

**DOMINANCE, EGALITARIANISM AND FRIENDSHIP
AT A DOG DAYCARE FACILITY**

by

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DEDICATION

To Bailey, Wallaby, and Junebug, my canine best friends. And to my mom for encouraging and inspiring me to follow my heart since the day I was born.

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ABSTRACT

This dissertation examines dominance, play, affiliation and social preferences in a group of 24 domestic dogs that socialize regularly at a dog daycare facility. In Chapter 1, we analyzed the frequencies and directions of aggression, submission, and dominance displays. Submission was the best indicator of dominance relationships and resulted in a significantly linear hierarchy in the group. Age was significantly correlated with dominance rank with older dogs out-ranking younger dogs. Muzzle-licking met most of the criteria for a formal display of submission in dogs, but was not displayed in most relationships. Only 29% of all possible pairs had discernable dominance relationships.

In Chapter 2, we examined the relationship between dominance and friendly behavior (play and affiliation) and identified four relationship styles among the dogs. Twenty-two percent of all possible pairs had known dominance relationships and also exchanged friendly behaviors (formal relationships), 21% of all pairs exchanged friendly behavior but had no discernable dominance relationship (egalitarian relationships), 50% of all pairs were never observed exchanging friendly or agonistic behaviors (non-interactive relationships), and 7% of pairs had known dominance relationships but did not exchange friendly behavior (agonistic

relationships). Friendly behavior was much more frequent than agonistic behavior, and we found a complex association between the two. Egalitarian relationships as well as play and affiliation were more common between males and females than in same-sex pairs. Relationship affinity (an index combining play and affiliation) did not significantly differ in formal versus egalitarian relationships, but the latter were significantly more equitable and playful.

In Chapter 3, we investigated patterns of third-party interventions during play. When dogs intervened during play between two group members, they directed either (1) a *playful* behavior at one of the dogs (the target), (2) an *affiliative* behavior at the target, or rarely, (3) an *aggressive* behavior at the target. Individual rank did not influence individual interventions rates. Rank relationships between interveners, targets and non-targets did not influence playful interventions. Dogs tended to target higher-ranking dogs during affiliative interventions and target lower-ranking dogs during aggressive interventions, but the latter were too infrequent to apply statistical analyses. Dogs tended to target their preferred partners (“friends”) during play more than support them (by targeting their opponents). We proposed that the dogs used interventions during play to promote and protect social relationships more than to practice agonistic intervention strategies.

INTRODUCTION

This dissertation examines social relationships in a group of 24 domestic dogs that socialize regularly at a dog daycare facility. Domestic dogs are an ideal study species for an investigation of social relationships. Recently, dogs have been called the “new chimpanzee” for studies of comparative social cognition (Bloom, 2004; Topal et al, 2009a). The long history of association between dogs and humans and social preferences for cooperative and altruistic human and canine social partners may have led to the co-evolution of prosocial behavior and socio-cognitive complexity in these two species (Nesse, 2007; Scheildt & Shalter, 2003; Topal et al., 2009a). Topal et al. (2009a) proposed that comparative studies of social behavior in humans, chimpanzees, dogs and wolves could contribute to another redefinition of what makes humans unique. Studies of the dog-human relationship are numerous and increasingly popular (review in Topal et al., 2009a), but far less is known about the relationships that dogs form with one another. A more thorough understanding of conspecific relationships among dogs in various settings will provide insight into the effects of domestication and social environment on behavior, facilitate cross-

species comparisons, and allow us to investigate the theory of co-evolution in humans and dogs.

Several comparative studies of social cognition in dogs and humans have revealed complex socio-cognitive abilities that are shared by dogs and humans but absent in wolves and chimpanzees (review in Topal et al., 2009a). For example, dogs and humans, but not chimpanzees or wolves, successfully use various forms of human directional gestures (e.g. pointing, gazing) to locate hidden objects (Hare & Tomasello, 2005). Human infants and pet dogs tend to rely more on human communicative gestures than on other visual and olfactory cues to locate objects revealing the importance of social and imitative learning in these two species (Pongracz et al., 2004; Szetei et al., 2003; Topal et al., 2009b). Like humans, dogs are sensitive to and selectively respond to the attentional state of humans suggesting that dogs may possess a rudimentary theory of mind (Call et al., 2003; Gacsi et al., 2004; Schwab & Huber, 2006; Viryani et al., 2004). In addition to socio-cognitive similarities between dogs and humans, it also appears that the attachments that humans form with their pet dogs and vice versa are analogous in several ways to the attachments that human parents and their children form with one another (review in Topal et al., 2009a).

Not only do dogs show cognitive similarities to humans, humans also display many characteristics of being domesticated: low rates of aggression, high levels of affiliation, cooperation and altruism, and an eagerness to please others (Leach, 2003; Nesse, 2007). Social selection is a subtype of natural selection in which an individual's reproductive fitness is influenced by the social preferences and choices

of others (Nesse, 2007). If being chosen as a social partner provides fitness benefits while social rejection leads to dire effects on fitness, selection will occur for prosocial behaviors and cognitive abilities that allow an individual to predict what others want. Social selection in both conspecific and cross-species relationships may have contributed to the evolution of similar social tendencies in humans and dogs. The prevalence of cooperation, affiliation, egalitarianism, morality, altruism, empathy, social anxiety, spitefulness and social preferences for cooperative and altruistic social partners in humans compared to chimpanzees support the notion that social selection has led to increased prosociality and complex socio-cognitive abilities in humans (Nesse, 2007). Dogs who were friendly and attentive to humans probably had a better chance of being fed and cared for by humans. In return, humans who were friendly and attentive to dogs likely received fitness benefits through warnings of danger, location of prey, and help in the hunt (Nesse, 2007; Scheildt & Shalter, 2003). Recent studies have provided evidence of increased prosocial behavior and socio-cognitive skills in dogs compared to human-reared wolves in their interactions with humans (Topal et al., 2009a). However, relatively little is known about social relationships that dogs form with one another and how they compare to conspecific relationships among wolves. Additional data on the social relationships among dogs (as well as additional data on social relationships among wild wolves) are needed to further assess the role of social selection in the evolution and possible co-evolution of canine and human social behavior.

In addition to theoretical contributions, studies of conspecific social relationships among dogs have substantial applied value. Dog parks and dog

daycare facilities where groups of dogs socialize are increasingly common all across urban America (Bennett, 2006). The primary concern at these parks and daycares is ultimately the safety of the dogs and their human companions (personal observation). A better understanding of social relationships between groups of pet dogs can contribute to more successful supervision and management of groups of dogs by applied dog professionals.

The following three chapters report the results of a year-long study of agonism, affiliation and social preferences among 24 dogs that socialize regularly at a dog daycare facility. With the data presented below, we aim to (1) deepen our understanding of agonism, affiliation and social preferences in dogs, (2) examine the effects of domestication and human influences on dog behavior, (3) foster cross-species comparisons between dogs, wolves and humans, and (4) contribute to the safe and effective management of dogs who congregate at dog parks, dog daycares and other places where dogs congregate.

CHAPTER 1
DOMINANCE AND ITS BEHAVIORAL MEASURES IN
A GROUP OF DOMESTIC DOGS

INTRODUCTION

The concept of dominance as it applies to social relationships in domestic dogs is currently a polemic topic in the field of applied animal behavior. In his best selling book, popular dog trainer and television personality Cesar Millan (2007) summarizes a common, long-held belief of many dog trainers, owners and enthusiasts around the world: “To dogs, there are only two positions in a relationship: leader and follower. Dominant and submissive. It’s either black or white. There is no in-between in their world” (p.118). However, applied animal behaviorists have recently questioned the usefulness of the dominance construct when discussing dog behavior (Bradshaw et al., 2009; Eaton, 2002; O’Heare, 2007; van Kerkhove, 2004). Some dog trainers think that applying dominance theory to dog-human relationships fosters aggression and combative relationships between dogs and their owners (Donaldson, 1996; O’Heare, 2007; Lindsey, 2000), and dominance has therefore become a controversial topic. One particularly contentious dog handling technique is an “alpha roll,” or pinning a dog down on his back, which can trigger aggression in dogs toward humans (Herron et al., 2009; Ryan, 2001). The mere

mention of the word dominance at a professional dog behavior seminar can trigger heated debates about whether dominance exists at all among pet dogs (McConnell, 2002; personal observation). Despite the debate surrounding the concept of dominance as it applies to pet dogs, few quantitative data have been published on the topic (Bradshaw & Nott, 1995; Bradshaw et al., 2009). In order to investigate the extent to which dominance applies to social relationships among neutered pet dogs, we recorded aggressive, dominant, and submissive behaviors among dogs that socialize regularly at a dog daycare facility.

The Concept of Social Dominance

Ethologists traditionally have used the concept of dominance to describe, explain and predict social relationships among animals living in groups (Hinde, 1974). Dominance implies a dyadic relationship that is fundamentally asymmetrical (i.e. A is dominant to B), and therefore, outcomes of competitive/aggressive encounters or behaviors related to the communication of status should be unidirectional (i.e. occur in only one direction in a dyadic relationship). Dominance can be analyzed at the level of the dyadic relationship and also at the level of the group to identify an overall social structure, if present. Pairwise relationships in a group may be transitive (i.e. A is dominant to B, B is dominant to C, and A is dominant to C), or circular (i.e. A is dominant to B, B is dominant to C, but C is dominant to A). If a dominance hierarchy is a useful model for describing relationships within a social group, hierarchies should be linear (i.e. triadic relationships should be transitive, and the number of circular triadic

relationships should be negligible) (Chase, 1974; Hinde, 1974; de Vries, 1995; Rowell, 1974; van Hoof & Wensing 1987).

In an agonistic dominance hierarchy, dominants influence or control the behavior of subordinates by means of intimidation, aggression or fighting ability (de Waal, 1989). Agonistic behaviors include those related to aggression, dominance, and submission. Submissive behavior is often considered a better indicator of dominance relationships than aggressive behavior, because aggression that is ignored and not met with submission may not indicate a mutually acknowledged dominance relationship (Rowell, 1974). As a consequence, measures of submission among mammals often result in higher levels of unidirectionality and linearity than do measures of aggression (Cafazzo et al., 2010; de Waal, 1986; 1989; Rowell, 1974; Schenkel, 1967; van Hoof & Wensing, 1987; Vervaecke et al., 2000). If dominance applies to relationships in a social group, agonistic interactions should occur in multiple relationships (Hinde 1974; van Hoof & Wensing, 1987). The coverage of dominance relationships can be assessed by calculating the proportion of unidirectional (1-way), bidirectional (2-way), tied and unknown relationships in a group (de Vries, 1995; van Hoof & Wensing 1987).

Dominance hierarchies range from despotic to tolerant. Tolerant dominance styles have also been described in literature as being "more egalitarian," meaning that dominants tolerate more counter-aggression from subordinates and allow them to win more competitive contests (Cooper & Bernstein, 2008; de Wall & Luttrell, 1985; Lehman & Bryson, 2008; Van Schaik, 1989; Vehrencamp, 1983). However, following Cooper & Bernstein (2008) we reserve the term *egalitarian* to refer to relationships in which there is no discernable dominance relationship based on agonistic behaviors or competitive

outcomes. In more despotic hierarchies, dominance relationships are more rigid, agonistic interactions are more unidirectional and linear, and aggression is infrequent but intense. In more tolerant hierarchies, bidirectional agonistic relationships and circular triads are more common, aggression is more frequent but less intense, and group members have a greater tendency to affiliate and reconcile after conflicts. Dominants are expected to be more tolerant and allow subordinates to win competitive contests more often when they benefit from the help and cooperation of subordinates, the cost of dispersal to another group is relatively low, and resources are more evenly distributed (Cooper & Bernstein, 2008; de Wall & Luttrell, 1985; Lehman & Bryson, 2008; Van Schaik, 1989; Vehrencamp, 1983).

