved. Detailed knowledge of individual dyads in Part 2 revealed an even deeper level of relationship variation. Each dog participated in several different types of relationships, and the relative prevalence of different submissive, dominance, and affiliative behaviours was specific to each dyad, even among dyads of the same type (e.g., formal dyads). In addition, several relationships changed over time, sometimes gradually but, in two instances, abruptly. The two abrupt changes showed that brief, unexpected eruptions of aggression can permanently alter the nature of a relationship. Bergman & Beehner (2015) have persuasively argued that the best measure of social complexity in nonhuman animals is the formation of highly differentiated social relationships. By this criterion, companion dogs clearly fit the bill.

Interactions among all the study dogs were more often affiliative than agonistic. Even submission, technically an agonistic behaviour, tended to be friendly in nature, usually involving muzzle-licking and tail wagging (Table 5; Trisko & Smuts, 2015). Even among the dogs in Part 2 who were subject to less human intervention than the daycare dogs, dominance displays were relatively rare and aggression was ritualized and mild. This is consistent with studies of free ranging dogs (Pal et al., 1998; Cafazzo, pers. comm.) and companion dogs at dog parks and shelters (Capra et al., 2011). Notably, during all the years of this study, dogs never experienced serious injuries in conflicts with familiar others.

4.2. Formal dominance vs. egalitarian relationships

Formal dominance relationships are thought to increase tolerance from dominants, encourage social bonding and reduce aggression (de Waal, 1986). Formal relationships among the study dogs were similar to those described for wolves (Schenkel, 1967; van Hooff & Wensing, 1987), feral dogs (Bonnanni et al., 2010a, b; Cafazzo et al., 2010) and companion dogs (Trisko & Smuts, 2015; van der Borg et al., 2015) characterized by unidirectional, usually friendly, submission; displayed by younger/lower ranking animals toward older/higher ranking animals. Subordinates often used muzzle licking together with other gentle affiliative behaviours to initiate friendly contact with dominants. Dominants sometimes ignored such overtures and sometimes even protested with mild growls or snarls, but at other times they responded by play fighting or displaying mutual gentle affiliation. Some of

the dyads in Part 2 had formal relationships that gradually became egalitarian. These patterns suggest that friendly submission functioned to test and strengthen bonds and increase social tolerance over time (Zahavi, 1977).

Egalitarian relationships (i.e., affiliative relationships with no observable imbalance of power) are rare in most species (Hand, 1986). Some studies of wolves (Zimen, 1981; Mech, 1999) and dogs (Bradshaw & Nott, 1995; Bradshaw et al., 2009) have hinted at the existence of egalitarian relationships, but to our knowledge, this is the first study to document that, in a species with linear dominance hierarchies, some dyads lack dominance relationships yet show affiliation. Such egalitarian relationships tended to occur most often in mixed sex dyads. This likely reflects the fact that in free-ranging dogs (Pal et al., 1998; Cafazzo et al., 2010) and wolves (Zimen, 1981; Jenks, 2011), competitive pressures are lower in mixed-sex compared to same-sex dyads. Egalitarian dyads were more likely than formal dyads to engage in mutual play fighting. This could be simply because they tended to be more friendly, but, alternatively, play fighting may sometimes be an alternative to formal dominance interactions as a way to balance cooperative and competitive pressures in relationships.

4.3. *Non-interactive, agonistic and unresolved relationships*

About half of the dyads at daycare never interacted aside from mutual sniffing, despite relatively small group enclosures and ample opportunity (hours spent together did not predict whether or not they interacted). The dog daycare environment was characterized by high numbers of dogs. Temporary groups contained 10–20 dogs at a time, but 80–100 different dogs attended the facility on a regular basis. Group membership changed often throughout the day and new dogs were introduced weekly. In these circumstances, establishing a relationship with every dog and negotiating dominance would require a lot of time, energy and social cognition. The ability to completely ignore a social partner who is in close quarters is probably another alternative strategy that dogs use to avoid conflict, and may have become more adaptive as the social environments of dogs changed from that of their wolf ancestors.

At daycare, male–male dyads were the most likely sex class to have non-interactive relationships, female–female dyads were the most likely to have agonistic relationships, and mixed-sex dyads were the most likely sex class to have egalitarian relationships. In a study of play at a dog park (Bauer & Smuts, 2007), male–male dyads were the least likely to play. These patterns

suggest that competitive pressures are higher for dogs of the same sex even when they are neutered and living with humans. On the other hand, many same sex dyads in the study had friendly and sometimes egalitarian relationships.

In Part 2, non-interactive relationships hardly existed among dogs who lived together, perhaps because it was difficult to ignore another dog in such close quarters. The Safi/Osa relationship abruptly changed to non-interactive after their fight, and two dogs not involved in the fight also stopped interacting with Osa, but these dogs were together for only 7 weeks; over longer time periods, avoiding interaction might have been difficult.

4.4. *Gentle affiliation*

Several studies have examined play fighting in dogs (reviewed in Smuts, 2014; Bradshaw et al., 2015), but, to our knowledge, this is the first quantitative study of gentle affiliative behaviours in dogs and the first evidence of reciprocity in affiliation. That is, over time, the daycare dogs were most likely to direct affiliation to dogs who showed affiliation toward them. In an experimental study, Romero et al. (2014) found that in dogs interacting with a familiar dog partner, an increase in oxytocin was associated with immediate reciprocity of affiliation. This rise in oxytocin appears to facilitate further social interaction, producing a positive feedback loop that is likely an important mechanism underlying social bond formation in dogs and other animals (Romero et al., 2014). Consistent with this view, Palagi et al. (2015) reported that during intraspecific play, dogs with longer associations showed increased rapid mimicry of the play faces and play bows of their partners.