The outcomes of competitive encounters can often be resource-specific and dependent on fluctuating motivational factors (e.g. satiety, fatigue) and situational contexts (e.g. the presence of potential allies), and therefore various measures of competitive dominance are often inconsistent (Bygott, 1979; de Waal, 1982; 1986; 1989; de Waal & Luttrell, 1985; Hand 1986; Rowell, 1966; Strum, 1982; Syme, 1974; van Hoof & Wensing, 1987). Despite inconsistencies in competitive dominance, in some species agonistic displays are consistently shown by only one member of a dyad and not by the other in several contexts (de Waal, & Luttrell, 1985; Flack & de Waal, 2007; Lu et al., 2008; Preuschoft, et al. 1995; Vervaeke et al., 2000). De Waal (1986) introduced the concept of formal dominance to account for the discrepancies between such unidirectional behaviors and inconsistent competitive outcomes. He defines formal dominance as “unequivocal communication of status” (de Waal, 1986, p. 459). In a formalized dominance relationship dominants may occasionally allow subordinates to

assert themselves in competitive encounters, provided they consistently express their subordinate status. Formal dominance is likely to be present in more despotic societies that are characterized by high levels of competition as well as social bonding among group members (de Waal, 1986). Discussions of formal dominance have emphasized the motivation of the subordinate to maintain friendly relations with the dominant in order to increase tolerance and sharing (de Waal, 1986; 1989; East et al., 1993; Lu et al., 2008; Preuschoft, 1999; Vervaeke et al., 2000).

To qualify as a formal indicator of status, a behavior should 1) be unidirectional, 2) be stable across different social contexts, 3) be expressed by different individuals and 4) coincide with agonistic dominance relationships (Table 1-1) (de Waal, 1986; 1989; de Waal & Luttrell, 1985; Vervaecke et al, 2000). Preuschoft (1999) makes a distinction between "(a) ritualized displays that are symptoms of acute emotional states (e.g., fear) and (b) formal status indicators that are symbols for a long-term social relationship (e.g., subordination)" (p. 91). For example, teeth-baring displays in rhesus, long-tailed and pig-tailed macaques are performed spontaneously by subordinates to dominants in contexts of non-hostile proximity (de Waal, & Luttrell, 1985; Flack & de Waal, 2007; Preuschoft, et al. 1995). By contrast, teeth-baring in chimpanzees is a typical emotional response to aggression. Therefore teeth-baring is considered to be a formal status display for macaques, but a ritualized display of fear for chimpanzees (Preuschoft 1999). Pant-grunting, however, is typically displayed by subordinate chimpanzees who approach and greet dominants in an affiliative context and is thus considered an indicator of formal status in this species (de Waal, 1986; 1996; Goodall, 1986; Takhata, 1990).

Chimpanzees do not pant grunt to unfamiliar conspecifics or during interactions with baboons, although they do use other communicative displays (e.g. play face) and occasionally seem to fear them (de Waal, 1986). Chimpanzees and rhesus macaques stop using pant-grunting or teeth-baring in periods of rank disturbances, and the signals reappear in dyads when the dominance relationship is stabilized (de Waal, 1982; 1986; 1989; de Waal & Luttrell, 1985). These observations led Preuschoft (1999) to propose the following additional criteria that may be used to classify a behavior as formal submission rather than fear (see above for the first 4 criteria): 5) displayed only to conspecifics (not predators), 6) displayed only to group members (not strangers), 7) displayed only in consolidated relationships (not during rank disturbances), 8) performed spontaneously (not induced by aggression), and 9) specialized use in non-hostile interactions (an additional display is used in hostile interactions).

Dominance in Wolves

Phylogenetic studies support an origin of the domestic dog from one ancestor, the wolf (*Canis lupus*) (Honeycutt, 2010; Pang et al., 2009; Vila et al, 1997; 1999). Wolf packs are traditionally described as having age-graded, linear agonistic hierarchies within each sex, with males dominant to females within each age class (Figure 1-1; Derix, 1994; Mech, 1970; Packard, 2003; Schenkel, 1947; 1967; van Hoof & Wensing, 1987; Zimen 1978; 1982). Van Hoof and Wensing (1987) calculated the linearity and directional consistency of several behaviors in a captive wolf pack and reported a linear agonistic hierarchy based on submissive, aggressive and dominant behaviors. Consistent with other reports of dominance in wolves (Mech, 1970; Lockwood, 1979; Schenkel, 1947; 1967;

Zimen 1978), submissive behaviors resulted in the highest levels of linearity and directional consistency (van Hoof & Wensing, 1987).

However, the majority of this dominance research in wolves was conducted on captive packs made up of related or unrelated individuals that were unable to disperse as they might in the wild (Derix et al., 1993; Lockwood, 1979; van Hoof & Wensing, 1987; Zimen 1976, 1978). The social environment in captive packs probably differs substantially from those in wild wolf packs. Mech (1999) argues that wild wolf packs are best described as families characterized by the division of labor. In the wild, wolf packs typically comprise a mated breeding pair and their offspring from one or more previous years (Mech, 1999; Packard, 2003; Vonholdt et al., 2008). Pups beg for food from their parents and older siblings, who assist in the care of the pups. Older siblings do not breed and defer to the breeding male and female who ultimately care for the entire family by defending the pack's territory and leading the pack's activities, movements and hunts (Mech, 1999; Peterson et al., 2002). In this type of nuclear family social structure, one might predict dominance hierarchies to be less linear than in captive packs of unrelated individuals (Figure 1-1) (Packard, 2003).

Mech's argument for relaxed dominance relationships in wild wolves was based mainly on his observations of a single wild wolf pack in Ellesmere Island, Canada. This pack was small compared to many packs in Yellowstone National Park, which are reported to vary in size from 5 to 37 wolves and are characterized by a wide range of familial pack structures (Vonholdt et al., 2008). The linearity and unidirectionality of dominance relationships have not yet been studied in Yellowstone wolves or in any wild wolf packs. However, observers agree that packs are led by a breeding male and female

who dominate all other individuals and initiate pack activities and movements (Peterson et al., 2002; Scott & Creel, 2004; Vonholdt et al., 2008). Peterson et al (2002), identified dominance relationships in 3 packs of Yellowstone wolves from dominance postures and submissive displays, and reported that “[d]ominant wolves were never observed exhibiting submission to other wolves” (p. 1407), suggesting that submission is unidirectional in wild wolf packs as well as captive ones.

Several behaviors have been proposed as formal indicators of rank in wolves. Schenkel (1967) describes two main forms of unidirectional submissive displays in wolves and dogs: active submission occurs when the subordinate wolf lowers her body and head and reaches up to lick the muzzle of the dominant wolf, and passive submission occurs when the subordinate wolf rolls over on her back and exposes her underside for the dominant’s inspection. These submissive behaviors are thought to be ritualized cub behaviors; active submission is derived from food begging behavior, and passive submission is derived from the posture that cubs assume when cleaned by their mothers (Schenkel, 1967). Observers have also described postures that indicate relative status in wolves. Low-posture is described as crouching with the legs bent, head kept low, ears back, tail down or tucked between the legs. High-posture is described as head and tail erect, ears forward with back and legs straight and stiff (Schenkel, 1967; Lockwood, 1979; van Hoof & Wensing, 1987). Van Hoof and Wensing (1987) report that active and passive submission as well as high and low posture show high levels of unidirectionality and coverage, remain unidirectional in several contexts, coincide with agonistic rank orders, and can therefore be considered as formal status displays in wolves. Preuschoft’s (1999) additional criteria for formal status displays have not been directly investigated in

wolves. However, Zimen (1978) reports that wolves do not display active/passive submission to wolves from other groups.

Schenkel (1967) defines submission as “the effort of the inferior to attain friendly or harmonic social integration” (p. 319). He also described another type of submissive display in wolves as “obstrusive submission” later described as “obnoxious submission” by Goodman et al. (1998). Schenkel (1967) gives the following description of the behavioral complex:

In obnoxious submission, wolves use behavior which is ostensibly submissive, but they do it so vigorously and persistently that they may actually displace a higher ranking animal. Sometimes the submissive wolf actually pursues the higher ranking wolf as it quickly leaves to avoid being tripped, poked, and effusively licked. The higher ranking wolf typically maintains confident expressive behaviors including growling, agonistic puckers, high tail carriage, locomotion characterized by stepping higher than usual, muzzle bites, etc. but also tends to leave the subordinate wolf rapidly. (p. 34)

Obnoxious submission may be a good example of dominant wolves allowing subordinates to assert themselves (e.g. by displacing dominants). Despite the obnoxious or pushy behavior, the actor consistently communicates her subordinate status by crouching and muzzle licking.

Dominance in Domestic Dogs

For tens of thousands of years, domestic dogs have been integrated into a wide range of human societies. Modern dogs live as hunters, herders, retrievers, draft animals, protectors, fighters, racers, service animals and human companions, just to name a few of their roles in human societies (Serpell, 1995). They live in urban, suburban, or rural environments with varying amounts of human interaction. Some dogs interact with few

or no other dogs, while others often live in large conspecific social groups (e.g. beagles, huskies). Some have a closed social group of other dogs that they live with, and some meet new dogs on a regular basis at dog parks, dog daycares and boarding kennels (personal observation). To further complicate the modern social environments of dogs, humans have significant influence on their behaviors, social partners and reproductive success, as well as access to food, shelter and medical attention. Given the wide range of social environments in which dogs live and the ubiquitous human influence on dogs' behavior for thousands of generations and in present environments, it seems likely that dominance relationships among domestic dogs differ from those of wolves. It is also very likely that conspecific dominance relationships vary in different social environments (e.g. feral dogs, working dogs, pet dogs living in the same household, groups of neutered pet dogs at dog daycares, etc).

Pal et al. (1998) recorded agonistic behavior among 12 free-ranging dogs in suburban India and reported linear dominance hierarchies in 2 groups of dogs based on the directions of aggression and submission, but the authors did not conduct statistical analyses of linearity, directional consistency or coverage. Cafazzo et al. (2010) measured the frequency and direction of aggressive, dominant, and submissive behaviors among a group of 27 free-ranging dogs living near suburban Rome and reported significantly linear dominance hierarchies based on all three types of agonistic behaviors. Submissive behavior showed the highest levels of linearity and directional consistency, rank was significantly correlated with age, older dogs outranked younger dogs, and males tended to out-rank females within age classes (Cafazzo et al, 2010). Cafazzo et al., (2010) report that "submissive-affiliative" behavior, akin to active submission described above for

wolves, fulfilled the criteria of formal submissive signals in their group of feral dogs. This behavior showed perfect directional consistency, did not vary in different social contexts (e.g. in the presence of food, receptive females, or in the absence of competition), and was predictive of agonistic rank orders. The coverage of submissive affiliative behavior (32% 1-way relationships) was lower than the coverage of total submissive behavior (72% 1-way relationships), so the authors suggest that measures of agonistic dominance based on total submissive behavior are more useful than submissive-affiliative behavior alone for ordering dogs in a consistent rank order. (Cafazzo et al., 2010). The authors did not directly address the relationship of the submissive display to fear, but the behavior was reported to commonly occur spontaneously in affiliative greetings among the dogs, and therefore does not seem likely to be a ritualized display of fear. Based on the studies described above, dominance does seem to be applicable to feral dogs (but see Bradshaw et al., 2009; van Kerkhove, 2004). However, the few studies of dominance in pet dogs living with humans have reported inconsistent results.

Bradshaw & Nott (1995) studied dominance interactions in groups of related female dogs and also in their litters. Hierarchies were constructed using the ratio of displacements in pairs of adult females and the ratio of 'dominant' and offensive play behaviors in pairs of puppies. The authors reported "partially transitive" hierarchies in the groups based on asymmetric relationships; statistical significance was reported for relationship asymmetry using chi-square goodness of fit tests, but linearity was not measured quantitatively (Bradshaw & Nott, 1995). Hierarchies in the groups of adult females were related to age with older females being more dominant, but the oldest individual did not always hold the "alpha" position (Bradshaw & Nott, 1995). Hierarchies

based on play in the litters were inconsistent when measured at different stages of development and did not coincide with competitive contests (Bradshaw & Nott, 1995). Bradshaw et al. (2009) calculated David's scores (Gammell et al., 2003) based on a combination of aggressive, dominant, and submissive behavior for 19 neutered male dogs living in a semi-permanent group at a re-homing shelter and reported some asymmetrical relationships, but no linear hierarchy. However, no statistical tests of linearity, directional consistency, or coverage were conducted.

In their study of role reversals during play in neutered pet dogs, Bauer and Smuts (2007) determined dyadic dominance relationships among some of the dogs based on consistently asymmetric postures (i.e. high-posture and low-posture) outside of the play context. Some dyads were said to have "relaxed" relationships with few status displays, and dominance relationships were unable to be determined in these dyads. The authors did not measure linearity, unidirectionality, or coverage of dominance relationships. However, mounts, muzzle bites, and muzzle licks were found to be unidirectional during play, a social context in which role reversals commonly occur in aggressive play behaviors, (i.e. attacks and pursuits). Bauer and Smuts (2007) proposed that these behaviors could be formal status signals that remain stable across social contexts. Other criteria for formal status signals have not been investigated in neutered pet dogs.

Studies of dominance relationships in domestic dogs suggest that the concepts of agonistic dominance hierarchies and formal submission apply to feral, sexually intact dogs. However, the applicability of agonistic and formal dominance to social relationships among neutered pet dogs remains unclear. We recorded the frequency and direction of agonistic behaviors among dogs that socialize regularly at a dog daycare

facility to address the following questions: 1) Are agonistic behaviors unidirectional and linear, and do they show high coverage? 2) How are individual factors such as age, sex, and size related to dominance relationships? 3) Do any agonistic behaviors meet the criteria for formal status signals?

METHODS

Subjects & Observations

The study was conducted at a dog daycare facility in Evanston, IL. Approximately 100 different neutered pet dogs attended the facility on a regular basis, from 1 to 5 days per week, with approximately 40 dogs present on any given day, Monday through Friday, 7am-7pm. Dogs were housed in 3 separate groups of approximately 10-20 dogs in outdoor or indoor enclosures approximately 1000-2000 square feet in size. Dogs arrived and left the facility at various times throughout the day, group membership fluctuated often, and new dogs were introduced to the environment on a regular basis. Behavioral observations were recorded in one of the 3 groups several days per week on 90 days distributed over the course of one year for a total of 224.4 hours of observations. We collected behavioral data on a total of 81 dogs, and 24 dogs were chosen for final analysis because they were in the group with each of the other 23 dogs for the longest amount of observation time. This group was made up of 12 males and 12 females of various pure and mixed breeds, ranging from 7 months to 11 years of age and 20 to 101 pounds (Table 1-2). We recorded all aggressive, dominant, and submissive behaviors among the dogs in the focal group using the *ad libitum* method for all-occurrence sampling (Altmann, 1974). Aggressive behaviors included *threats* and *conflicts*, dominant behaviors included *muzzle*

bites, high-posture, mounts, and chin-overs. Submissive behaviors included *muzzle licks, low-posture, passive submission, and retreat*. Detailed descriptions of all behaviors can be found in Table 1-3. Active submission and obnoxious submission, as described in wolves, are behavior complexes that combine muzzle licking and a low-posture. If a dog displayed the full complex of active or obnoxious submission the behavior and the posture were recorded separately (e.g. active submission was coded as a muzzle lick and a low-posture). We considered behaviors and postures separately because posture was often difficult to determine in our study dogs due to morphological variation (e.g. floppy ears, a cropped tail, a bushy coat of fur, large discrepancies in size).

We distinguished *passive submission* from *voluntary downs* during play (Bauer & Smuts, 2007; Ward et al., 2008) as follows. For the behavior to be recorded as passive submission during play, the actor had to pause and remain still for at least one 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 and play did not pause while the recipient sniffed the actor. Bauer and Smuts (2007) found that subordinates perform a significantly higher proportion of voluntary downs (and other self-handicapping behaviors) than dominants, but voluntary downs can sometimes be bidirectional during play in adults (Bauer & Smuts, 2007) and in young littermates (Ward et al., 2008).

It is important to note that human supervisors at the dog daycare facility had a significant influence on the dogs' social interactions. Most threats were immediately followed by 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 including physical contact was immediately interrupted with verbal or physical means (e.g. physically restraining one or both dogs), and the dogs involved were separated from the other group members and confined to a crate for 3-5 minutes immediately following a conflict. Pairs of dogs that had several conflicts, as well as those that human supervisors thought might be likely to get into conflicts, were housed in separate groups. Dogs that approached in a high-posture or mounted another dog were interrupted. If play-fighting behavior was thought to be too rough, if several dogs were involved in a single interaction, and to prevent threats and conflicts, dogs were often called over by human supervisors and were rewarded with a piece of kibble for halting their social interactions. Dogs that initiated several conflicts or caused an injury more severe than a few small scratches were excluded from the facility. In summary, relatively aggressive dogs were not permitted in the group, aggressive behavior was punished, and the absence of aggressive behavior was reinforced. Therefore, the frequencies of threats, retreats, conflicts, high-posture and mounts among the dogs were undoubtedly reduced by human intervention.

Statistical Analyses

In order to investigate agonistic dominance relationships among the dogs, the frequencies of aggressive, dominant, and submissive dyadic interactions were used to construct 3 matrices with actors on the vertical axis and recipients on the horizontal axis. For analyses, all matrices of submissive behavior were transposed, moving recipients to the vertical axis and actors to the horizontal axis; this allowed us to compare aggression

or dominance emitted with submission received. All matrix analyses were performed using MatMan 1.1 (Noldus Information Technology). For each behavioral matrix, linearity of dominance relationships were assessed using de Vries (1995) improved version of Landau's index of linearity (Landau, 1951), which corrects for unknown and tied relationships (h'); 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 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 behavior was performed in the direction of the higher frequency within each dyad (H) minus the total number of times the behavior occurred in the direction of the lower frequency within each dyad (L), divided by the total number of times the behavior was performed by all individuals: $DCI = (H - L)/(H + L)$ (van Hoof & Wensing, 1987). To assess the coverage of a behavioral category, we calculated the number and proportion of unknown relationships (dyads in which the behaviors did not occur in either direction), 1-way relationships (only one dog in the dyad performed the behaviors), 2-way relationships (both dogs in the dyad performed the behaviors), and tied relationships (both dogs perform the behaviors the same number of times).

Each dyad was observed in the study group together for a different number of hours. To assess the effects of time observed together on the presence of a unidirectional dominance relationship, we constructed a matrix of dyadic observation hours and a matrix of known dominance relationships (1-way relationship = 1, unknown dominance

relationship = 0) and performed a rowwise matrix correlation between these two matrices.

In order to investigate the relationship between dominance rank and age (in months), and between rank and size (in pounds), we calculated Kendall *tau* correlations. To compare dominance relationships in same-sex relationships with those between the sexes, we constructed a matrix of “sameness of sex” (1 = same-sex, 0 = cross-sex) and compared them to the matrices of aggression, dominance, submission, and the presence or absence of a known dominance relationship using rowwise matrix correlations. Rowwise matrix correlation methods use row totals to control for individual differences in behavior; K_r test statistics and Kendall’s $tau_{rw,av}$ are presented (de Vries, 1993; Hemelrijk, 1990).

In order to investigate formal submission in dogs, separate matrices were constructed of the frequencies of each agonistic behavior. Directional consistency (DCI), and the number and proportion of 1-way relationships were calculated for each agonistic behavior matrix. As an additional measure of coverage, we calculated the percentage of dogs in the study group that performed each behavior at least once. In order to determine whether the behavior was multi-contextual, we noted whether or not the behavior was observed in both playful and non-playful interactions. Behaviors were classified as playful if both dogs had relaxed, fluid body postures and facial expressions, exaggerated bouncy movements, and engaged in mutual play-fighting behaviors (e.g. play bite, jump on, chase) (Bauer & Smuts, 2007; Ward et al., 2008; 2009). If mutual play occurred within one minute before or after the behavior was displayed, the behavior was classified as occurring in a playful context. In order to assess the correlations of each behavior with

agonistic relationships, we performed rowwise matrix correlations to determine if the matrix structure of each submissive and dominant behavior corresponded to the matrix structure of aggressive behaviors. In order to determine whether a behavior indicated subordination rather than fear, we calculated the percentage of times that each behavior was immediately preceded by aggression from the recipient. Aggression by definition cannot be a formal status display, but threats and conflicts are included in our analysis in order to examine the intensity of aggression and the relationship between the rank orders based on aggression and submission. Aggression was never classified as playful whether or not it occurred within one minute of play behaviors. The number of threats and conflicts triggered by aggression refers to instances of counter aggression.

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

RESULTS

Agonistic Dominance

The matrix of total submission (Table 1-4) ($N = 609$) resulted in a significantly linear hierarchy ($h' = 0.258$, $P = 0.014$), showed the highest level of directional consistency (DCI = 0.971), and the highest level of coverage (29.4% 1-way relationships). The matrix of total aggression ($N = 160$) also resulted in significant linearity ($h' = 0.236$, $P = 0.036$), a fairly high level of directional consistency (DCI = 0.825), and a level of coverage similar to that of total submission (25.7% 1-way relationships). The matrix of total dominance ($N = 219$) did not result in significant linearity ($h' = 0.135$, $P = 0.770$) and resulted in the lowest levels of directional

consistency (DCI = 0.790) and coverage (9.8% 1-way relationships) (Table 1-5). The presence of a known dominance relationship was not significantly correlated with dyadic observation hours ($K_r = 414$ $P = 0.210$).

Age, Size, Sex & Individual Differences

The matrix based on total submission was significantly linear, and showed the highest level of linearity, directional consistency, and coverage of the three types of agonistic behavior (Table 1-5). Therefore, we chose this matrix to apply the procedure proposed by de Vries (1998) to reorder the dogs in the dominance order most consistent with a linear hierarchy (Table 1-4) and used this rank order to correlate rank with age and size.

Dominance rank was not correlated with weight ($\tau = 0.029$, $P = 0.862$).

Dominance rank was significantly and positively correlated with age ($\tau = 0.514$, $P < 0.001$). The rank order did not perfectly coincide with age (Table 1-2), but the older dog was dominant in 74 (91%) of the 81 1-way relationships. In six of the seven relationships in which the younger dog was dominant, the dyad was within one year of age. Further, age was estimated for 2 of the 3 younger/dominant dogs because they were adopted as young adult dogs. In the one case of a younger/dominant dog in a dyad with an age difference greater than one year, the dyad was 18 months apart and had the largest size difference in the group; the younger dominant dog was a Newfoundland (101 lbs.), and the older submissive dog was a pug (20 lbs.).

Aggression was significantly more frequent in same-sex than in cross-sex dyads ($K_r = 187$ $P = 0.039$). The frequency of submission and dominance displays did not

significantly differ within or between the sexes (submission: $K_r = 80$ $P = 0.392$; dominance: $K_r = 59$, $P = 0.248$). Dominance relationships based on 1-way submission were more frequent in same-sex than in cross-sex dyads ($K_r = 264$ $P = 0.022$).

There was large variation in the number of known dominance relationships that each dog formed; one dog (fd) had zero 1-way relationships; nine dogs had between one and four 1-way relationships; ten dogs had between five and ten 1-way relationships and five dogs had between 11 and 15 1-way relationships (Table 1-2).