Although gentle affiliation was reciprocal in the group as a whole, in more than a quarter of the dyads gentle affiliation was highly skewed, with one partner, usually the subordinate, giving much more gentle affiliation than the other. Gentle affiliation was often paired with friendly submission in formal dyads and was directed up the hierarchy, but dominants also sometimes offered gentle affiliation to subordinates, and in many egalitarian dyads gentle affiliation was exhibited in both directions. The skewed affiliation in many formal relationships demonstrates a general asymmetry in the motivation to interact; subordinate/younger dogs seem to be more motivated to affiliate with dominant/older dogs than vice versa. The findings that younger/subordinate dogs self handicap more often and display more play signals support this notion (Bauer & Smuts, 2007).

When gentle affiliation occurred in non-submissive contexts, it often resembled courtship behaviours described in intact wolves and dogs (e.g. nose nudges and licks to the ear, genital licks, etc.) (Handelman, 2008). Some dyads, such as Bahati and Tex, engaged in elaborate, prolonged courtship play for years (see Table 5, key to column 7 for details). Courtship-like behaviours appeared to be more common in mixed sex dyads, but they were sometimes exchanged in same-sex dyads as well. To our knowledge, courtship-like behaviours in spayed/neutered dogs have not been reported elsewhere, and this intriguing behaviour deserves further study.

4.5. *Friendship and its benefits*

Dogs in this study showed a striking tendency to form highly differentiated, mutual social bonds, or friendships. Although sex class and presence/absence of dominance affected relationships in various ways, as summarized at the end of Part 1 and in Part 2, friendships occurred in all of the sex class/dominance combinations. Given the prevalence of conspecific friendships in dogs, we hypothesize that dogs receive benefits from having dog friends, both ultimate and proximate.

Our study does not allow us to address the question of ultimate benefits directly since these dogs did not reproduce. However, some of their interactions hint at benefits that might manifest in other contexts. For example, dogs in Part 2 showed other-regarding behaviours when they scared away unfamiliar dogs threatening a friend and when they seemed to inform BS that a housemate was locked out. A quick perusal of YouTube provides many anecdotal examples of dogs who remained close by or even rescued a dog friend who was lost, sick or injured, and, although difficult to assess scientifically, at least some of these examples provide evidence that dog friends help each other in ways that could contribute to fitness. Studies of free-ranging dogs suggest possible benefits of strong conspecific bonds. Bonanni et al. (2010a) showed that younger dogs tended to follow older dogs with whom they had affiliative relationships. Followers could benefit from letting more knowledgeable elders guide them, and leaders could benefit by having followers close by to support them in intergroup encounters (Bonanni et al., 2010b). Pal (2005) reported that some free-ranging females favored a single male dog as a mate, and those males later invested in that female's offspring. Cafazzo et al. (2014) found that males who showed the most affiliation and least aggression toward oestrous females, and who were most frequently approached

by oestrous females, had the highest copulation success. These findings indicate that strong mixed-sex social bonds promote reproductive success. Dog friends could also function as valuable coalition partners. Coalitions have not been studied in detail among domestic dogs, but they have been described in intergroup contests among free-ranging dogs (Bonanni et al., 2010b; Pal, 2014) and within groups of dogs living with humans in a laboratory setting (Scott & Fuller, 1965). In captive wolves, such coalitions also occur within packs and sometimes contribute to dominance reversals that in turn influence reproductive success (Zimen, 1981; Cordoni & Palagi, 2008; Jenks, 2011). We hope researchers will investigate the possibility of similar within-pack coalitions in free-ranging dogs.

Across a wide array of taxa, affiliative behaviour and intraspecific social bonds have been associated with lower heart rates, reduced stress, improved immune function and enhanced longevity (Kaplan et al., 1991; Feh & de Mazières, 1993; Hennessey et al., 2008; Wittig et al., 2008; Silk et al., 2010; Archie et al., 2014). In dogs, the exchange of affiliation with conspecifics triggered the release of oxytocin, a hormone associated with social bonding and positive emotions, and the release of oxytocin may, in turn, increase the motivation to maintain long-term affiliative bonds with particular individuals (Romero et al., 2014). Boissy et al. (2007) proposed that play and affiliation are some of the best behavioural indicators of positive emotions in animals, and Palagi et al. (2015) suggested that during play, rapid mimicry between partners promotes contagion of such positive emotions. Thus, dogs' tendencies to form friendships allow them to transcend differences in sex, age, size and rank to create relaxed, compatible partnerships that likely add to their quality of life.

In sum, we found that companion dogs display considerable complexity in their social interactions with other dogs. Social relationships were differentiated: some dogs ignored each other altogether, whereas others formed strong, mutual social bonds, or friendships. These bonds were often enduring but also subject to change over time. This study contributes to our growing understanding of animal social bonds (Seyfarth & Cheney, 2012) and emphasizes that we can gain considerable insight into animal friendship in our own backyard.

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