Formal Dominance

Muzzle licks did not occur in a low proportion of relationships (18%), but when they did occur, they met the criteria for a formal display of submission. Muzzle licks ($N = 364$) were highly unidirectional ($DCI = 0.961$) and remained stable in both playful (23%) and non-playful contexts (77%). The muzzle lick rank order was significantly correlated with the agonistic rank order ($tau = 0.77$, $P < 0.0001$). The matrix of muzzle licks received was significantly correlated with the matrix of aggression emitted ($tau_{rw,av} = 0.31$, $P = 0.001$), but muzzle licks were never induced by aggression. Muzzle licks occurred more often than any other agonistic behavior and were performed in the highest proportion of relationships and by the highest proportion of dogs (58%). Bi-directional muzzle-licking occurred in 4 (1%) pairs. It is noteworthy that these 4 pairs of dogs also had particularly close and friendly relationships, exchanging other affiliative and playful behaviors at relatively high rates.

Low-posture, passive submission, and retreats were perfectly unidirectional, but showed lower coverage than muzzle licks and were sometimes induced by aggression

(see Table 1-8 for all results). Muzzle bites and high-posture resulted in very low coverage but met all of the other criteria for a formal status signal (i.e. unidirectional, multi-contextual, related to agonistic relationships, not induced by aggression). Mounts were perfectly unidirectional and showed relatively high coverage, but mounts and chin-overs were not correlated with aggression or with agonistic relationships and therefore do not seem to be related to status communication in dogs. With the exception of aggressive behaviors and retreats, all behaviors were observed in both playful and non-playful contexts. Threats (N = 142) showed high directional consistency (DCI = 0.905), relatively high coverage (26.8%), and produced a rank order that was correlated with the agonistic rank order based on submission ($\tau = 0.49$, $P = 0.0009$). Conflicts (N = 19) showed low directional consistency (DCI = 0.368) but did correlate with agonistic rank order ($\tau = 0.46$, $P < 0.0019$). Counter aggression was rare for threats (2%) but common for conflicts; 13 conflicts were initiated, and 6 (46%) of these conflicts involved counter aggression. In general aggressive behaviors were low intensity; the majority of aggressive behavior was threats (88%) and the conflicts never resulted in injury.

DISCUSSION

To our knowledge, this is the first systematic quantitative study of the linearity, directional consistency and coverage of dominance relationships in a large group of pet dogs living closely with humans. We found significantly linear hierarchies based on submissive and aggressive behaviors. Age was a more important factor than sex or size affecting dominance relationships with older dogs out-ranking younger dogs. Muzzle-licking appears to be a display of formal submission when it occurs, but coverage of

muzzle-licking and other agonistic behaviors was low. Most dogs had some known dominance relationships based on 1-way submission, but dominance relationships were discernable in less than a third of all possible pairs. The results of this study suggest that agonistic and formal dominance can be appropriately used to describe some, but not all, social relationships in groups of pet dogs. The fact that a linear dominance hierarchy was present in the study group despite the fact that humans rewarded tolerance and sharing, punished aggression, and excluded more aggressive dogs from the social environment suggests that dominance is a robust component of dog-dog relationships.

Agonistic Dominance

Submissive behavior was the most common form of agonistic behavior, was highly unidirectional and resulted in a significantly linear hierarchy. Aggressive behavior also resulted in a linear hierarchy and showed fairly high directional consistency, but was not as unidirectional as submissive behavior. Threats were much more frequent and unidirectional than conflicts. Dominance related behavior resulted in the lowest directional consistency and was not significantly linear, and this was probably influenced by the low frequency of dominance displays among the dogs. Further, mounts and chin-overs were uncorrelated with the distribution of aggression and the agonistic rank order, and contributed to the high number of circular triangles and low directional consistency in dominance related behaviors. Muzzle bites and high-posture were significantly correlated with aggression and the agonistic rank order and were perfectly unidirectional. These behaviors resulted in very low coverage in this study, but they do seem to be related to the communication of status. As in other studies (Cafazzo et al., 2010; de Waal,

1982; Van Hoof & Wensing, 1987; Vervaecke et al., 2000), we found that submissive behaviors, rather than aggressive or dominance related behaviors, most clearly indicated dominance relationships among the dogs and rank order within the group.

Our results are in accordance with similar studies of unidirectionality and linearity in captive wolves and feral dogs (Cafazzo et al., 2010; Van Hoof & Wensing, 1987) but conflict with the results of recent study of dominance among pet dogs conducted by Bradshaw et al. (2009). They reported no linear hierarchy among their group of neutered male shelter dogs, but the behaviors they measured and their methods of analysis differ from those in this study and other studies of wolves and dogs (Cafazzo et al., 2010; Van Hoof & Wensing, 1987). Bradshaw et al. (2009) calculated David's scores (Gammell et al., 2003) which measured weighted proportion of wins and losses in agonistic encounters based on a combination of aggressive, dominant, and submissive behaviors (Bradshaw et al., 2009). Their list of submissive behaviors included "crouch, avoid, displacement, lick/yawn, [and] run away" (p. 140). A detailed description of the behavior "lick/yawn" is not included in the article, but this most likely refers to a dog licking its own lips and/or yawning, behaviors that have been described as calming or appeasement signals to other dogs (Rugaas, 1997). Muzzle licking, active submission, and passive submission did not appear to be included in the submissive behaviors measured by Bradshaw et al. (2009), but these behaviors made up the majority of the submissive behavior that we observed in the study group. In the Bradshaw et al. (2009) study, dogs that had fewer than 5 agonistic interactions were not included in the final analysis, the number of observation hours was not reported, no tests of linearity or directional consistency were conducted, and the behavioral matrices and ages of the dogs were not given. It may be that a linear hierarchy

was present in the group of dogs studied by Bradshaw et al. (2009) but was not revealed by their methods. Also, it seems likely that dominance relationships are highly dependent on the specific social environment. Hierarchies could be linear in some groups of dogs but not others.

In the present study group, only about one third (29%) of all possible dyads had discernable dominance relationships (Table 1-5). This is not because bidirectional relationships were common (bidirectional submission occurred in only 1% of dyads; Table 1-4), but rather because many dyads (69%) were never observed exchanging agonistic behaviors. In some of these unknown dominance relationships, the dyads engaged in mutual social play or other affiliative behaviors but did not display rank-related behaviors, and other dyads were never observed interacting (Ch. 2). Dominance does not seem to be a concept relevant to dyads that affiliated but did not display agonistic behavior. For the dyads that avoided each other, we suggest three possibilities: (1) agonistic interactions occurred outside of the observations and the subordinate avoided the dominant from that point on, (2) both dogs avoided each other because neither wanted to submit or behave aggressively, or (3) dominance was not applicable to the relationship. The ability to ignore other dogs can be effective in preventing conflicts (personal observations), and is a canine social skill that is welcomed by human supervisors for dogs in the dog daycare environment.

Coverage of dominance relationships was higher in captive wolves (98% in 235 observation hours; Van Hoof & Wensing, 1987) and feral dogs (72% in 630 observation hours; Cafazzo et al., 2010) than in our group of neutered pet dogs (29% in 224 observation hours). The most obvious explanation for the lower coverage is the degree of

human influence on behavior. Our study dogs were all neutered, completely eliminating mating competition. Pieces of kibble were occasionally evenly distributed to the dogs, and larger meals were given outside of the group setting, eliminating most of the competition for food. Humans evaluated the dogs' behavior prior to including them in the larger social groups. Only dogs that displayed very little aggressive behavior were allowed to attend the facility, and dogs that displayed injurious or frequent aggression were not allowed to return. As discussed in the methods section, most aggression was immediately interrupted by humans, and in some cases, dogs were actually reinforced with food rewards for refraining from displaying aggressive behaviors. Human supervisors punished aggression (i.e. verbal correction or separation from the group), and reinforced non-aggression. For example, if a dog looked like she was about to initiate submissive contact with a dog that tended to be intolerant of submission, or an active young dog accidentally bumped into an older dog that was resting, the human supervisor would interrupt and redirect the dogs by calling one or both of the dogs over to sit for a piece of kibble, thereby preventing an agonistic interaction and potentially reducing the likelihood of agonistic behaviors in the future. Bailey, for example, the highest-ranking dog in the agonistic hierarchy, is typically intolerant and responds with a threat if another dog bumps into her. She has been given a piece of kibble when this happened so often that she has begun to look immediately to a human supervisor and trot over for a treat after getting bumped, rather than threatening the guilty party. In summary, human influence most certainly reduced the coverage of dominance relationships among our study dogs suggesting that dominance relationships would be more prevalent among dogs in the absence of human intervention.

The degree of social flux for the Italian feral dogs and for the dogs in the current study may have contributed the lower coverage of dominance relationships than found in wolves. The captive wolf pack studied by van Hoof and Wensing (1987) contained 17 wolves consisting of a mated pair and selectively chosen offspring of several generations that spent all of their time together. Animals were not given the opportunity to disperse, but the pack's familial structure was within the range of pack structures observed in the wild. In Cafazzo et al.'s (2010) study of feral dogs, a total population of 100 dogs fed from the same feeding site, and smaller distinct groups of dogs were apparent that socialized frequently within the larger population (Bonanni et al., 2010), but temporary group membership fluctuated regularly (Cafazzo et al., 2010). The social structure in our study was somewhat similar to the Italian feral dogs. Eighty-one total dogs were observed in temporary daily groups of 10-20 dogs. The 24 dogs chosen for analysis were those that attended the facility most frequently and spent the most time socializing together, representing a core group; the obvious difference is that humans determined group membership. We did not find that dogs with known dominance relationships spent significantly more time in the study group together, but the constant fluctuation in group membership at the daycare facility undoubtedly influence the relationships that the dogs formed with one another. The feral dogs and study dogs had a much larger number of possible social partners than did the wolves in the captive pack. As the number of possible individuals increases, the possible dyads increase exponentially. Establishing and maintaining a dominance relationship with every other individual that a dog encountered would require significant amounts of time and energy. If two dogs encounter one another infrequently and there is little need for them to directly compete for

resources, it may be advantageous for that dyad to avoid social interactions and peacefully co-exist without establishing a dominance relationship (see Chapter 2 for further consideration of pairs of dogs without known dominance relationships).

Finally, the tendency of dogs to engage in agonistic interactions with one another may have been reduced by thousands of generations in which they have associated closely with humans. Since dogs split from wolves an estimated 40,000-135,000 years ago (Schleidt & Shalter, 2003) their group structures have become more variable and fluid, and cooperative hunting and communal pup care have become less important for their reproductive success (Serpell, 1995). For dogs as opposed to wolves, it is likely that being friendly toward humans resulted in greater fitness benefits than establishing dominance relationships with conspecifics. This general pattern is clearly true for some dogs more than others. In the Italian feral groups for example, conspecific relationships are probably much more important for fitness than for pet dogs living in human households. Over the course of domestication there was probably genetic transfer between dogs living closely with humans and those who more or less bred on their own (Serpell, 1995). Even today, pet dogs escape their human-opposed confines and mate on their own accord. It is likely that both dog-human relationships and dog-dog relationships have had fitness consequences for dogs (Smuts, 2010). In general, the range of variation between the social environments of dogs is much greater than for wolves as a result of their associations with humans. Perhaps what has been selected for in dogs since their split with wolves is *social flexibility*, or the capacity to develop several different types of social relationships with different individuals depending on the particular social environment. However, the data on dominance in captive and wild wolves (Van Hoof &

Wensing, 1987; Mech, 1999; Sands & Creel, 2004), the large variation observed in pack size and composition (Vonholdt et al., 2008), and their wide range of feeding habits based on the availability of prey (Meriggi et al., 1996) suggest that wolves might be just as socially flexible as dogs when it comes to conspecific relationships, and the lower coverage of dominance relationships in this study versus studies of wolves may be due to different social environments rather than genetic differences between these two species. More studies of dominance in wild wolf packs are necessary to assess the behavioral changes that have taken place in dogs over the course of domestication.

Age, Sex, Size and Individual Variation

Consistent with other studies of wolves and dogs (Bradshaw & Nott, 1995; Cafazzo et al., 2010; van Hoof & Wensing, 1987), we found that age was significantly correlated with rank; younger dogs tended to submit to older dogs (see Chapter 2 for further discussion of the effects of age on dominance relationships in dogs). Size did not influence dominance relationships; weight was uncorrelated with rank.

Aggression was more frequent in same-sex pairs than between males and females, but submission and dominance displays were not different between same-sex and cross-sex relationships. Unidirectional dominance relationships did occur between dogs of opposite sexes, but dominance relationships were more common in same-sex than in cross-sex pairs. These results suggest that competition is greater within sex than between the sexes, even for neutered dogs.

Some dogs formed more dominance relationships than others, suggesting that individual differences affect dominance relationships among dogs. As a species, dogs

appear to engage in nearly all of the conspecific social behaviors observed in wolves (Abrantes, 1997; Handelman, 2008), but individual variation in the behavioral repertoires of dogs is huge. For example, some dogs display affiliative behaviors but never display agonistic behavior. Some dogs display only aggressive behavior toward any other dog they encounter. Some dogs display muzzle-licking but do not display low-posture or passive submission. Most dogs engage in social play, but some dogs do not. Some dogs perform almost all the social behaviors observed in wolves, while others perform only a few. Goodwin et al. (1997) found that more anatomically paedomorphic dog breeds displayed fewer agonistic signals than less paedomorphic breeds. When considering differences in conspecific relationships between those reported here and those in wolves, it is difficult to tease apart the effects of domestication and selective breeding from the effects of social environment. Further studies of conspecific relationships among dogs and wolves and breed comparisons of social behavior are needed to address these issues.

Formal Dominance

Muzzle licks met most of the criteria for a formal display of submission in dogs, but they did not occur in a high percentage of relationships (Table 1-6). The coverage of 1-way muzzle-licking relationships was low (18%), but the majority of the dogs in our study (58%) displayed muzzle-licking at least once. Muzzle-licking showed the highest coverage of all submissive or dominance-related behaviors and showed very high directional consistency; only 1% of dyads had bidirectional relationships. In our study, social context did not vary according to competition for food or mates, but muzzle licks (and all other submissive behaviors) remained unidirectional in playful and non-playful

contexts. Muzzle licks coincided with other measures of agonistic dominance and were never triggered by aggression. All other submissive behaviors were at times triggered by aggression and may be related to the expression of fear. Muzzle bites and high-posture met most of the criteria for a formal status display (i.e. unidirectional, multi-contextual, coincide with agonistic relationships, not induced by aggression), but the coverage of these behaviors was very low in our study (3% and 2% respectively). Muzzle-licking in this study is analogous to active submission in captive wolves and submissive-affiliative behavior in feral dogs, which appear to be formal status indicators in these animals (Cafazzo et al., 2010; Van Hoof & Wensing, 1987). Our findings suggest that when one dog licks another's muzzle, it is usually a reliable indicator of a formal dominance relationship. However, muzzle-licking occurred in a low proportion of relationships in this group of neutered pet dogs with fluctuating group membership, low levels of resource competition, and strong human influence on behavior. Bi-directional muzzle-licking occurred in four pairs (1%); three were in male-female pairs, one was between females, and all four had particularly friendly relationships, exchanging playful and affiliative behaviors often (see Chapter 2 for more information on friendly relationships in this group). Muzzle-licking was a good indicator of which dog was dominant in the present study group, but it is possible that bi-directional submission is more common in pairs of dogs that are very familiar with one another, such as those living in the same household. Future studies of the development of dominance relationships among dogs over time are needed to address this possibility.

Mounts were unidirectional, but mounts and chin-overs did not coincide with agonistic relationships. These behaviors are generally considered to be displays of

dominance in wolves and dogs (Abrantes, 1997; Handelman, 2008; Lindsey, 2001). However, in their study of dominance in captive wolves, van Hoof and Wensing (1987) found mounts and “head ons” (equivalent to chin-overs) were more closely related to affiliative behaviors than to behaviors related to status communication. Mounts were unidirectional in the present study group, but we found that subordinates often mounted dominants. For example, Benny, the lowest-ranking male in our group, mounted the highest number of dogs, all females, including those he submitted to. In two male-male dyads, the subordinates regularly mounted the dominants. In two of the cross-sex pairs with bidirectional muzzle licking relationships, the females regularly mounted the males, and in the other the male regularly mounted the female. Chin-overs were often bidirectional (DCI = 0.7), and bidirectional mounts were also observed in dyads that were not included in the final analysis. Mounts and chin-overs seem to be attention-getting behaviors that often instigate play. Most dogs do not tolerate being mounted (personal observations), so mounting is an effective way to get a reaction from an aloof social partner (see Chapter 2 for further analysis of the relationship between mounts, chin-overs, and affiliation). It seems that dominants sometimes allow role reversals with mounts and chin-overs, at least in playful contexts, as they do with many play-fighting behaviors (Bauer & Smuts, 2007), but submissive behaviors, especially muzzle-licking, seem to clearly communicate status in both playful and non-playful contexts.

In theory, formal submission should facilitate tolerance and reduce aggression from dominants (de Waal, 1982; 1986). However, we observed several interactions in which muzzle licking or other spontaneously emitted submissive behaviors actually triggered a threat or even a bite from another dog. Perhaps muzzle licks trigger

aggression in less familiar dyads but foster tolerance over time as the relationship develops. Anecdotal observations suggest that muzzle licking is more often tolerated in very close relationships, such as dogs that live in the same household, and aggression may become less intense and less frequent over time in formal dominance relationships. Future studies are needed to investigate this possibility.

Chance (1967) proposed that attention structure was the basis of rank orders in primates, with high-ranking animals being the focus of attention for subordinates. This, he argued is the social mechanism that allows high-ranking animals to lead the group in movements and activities. In a study of leadership behavior in 3 wild wolf packs in Yellowstone National Park, Peterson et al. (2002) found that breeding males and females led the majority of their pack's travels and activities. In another study of two groups of dog in the same Italian feral dog population studied by Cafazzo et al., (2010), Bonanni et al., (2010a) found that dogs who received affiliative submission were more likely to lead and be followed by others than were dogs that received more agonistic submission. As mentioned above, Bailey, the highest-ranking dog in our group, was typically intolerant of submission and proximity of younger dogs. Muzzle licks and active submission only made up only 32% of the submission that Bailey received. The second ranking dog in the agonistic hierarchy, a female named Charlie, was the highest-ranking dog based on muzzle licks alone. Muzzle licks and the full behavioral complexes of active submission and obnoxious submission made up 98% of the submission that she received. When Charlie entered the group, other dogs would often crowd around her and lick her muzzle. Her usual response was to retreat from the attention; she was very tolerant of the other dogs, but she was somewhat shy, and when she received too much attention she

responded with a mild growl or snap to end the interaction. Most of the time she kept to herself or affiliated with a few close friends, but she was often the focus of attention, submission, affiliation, and play invitations from other dogs. As these examples illustrate, some dogs seem to be more tolerant toward subordinates than others. More tolerant dogs are perhaps more likely to be the center of attention and therefore more successful leaders (Bonanni et al., 2010).

Why Do Linear Hierarchies Emerge in Dogs?

Dominance hierarchies likely emerge in groups of neutered pet dogs because they retain many of the social strategies that were adaptive in their wolf and early dog ancestors (Smuts, 2010). In wolves, dominance hierarchies likely contribute to a pack's success in cooperative hunting and raising young. The top ranking male and female are typically the only animals that breed (Mech, 1999; Vonholdt et al., 2008; Zimen, 1978). They take the lead during hunts, travel, and territorial defense, but the cooperation of other pack members is crucial for successful group hunts and pup care (Mech, 1999; Packard, 2003; Peterson et al., 2002). Bonanni et al. (2010a; 2010b) found that groups of feral dogs compete for territories and food resources and these groups tended to follow the lead of only a few high-ranking individuals in the group. Over the course of domestication, dogs came to rely primarily on humans for food, but it is likely that social relationships with other dogs remained (and still remains) important for survival and reproductive success for many feral and semi-feral dogs (Smuts, 2010). Formal dominance relationships may facilitate cooperation and clear behavioral roles allowing groups to successfully secure food and compete with other groups. Deferring and literally

“kissing up” to older animals is likely to be adaptive for wolves and feral dogs, and pet dogs appear to retain this behavioral tendency, despite the effects of domestication, castration, fluctuating group membership, and little need to compete for resources.

Although dominance relationships in neutered dogs no longer are adaptive in terms of securing mating opportunities or resources, they may provide short-term benefits by reducing aggression. If dog A threatens dog B, B may learn to stay out of A’s way to avoid future conflicts. If B submits to A, A may learn that B will probably submit in future interactions without the need for serious aggression. Submission given and aggression received were correlated in the study dogs, but aggression was very mild (84% threats). It is possible that dominance relationships decreased the intensity and frequency of aggression. Future studies of the development of agonistic behavior in social relationships in dogs are necessary to test this hypothesis by determining whether aggression decreases over time as clear dominance relationships are formed.

How Do Linear Hierarchies Emerge in Dogs?

The probability of finding linear hierarchies by chance alone is low and decreases as group size increases (Jameson, et al., 1999). However, they occur more often than expected by chance in many species including humans (Roseth et al., 2007). Chase et al. (2002) tested two hypotheses in cichlid fish to explain the emergence of linear hierarchies: ‘individual attributes,’ where rank is predetermined by differences in dominance ability, and ‘social dynamics,’ where rank is established by social processes and hierarchies are not predetermined by relative individual attributes. The authors reported that although individual characteristics play a significant part, social dynamics

are also necessary for the high proportions of groups across species in which linear hierarchies are formed (Chase et al., 2002). In domestic dogs, it seems likely that individual attributes and social dynamics both play a role in establishing dominance relationships. The higher-ranking dogs in our group tended to be older and socially aloof.

A dog's scent probably also plays a big role in the way others interact with him, although this is difficult to test with the current methodology. All the dogs included in our study were neutered, but behavioral anecdotes suggest that dogs tend to engage in agonistic interactions more often with intact males than with neutered dogs of similar age. Specifically, younger dogs seem more likely to display submissive affiliation to intact males, and older dogs (especially other males) seemed more likely to display aggression to intact males (aggressive behavior displayed *toward* intact males, not by them, led to the requirement that all dogs at the facility must be neutered). Scent presumably allows dogs to easily distinguish intact from neutered males.

Scent may also be involved in determining another dog's age. Winner effects, loser effects, and bystander effects are also likely to play a part in the formation of dominance relationships among dogs. We propose two possible social rules combining individual attributes and social dynamics that may contribute to the emergence of a linear hierarchy in dogs: Social Rule #1) "If the other dog smells older than me, displayed dominance or aggression to me in the past, and other dogs submit to her, I will submit." Social Rule #2) "If the other dog smells younger than me, displayed submission to me in the past, and submits to other dogs, I will not submit.

Applied Considerations

Having shown that dominance is a concept that can be applied to social relationships among dogs, we wish to return to the applied debate discussed at the start of this chapter. Some dog trainers feel that because dogs are descended from wolves who supposedly show rigid dominance hierarchies, humans need to assert dominance over their pet dogs through forceful methods of training and punishment. However, studies of wolves show that dominance is usually expressed through postures and displays rather than overt aggression, aggressive behavior is mild and ritualized, alpha wolves are not necessarily the most aggressive individuals in the pack, and relationships in wolf packs tend to be more affiliative than combative in nature (Lockwood, 1987; Mech, 1999; Sands & Creel, 2004; van Hoof & Wensing). Similarly, in the study group, status communication occurred mainly through ritualized threats, gestures and postures rather than through aggressive physical contact, which was rare. For example, we never observed an “alpha roll” among our study dogs. In fact, dominance relationships in this group were most commonly expressed through affiliative displays of submission. High-ranking dogs were usually aloof and tended to receive submission much more often than they imposed their dominant status on other dogs (Chapter 1). If dogs rarely use force to assert dominance over other dogs, why deem it appropriate for humans to use force when interacting with dogs? The use of alpha rolls, and other combative, punishment-based dog training methods can trigger fearful and aggressive responses in dogs (Blackwell et al., 2007; Herron et al., 2009; Ryan, 2001), and are less effective in achieving desirable behavior from dogs than reward-based approaches based on positive reinforcement (Hiby et al., 2004; personal observation).

Table 1-1. Criteria for formal status displays

-
- 1) Display should be unidirectional.**
 - 2) Display should be stable across multiple contexts.**
 - 3) Display should coincide with agonistic dominance relationships.**
 - 4) Display should not be a conditioned fear response.**
-

From de Waal (1986) & Preuschoft (1999)

Table 1-2. Study subject information

Dog	Initials	Sex	Age	Size	Breed	# Dominant^a	# Subordinate^b
Bailey	BA	F	116 mo.	42 lbs.	Basenji mix	10	0
Charlie	CH	F	71 mo.	84 lbs.	Husky mix	9	0
Junebug	JB	F	94 mo.	24 lbs.	Beagle	10	1
Cody	cd	M	76 mo.	74 lbs.	Airedale	6	1
Happy	hp	M	140 mo.	29 lbs.	Beagle mix	4	0
Wrigley	wr	M	37 mo.	70 lbs.	Golden retriever	2	1
Wallaby	wa	M	39 mo.	63 lbs.	Cattle dog mix	9	6
Lily H	LH	F	41 mo.	100 lbs.	Scottish deerhound	9	3
Lily A	LA	F	43 mo.	59 lbs.	Belgian tervuren	5	3
Freedom	FR	F	65 mo.	43 lbs.	Labrador mix	2	1
Taggart	tg	M	66 mo.	72 lbs.	Vizsla	0	1
Maggie	MG	F	40 mo.	48 lbs.	Boxer mix	3	7
Rex	rx	M	29 mo.	54 lbs.	Portuguese water dog	3	4
Molly	ML	F	20 mo.	101 lbs.	Newfoundland	2	2
Fielding	fd	M	45 mo.	20 lbs.	Bichon mix	0	0
Sawyer	sy	M	41 mo.	80 lbs.	Spinone Italiano	0	1
Buddy	bd	M	19 mo.	76 lbs.	Tibetan mastiff mix	1	2
Mason	ms	M	28 mo.	43 lbs.	Vizsla	1	4
Lionel	li	M	42 mo.	88 lbs.	Labrador retriever	2	3
Riley	RI	F	7 mo.	50 lbs.	Boxer mix	0	3
Mindy	MD	F	38 mo.	21 lbs.	Pug	2	5
Lizzy	LZ	F	40 mo.	70 lbs.	Golden-doodle	2	5
Benny	bn	M	30 mo.	55 lbs.	Golden-doodle	0	15
Sachi	SA	F	16 mo.	48 lbs.	Vizsla	0	13

^a Number of dyadic relationships in which dog only receives submission.

^b Number of dyadic relationships in which dog only emits submission.

Table 1-3. Ethogram of agonistic behaviors

Behavior	Description
Aggressive	
Threat	A directs a mild display of aggressive behavior at R, that may include any of the following behaviors: barking, growling, staring, lip curling, and/or snapping, but A makes no body contact or bite contact with R.
Conflict	A directs aggressive behavior at R that may include any of the behaviors listed above for threat, and also includes one or more of the following behaviors: 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.
Crouch	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 behavior from R.

Adapted from Van Hoof & Wensing, 1987; Handleman, 2008

Table 1-4. Matrix of total submission

Actor	Recipient																								
	BA	GH	JB	cd	hp	wr	wa	LH	LA	FR	tg	MG	rx	ML	fd	sy	bd	ms	li	RI	MD	LZ	bn	SA	
BA	*																								
GH		*																							
JB	1		*																						
cd	2			*																					
hp					*																				
wr						*																			
wa	2	1	6	157	4	1	*	1																	
LH		19	1	2			2	*																	
LA	2	1	2						*																
FR		2								*															4
tg			1								*														
MG	4	1	1	3			1	1	1			*													
rx							2	1	1			1	*												
ML			1										1	*											
fd															*										
sy												1				*									
bd							1	1									*								
ms		1		2			7	6									*								2
li					1			1	3									*							
RI	2		2				1												*						
MD	1	1					6	3		4				1							*				
LZ	5				1		34	2		6								4							
bn	1	109	5	5	6	4	2	12	5	12		2						3	2		1	4	*		1
SA	5	30	3	1			8	22	1		3	12	1				1				1	1	3	*	

Lower case initials are males; upper case initials are females. Highlighted values are 2-way relationships.

Table 1-5. Linearity, unidirectionality and coverage of agonistic behaviors

	<i>N</i>	<i>h'</i>	<i>Two-tailed p-value</i>	DCI	Unknown 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%)

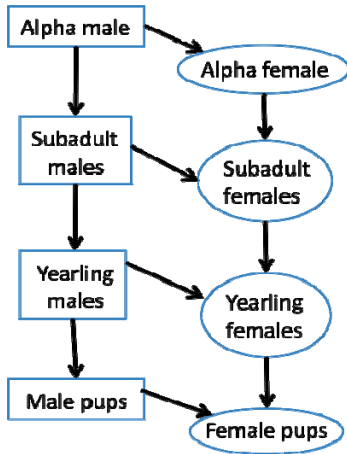
Table 1-6. Possible formal status displays in dogs

	<i>N</i>	DCI	Performed in playful and non-playful contexts	1-way Relationships	2-way Relationships	Dogs that performed the behavior	Correlation w/ Aggression (<i>rs</i>)	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%)
Crouch	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%)
Conflict	19	.368	N/A	6 (2.2%)	4 (1.5%)	6 (25%)	N/A	6 (46.2%)

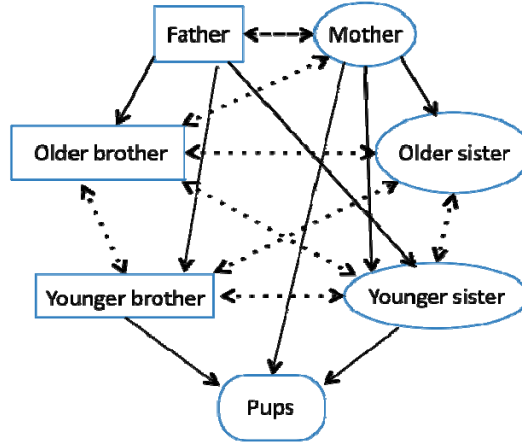
* Statistically significant; two-tailed p-value < 0.05

Figure 1-1. Two models proposed for dominance relationships in a wolf pack

a) Sex/Age Graded Hierarchy



b) Family



Adapted from Packard (2003)

CHAPTER 2
DOMINANCE, EGALITARIANISM, PLAY AND AFFILIATION
IN DOMESTIC DOGS

INTRODUCTION

In groups of neutered pet dogs, competitive pressures for food and mates are significantly lower than they are in groups of intact free-ranging dogs and wolves. Despite low levels of food and mating competition, we found a linear dominance hierarchy based on unidirectional submission and aggression in a group of 24 neutered pet dogs at a dog daycare facility (Chapter 1). However, asymmetrical dominance relationships were only discernable in 29% of all possible dyads. The absence of agonistic interactions in over two-thirds of the dyads indicates the need to expand our focus beyond agonism if we are to fully understand canine social relationships. In this chapter, we examine patterns of play and affiliation in the study group and how these friendly behaviors are related to agonism. As a result of these investigations, we propose the existence of 4 different relationship styles in domestic pet dogs.

Dominance and Egalitarianism

Dominance is presumed to be one of the primary mechanisms that help gregarious animals balance competitive and cooperative pressures in social groups (de Waal, 1986;

Hinde, 1974). Dominance (i.e. an accepted imbalance of power or “bias” in a relationship) can help resolve conflicts over ecological resources such as food and mates, and can also be used to resolve *conflicts of interest*. For example, conflicts of interest can occur when deciding the direction in which a group moves, which member of a mated-pair will tend to the young, or whether or not two individuals will maintain proximity (Hand, 1986). While the presence of a predetermined “winner” in most social conflicts can easily resolve such competitive encounters through despotic (i.e. biased) means, these conflicts can also be resolved through egalitarian processes. Hand (1986) discusses egalitarianism in terms of the resolution of proximate social conflicts, stating “a continuum exists between a fully egalitarian relationship in which each member wins 50% of the conflicts, and a strictly dominance/subordination relationship in which one individual wins 100% of the conflicts.” (p. 208). She outlines situations in which social conflicts can be resolved without a dominance relationship, such as sharing, adhering to rights of possession, communicating degrees of relative motivation, and mutually avoiding conflicts.

Egalitarian relationships should be favored when the cost of winning a competitive encounter is high and the cost of losing is low, such as in relationships between pair-bonded mates or parents and offspring and in environments where resources are plentiful (Hand, 1986). However, empirical data on purely egalitarian relationships in which two individuals interact but have no discernable bias of power in their relationship are extremely rare in the existing literature on non-human animal behavior (but see Swedell, 2002). In a social group, dominance styles can range from *despotic* (i.e. competitive and agonistic encounters are more biased toward dominants) to *tolerant* (i.e.

dominants tolerate more counter-aggression by subordinates and subordinates win more competitive contests). Tolerant dominance styles have been described in literature as being "more egalitarian." However, following Cooper & Bernstein (2008), we reserve the term *egalitarian* to refer to relationships where there is no discernable dominant/subordinate. In the more despotic societies, dominance relationships are more rigid, agonistic interactions are more unidirectional and linear, and aggression is infrequent but intense. In more tolerant societies, bidirectional agonistic relationships and circular triads are more common, aggression is more frequent but less intense, and group members have a greater tendency to affiliate and reconcile after conflicts (De Waal & Luttrell, 1985). Despotic versus tolerant dominance styles have been compared in different species (Cooper & Bernstein, 2008; de Waal & Luttrell, 1985; Jaeggi et al., 2010), in different social groups within a species (Sapolsky & Share, 2004), and in different sexes within a group (Preuschoft et al., 1998; Stevens et al., 2007). Certain species, groups, or sexes have been found to be more despotic than others. The degree to which dominants can bias resources or social interests in their favor is limited by subordinates' options outside of the group and the relative benefits of group-living. Tolerant dominance styles should be favored when the benefits of group-living are high, the risks of dispersal are low, and resources are evenly distributed (Cooper & Bernstein, 2008; de Wall & Luttrell, 1985; Lehman & Bryson, 2008; Van Schaik, 1989; Vehrencamp, 1983).

Affiliation and Aggression

In the short term, affiliation and aggression appear to have opposite effects on a relationship. Aggression appears to have a *dispersive* effect (i.e. distance-increasing), while affiliation appears to have a *cohesive* effect (i.e. distance-decreasing). In Chapter 1 we found that dominance relationships in the study dogs were characterized by asymmetrical aggression. However, the large majority of aggression (88%) observed among the study dogs consisted of threats (i.e. aggressive displays with no physical contact), and conflicts never resulted in injury. Submission was much more common than displays of aggression or dominance, and the most common form of submission was affiliative in nature (i.e. muzzle-licking). Aggression did not immediately trigger muzzle-licking, but this behavior was positively correlated with the receipt of aggression (Chapter 1).

In his influential paper on dominance and social bonding in primates, de Waal (1986) discusses empirical data showing an association between aggression and affiliation in social relationships. Subordinates likely use affiliation to temper aggression and foster tolerance from dominants (de Waal 1986, Schino & Aureli, 200). In primate groups, grooming is often directed up the dominance hierarchy, although this tendency can be weak or absent in species with more relaxed dominance styles (Cords et al., 2010; Puga-Gonzalez et al., 2009; Schino & Aureli, 2008). Numerous studies have also shown that pairs of animals in several species, including domestic dogs and wolves, tend to *reconcile* after an aggressive encounter. This means that the pair is more likely to exchange friendly behavior in the time period immediately following a fight than during a similar time period on a different day without an aggressive exchange (Aureli et al.,

2002; Cools et al. 2009; Cordoni & Palagi, 2008). Increased rates of affiliation after conflicts are more common in dyads with closer social bonds, suggesting that reconciliation serves to repair and strengthen bonds in valuable social relationships (Aureli et al., 2002). Conflict involving aggression followed by increased rates of affiliation appears to indicate social bonding more accurately than the absence of conflict. Thus, aggression and affiliation in close social relationships seem to be inextricably linked.

Play and Affiliation

In this study we recorded two types of friendly behaviors among dogs: *play* and *affiliation*. During play fights, animals compete to ‘win’ the interaction by biting, chasing, pushing, and pinning each other to the ground, as they do during aggressive interactions (Bauer & Smuts, 2007; Bekoff, 1974; Biben, 1998; Fagen 1981; Palagi, 2006; Palagi et al., 2004; Paquette, 1998). Play-fighting also contains cooperative elements that distinguish it from real fighting, including special play signals to communicate playful intent, self-handicapping (voluntarily using less than full force or putting oneself in a vulnerable position), and role reversal (subordinates assuming winning or dominant roles) (Bauer & Smuts, 2007; Bekoff, 1974; Biben, 1998; Fagen, 1981; Spinka et al. 2000). Play-fighting in young mammals is probably important for the development of competitive abilities and nuanced social skills that are important to reproductive success in adulthood (Bekoff, 1974; Fagen, 1981; Pellis et al., 2005; Spinka et al., 2000; Ward et al., 2008; 2009). In terms of short-term social benefits for juvenile and adult players, play-fighting in mammals has been proposed to (1) strengthen social

bonds and increase trust between social partners and/or (2) assess the competitive abilities of others without the risks involved in overt aggression (Bauer & Smuts, 2007; Bekoff, 1974; Biben, 1998; Cordoni, 2009; Drea et al., 1996; Fagen, 1981; Palagi, 2006; Palagi et al., 2004; Pellis et al., 2005; Ward et al., 2009; Zimen, 1978).

Domestic dogs are frequent and vigorous players as juveniles and adults (Bauer & Smuts, 2007; Horowitz, 2009; Ward et al., 2008; 2009). Bauer and Smuts (2007) studied asymmetry during bouts of play-fighting among familiar but unrelated dogs and found that dominant dogs assumed the winning role during play significantly more often than did subordinate dogs. Similarly, Ward et al., (2008) found that certain puppies assumed the winning role significantly more often than others when playing with their littermates. Puppies also showed preferences for certain littermates, and these preferences became stronger over the course of development (Ward et al., 2008). In a study of third party interventions during play in these litters, Ward et al. (2009) found that interveners tended to target the dog in the losing position during play. Interventions were unrelated to partner preferences, and puppies did not reciprocate support during play fights. Aggressive fights and submission were not observed in the litters, and the authors propose that puppies use play to develop stable social relationships with littermates and to opportunistically practice being in the offensive role against other dogs (Ward et al., 2008; 2009).

Wolves also engage in play-fighting well into adulthood (Cordoni, 2009; Mech, 1970; Zimen, 1978). Adult wolves play more frequently in the summer months when mating competition is low (Cordoni, 2009; Mech, 1970; Zimen, 1976; 1978) Cordoni (2009) found that wolves tended to play most often with group members that were close

in rank. In this captive pack, play distribution was not related to “relationship quality” measured by friendly body contact and agonistic support frequencies (Cordoni, 2009). The author suggests that wolves use play to assess the competitive abilities of potential competitors more than to strengthen social relationships

Affiliative behaviors (e.g. grooming, friendly body contact) are thought to eliminate parasites, reduce stress, strengthen social bonds and aid in the resolution and reconciliation of conflicts among group members (Aureli, 2002; de Wall, 1986; Palombit et al., 1997). In a photo illustrated encyclopedia of canine behavior, Handelman (2008) describes several types of *affiliative* behaviors in dogs that are distinct from play-fighting behaviors including *muzzle licks*, *nuzzles*, *head presses*, *nibbles*, *nose nudges*, and *hip nudges*. Behavioral descriptions are given in Table 2-1. In Chapter 1, we found muzzle-licking, an affiliative behavior, to signal submission among the dogs in the study group. Similarly, Cafazzo et al. (2009) found that “submissive-affiliative” behavior (i.e. muzzle-licking and low tail wagging) signaled submission in a group of feral dogs living on the outskirts of Rome. It is likely that muzzle-licking and other affiliative behavior serve to strengthen social relationships among dogs. However, to our knowledge the affiliative behaviors described by Handelman (2008) (other than muzzle licks) have not been studied quantitatively in dogs.

Affiliative behaviors among wolves, sometimes referred to as *affection* or *friendliness* in the literature, are observed in the context of care-taking, courtship, and during friendly greetings after periods of separation (Mech, 1970; Packard, 2003; Zimen, 1978). Affiliation is thought to strengthen pair bonds between mates and increase the cohesion and cooperation of pack members necessary for cooperative hunting, territorial

defense, and communal pup care (Mech, 1970; Packard, 2003; Zimen, 1978). Mounts and chin-overs are observed during mating and courtship, but they are also thought to signal dominance in dogs (Abrantes, 1997; Handelman, 2008; Lindsey, 2001). In Chapter 1, however, we found that mounts and chin-overs were not correlated with other agonistic behaviors (Chapter 1). Van Hoof and Wensing (1987) found these behaviors to be more closely associated with affiliative behaviors than with agonistic behaviors in wolves. We included these behaviors in this study to consider the possibility that mounts and chin-overs also represent affiliation in dogs.

To investigate the frequency, distribution and associations between play, affiliation and agonism in dogs, we used data collected on a group of 24 neutered pet dogs that socialize regularly at a dog daycare facility in Evanston, Illinois to examine the nature of dominance, egalitarianism, play and affiliation among dogs. We began by examining the characteristics and patterns of friendly behaviors in the study group with a focus on the common but seldom-studied affiliative behaviors. Next, we investigated the relationship between affiliation, aggression, and dominance in social relationships. Finally, we identified 4 different relationships styles in groups of pet dogs, and compared friendly relationships in pairs that have an established dominance relationship to those that lack a discernable dominance relationship because they did not exchange agonistic behaviors.

METHODS

Subjects and Observations

Behavioral observations were conducted on 24 dogs that socialize regularly at a dog daycare facility in Evanston, IL. Group membership, which fluctuated daily and throughout the day, was determined by human supervisors who commonly interrupted aggressive interactions among the dogs. Aggressive, submissive, dominant, playful, and affiliative behaviors were recorded using all occurrence sampling (Altmann, 1974) several days a week on 90 different days distributed over the course of one year for a total of 224.4 hours of observation. See Chapter 1 for additional information on the dog daycare facility, study subjects, and the nature of human involvement during interactions. Note that we were unable to investigate reconciliation behavior directly through standard observational methods because dogs that were involved in conflicts or threatened one another frequently at daycare were regularly given crated time-outs and/or separated into different groups.

Behavioral Definitions

Mutual play was recorded in dyads if both dogs displayed relaxed body postures, facial expressions and exaggerated, bouncy locomotion accompanied by one or more of the following behaviors: *play bite*, *body slam*, *jump on*, *tackle*, *nose punch*, *stand over* or *sit on* (see Bauer & Smuts, 2007; Ward et al, 2008; 2009; Handelman, 2008 for behavioral descriptions of each play behavior). During play bouts between dogs, behaviors are exchanged so rapidly that it is extremely difficult to quantify each individual behavior without frame-by-frame analysis of videotaped interactions as utilized in other studies of dog play (e.g. Bauer & Smuts, 2007; Ward et al., 2008; 2009). Therefore, we recorded play in minutes rather than recording each distinct play behavior.

Affiliation was recorded in dyads that exchanged any of the following behaviors: *muzzle licks*, (non-muzzle) *licks*, *nuzzles*, *nose nudges*, and *hip nudges* (see Table 2-1 for ethogram). Affiliative behaviors occurred infrequently enough to code each behavior individually, and therefore frequencies of each behavior were recorded for each dyad. Affiliative behaviors were primarily observed during mutual play bouts, but only occasionally in the absence of social play.

Aggression, submission, dominance displays, mounts and chin-overs were also recorded (see Tables 1-3 & 1-8), and a significant linear dominance hierarchy was found in the group ($h' = 0.258$, DCI = 0.971, two-tailed $p = 0.014$). Dominance relationships based on unidirectional submission were discernable in 81 of the possible 276 (29%) dyads. See Chapter 1 for additional information on the behaviors and statistical methods used to determine dominance relationships in the study group.

Relationship Styles

Based on the presence or absence of a discernable dominance relationship and the presence or absence of affiliation, we split the dyads into 4 distinct relationship styles. *Formal* dominance relationships included unidirectional submission and affiliation (N = 61). *Egalitarian* relationships included bidirectional or no submission and affiliation (N = 58). *Agonistic* dominance relationships included unidirectional submission and no affiliation (N = 20). *Non-interactive* relationships included no submission and no affiliation (N = 137) (Table 2-3).

Affinity, Equity, and Play

To compare friendly behavior in relationships with or without discernable dominance relationships, we examined differences between formal and egalitarian relationships. To measure the relative level of *affinity* in pairs of dogs, we added the number of minutes spent playing together to the number of affiliative behaviors exchanged in each dyad to compute a composite index of play and affiliation. This affinity index (A_{ab}) was computed as follows (adapted from Silk et al., 2006 & Thompson, 1996):

$$A_{ab} = \frac{I_{ab}}{\left(\frac{I_a + I_b}{2}\right)}$$

where I_{ab} is the rate of affiliation between a and b (calculated by dividing the number of minutes that a and b spent playing together and the number of affiliative behaviors exchanged, by the number of hours that the dyad was present in the study group), I_a is a 's average rate of affiliation with all 23 of the other study dogs, and I_b is b 's average rate of affiliation with all 23 of the other study dogs. This calculation resulted in an affinity index for each dyad that controlled for the dogs' individual tendencies to engage in friendly social behavior. Dyadic affinity scores ranged from zero (i.e. agonistic and non-interactive dyads) to 13.2 indicating that the dyad engaged in friendly behavior with one another 13 times more often than they did so with all other dogs on average.

To assess whether friendly behavior was balanced or skewed in social relationships, we calculated relationship equity (E_{ab}) as follows (adapted from Mitani, 2009 & Silk et al., 2006):

$$E_{ab} = 1 - \left| \frac{f_{a \rightarrow b} - f_{b \rightarrow a}}{f_{a \leftrightarrow b} + f_{a \leftrightarrow b}} \right|$$

where $f_{a \rightarrow b}$ is the total number of friendly behavior (i.e. affiliative behaviors and play minutes) that a directed at b , $f_{b \rightarrow a}$ is the amount of affiliation that b directed at a , and $f_{a \leftrightarrow b}$ is the total amount of affiliation exchanged between a and b . Relationship equity scores ranged from zero indicating that friendly behavior was completely skewed to one indicating that friendly behavior was completely equitable. To compare levels of play in formal and egalitarian relationships, we calculated the proportion of play minutes relative to the total amount of friendly behavior exchanged for each dyad.

Statistical analyses

MatMan 1.1 (Noldus) was used for all matrix analyses. The directional consistency index (DCI) of each behavior matrix was calculated as the total number of times a behavior was performed in the direction of the higher frequency within each dyad (H) minus the total number of times the behavior occurred in the direction of the lower frequency within each dyad (L), divided by the total number of times the behavior was performed by all individuals: $DCI = (H - L)/(H + L)$ (van Hoof & Wensing, 1987). We also calculated the number of 1-way relationships (only one dog in the dyad performed the behaviors), 2-way relationships (both dogs in the dyad performed the behaviors), and the total number of study dogs that performed each behavior. For analyses comparing matrices of behavioral frequencies, we corrected for variation in the opportunity for each dyad to interact by dividing each behavior matrix by a matrix of dyadic observation hours to create a corrected behavior matrix. To test whether behaviors were directed up or down the hierarchy, these corrected behavior matrices were compared with a matrix of the “relative rank of recipient” (1 = higher-ranking, 0 = lower-ranking). We used rowwise

matrix correlations to calculate Kendall's K_r statistics. Rowwise matrix correlations permute rows and columns in a matrix independently to control for individual differences in behavioral tendencies (de Vries, 1993; Hemelrijk, 1990). In order to assess whether affiliation was reciprocal, we performed a rowwise matrix correlation on affiliation and its transposition. In order to compare behaviors in same-sex and female-male (FM) dyads, we constructed a matrix of "sameness of sex" (1 = same-sex, 0 = FM) (Vervaecke et al., 2000b).

In order to compare dyads with formal and egalitarian relationships, we used repeated measures linear mixed models (LMMs) and generalized linear mixed models (GLMMs) using SAS 9.2. Repeated measures LMMs and GLMMs account for the lack of independence between dyads (one individual appears in several dyads within a social group) by controlling for random error effects for each individual. LMMs were used to compare affiliation indices, affiliation equity, and the proportions of play to total affiliation in formal versus egalitarian relationships. Log transformations were used to normalize the distributions and fit the LMMs. GLMMs were used to compare the frequencies of the 4 relationship styles in same-sex and FM dyads. For all statistical analyses, two-tailed probabilities are reported. Results were considered statistically significant at probabilities less than or equal to 0.05. Tukey's adjustments were applied for multiple comparisons.

RESULTS

Patterns of Play and Affiliation

The frequency, directional consistency, and coverage for play and affiliative behaviors among the study group are presented in Table 2-2. Minutes of play ($N = 2,430$) were more frequent than instances of affiliation ($N = 1,284$), but the coverage of affiliation was higher than the coverage of play. All 24 study dogs (100%) displayed some form of affiliative behavior, and affiliation was exchanged in a total of 106 dyads (38%). 23 dogs (96%) engaged in mutual play with at least one other dog, and mutual play occurred in 54 dyads (20%). Play and affiliation were significantly correlated with each other ($K_r = 993, P = 0.001$).

Affiliation showed a fairly high level of directional consistency ($DCI = 0.713$) and significant reciprocity ($K_r = 1069, P = 0.001$). Mutual play was completely bidirectional by definition (see Behavioral Definitions). Play and affiliation were significantly more common in FM dyads than in same-sex dyads (play: $K_r = -421, P = 0.001$; affiliation: $K_r = -408, P = 0.001$). Mounts and chin-overs were significantly correlated with each other ($K_r = 90, P = 0.001$), with play (play & mounts: $K_r = 217, P = 0.001$; play & chin-overs: $K_r = 266, P = 0.001$), and with affiliation (affiliation & mounts: $K_r = 214, P = 0.001$; affiliation & chin-overs: $K_r = 283, P = 0.001$). Chin-overs occurred more often in FM than in same-sex dyads ($K_r = 132, P = 0.008$). Mounts were slightly, but not significantly more common in FM than in same-sex dyads ($K_r = 85, P = 0.101$).

Affiliation, Aggression and Dominance

Affiliation given was significantly correlated with aggression received ($K_r = 293$, $P = 0.010$). Play did not show a significant correlation with aggression received ($K_r = -114$, $P = 0.152$). Affiliation was directed up the hierarchy ($K_r = 398$, $P = 0.008$), while aggression was directed down the hierarchy ($K_r = -268$, $P = 0.029$). Aggression was never observed to trigger affiliation, but affiliation did trigger aggression on 40 occasions (3% of all affiliation). Triggers of all aggressive acts were as follows: 67 (42%) were triggered by intolerance of proximity (the recipient moved closer to, but did not attempt to interact with actor), 40 (25%) were triggered by the receipt of affiliation, 15 (9%) were triggered by mutual play or play attempts, 15 (9%) were triggered by other aggressive behaviors, 13 (8%) were spontaneous (actor approached and aggressed the recipient), 6 (4%) were triggered by the proximity of food or a toy, and in 4 cases (3%) the trigger was undetermined.

Affinity, Equity and Play in Formal vs. Egalitarian Relationships

There was large variation in the number of hours that each dyad was present in the study group during observations (4 to 217 hours). Therefore, we wanted to rule out the possibility that relationship style could be a function of how much time the dogs were observed in the group together. The mean number of dyadic observation hours was not significantly different in any of the relationship styles (LMM: $F_{3,228} = 2.02$, $P = 0.112$).

The mean affinity indices did not differ between egalitarian and formal relationships (LMM: $F_{1,117} = 0.03$, $P = 0.866$), but affiliation was significantly more equitable in the former than the latter (LMM: $F_{1,117} = 11.77$, $P = 0.001$). Also, the

proportion of play relative to total affiliation was significantly higher in egalitarian than in formal relationships (LMM: $F_{1,117} = 7.76$, $P = 0.007$) (Figure 2-1).

The Effects of Sex, Age and Size on Relationship Style

Egalitarian relationships were more common in FM dyads than were formal relationships (GLMM: $t = 2.89$, $P = 0.004$), agonistic relationships (GLMM: $t = -2.86$, $P = 0.005$) and non-interactive relationships (GLMM: $t = -2.97$, $P = 0.003$). Neither age difference (in months) (LMM: $F_{3,228} = 1.43$, $P = 0.263$) nor size difference (in pounds) (LMM: $F_{3,228} = 1.25$, $P = 0.291$) were significantly different in any of the four relationship styles.

DISCUSSION

In general, social interactions among the study dogs were highly affiliative in nature. The frequency and coverage of friendly behaviors (i.e. play and affiliation) in the study group (N = 3714, 100% of dogs, 43% of relationships) were notably higher than frequency and coverage of aggression and dominance displays (N = 379, 75% of dogs, 29% of relationships) (Chapter 1). Mounts and chin-overs (N = 143) were more closely associated with affiliation than with dominance. If mounts and chin-overs are added to the other affiliative behaviors, the difference between affiliation and agonism becomes even greater. We identified four different types of relationship styles among the dogs based on dominance and affiliation: formal relationships were characterized by affiliation and 1-way submission (22%), egalitarian relationships showed affiliation but lacked a discernable dominance relationship (21%), agonistic relationships were characterized by

1-way submission but no affiliation (8%), and non-interactive relationships showed no submission or affiliation (50%).

Despite the relative infrequency of agonism, affiliation among the dogs was associated with aggression, dominance, and the negotiation of social conflicts. Affiliation (but not play) was correlated with the receipt of aggression and was directed up the hierarchy. Affiliation was also reciprocal in relationships meaning that subordinates initiated most affiliative interactions, but affiliation was also reciprocated by dominants, at least some of the time. Dominants appear to have had a social preference for affiliative subordinates. Aggression was directed down the hierarchy and was highly ritualized; most instances of aggression were threats (88%), and aggressive contact was never injurious (Chapter 1). The large majority of aggression was triggered by social proximity and affiliation attempts from other dogs (78%), but only 3% of all displays of affiliation were met with aggression. Only rarely did dogs spontaneously approach others and display aggression (8%). Also, aggression was rarely triggered by contests over the possession of food or other objects (4%). These findings reveal a very tolerant dominance style in the group and suggest that social conflicts among neutered pet dogs in the dog daycare environment involve conflicts over personal space and the negotiation of social relationships rather than competition for ecological resources (i.e. food).

In Chapter 1, we found a strong tendency for older dogs to dominate younger dogs. These patterns of affiliation and aggression and their relationship with dominance and age demonstrate a general asymmetry in many relationships in the motivation to interact. In general, subordinates (i.e. younger dogs) seem to be more highly motivated to interact with dominants (i.e. older dogs) than vice versa. The findings that

younger/subordinate dogs self handicap more often and display more signals that communicate friendly intent during play also support this notion (Bauer & Smuts, 2007). A greater motivation to interact on the part of the younger animal would be adaptive in social systems where older, dominant animals lead and assist younger, subordinate animals in the procurement of food and territorial defense as is observed in wolves (Mech, 1999; Peterson et al., 2002) and some groups of feral dogs (Bonanni et al., 2010b). Dominants are also likely to receive benefits from maintaining affiliative relationships with subordinates who are often kin and may provide assistance with pup care and intergroup contests (Packard, 2003; Bonanni et al., 2010b). This would favor tolerance and occasional reciprocation of affiliation from dominants, but dominants are probably less dependent on subordinates for their basic survival than vice versa. In free-ranging canine social groups, solitary life is risky. Many young and inexperienced animals would likely starve or get killed without the assistance and tolerance of older animals. This would explain the patterns that we find over and over in dogs and wolves of younger animals literally “kissing up” to older animals (Bonanni et al., 2010a; 2010b; Cafazzo et al., 2010; Lockwood, 1979; Mech, 1970; 1999; Schenkel, 1967; van Hoof & Wensing, 1987; Zimen 1978). This general rule of affiliation and deference towards older dogs seems to explain the existence and the nature of dominance/submission in dogs.

However, we also found a similar number of equally affiliative, egalitarian relationships in which the distribution of affiliation was significantly more equitable than it was in formal relationships. Play accounted for a greater proportion of total affiliation in egalitarian relationships than it did in formal relationships, and the former lacked a discernable asymmetry in power. It is difficult to compare the egalitarian relationships we

found among the study of dogs with those in other nonhuman species, because empirical data on fully egalitarian yet affiliative relationships are scarce in the literature on nonhuman animals. We found one study of female hamadryas baboons that provided evidence of affiliative relationships in pairs where a dominant and subordinate were not discernable (Swedell, 2002). Given that (1) there is a lack of data on egalitarian relationships, (2) egalitarian relationships were as common as formal dominance relationships in our study group, and (3) there have been several recent publications that question the applicability of dominance to domestic dogs (Bradshaw et al., 2009; Eaton, 2002; O’Heare, 2007; Van Kerkhove, 2004), one might predict that egalitarian relationships are more common in domestic dogs than in most non-domesticated social species. Alternatively, it could be that relationships that are both affiliative and fully egalitarian do occur in other nonhuman species but have not been reported in the literature. Future studies on within-group relationships that completely lack an aspect of dominance are needed to properly assess the frequency of egalitarianism in social mammals.

The nature of dominance among wolves, dogs’ closest living relatives (Vila et al., 1997; 1999), has been a subject of scrutiny (Lockwood, 1979; Mech, 1999; Packard et al., 2003). Cooperative hunting, communal pup-care, long-term pair bonding, and close social bonds are typical of wolf societies (Macdonald, 1983; Mech, 1970; 1999; Packard, 2003; Zimen, 1978). These social characteristics favor high levels of affiliation and cooperation and low levels of aggression among pack members (Drea & Carter, 2009; Hinde, 1974). However, food and breeding opportunities are not evenly distributed among pack members. In most wolf packs, breeding rights are restricted to one female

and one male (Vonholdt et al., 2008) who also lead cooperative hunts and have priority access to kills (Packard, 2003; Peterson et al., 2002). Such skewed resource distribution increases competitive pressures between group members and favors stricter, more despotic dominance hierarchies (Hinde, 1974; Lehmann & Bryson, 2008; Van Schaik, 1989). Studies of dominance relationships in wild wolves are rare (Mech, 1999; Peterson et al., 2002; Sands & Creel, 2004) and the degree of social bias within wolf packs has not been studied quantitatively. Studies of captive wolf packs suggest dominance styles among wolves that are despotic in some respects with linear hierarchies and unidirectional aggression (Derix et al., 1993; van Hoof & Wensing, 1987; Zimen, 1978). On the other hand, aggression is highly ritualized within wolf packs and social relationships are characterized by post-conflict reconciliation (demonstrated in captivity) and high levels of affiliation, suggesting a more tolerant than despotic dominance style (Cordoni & Palagi, 2008; Lockwood, 1979; Mech, 1970; 1999; Packard, 2003; van Hoof & Wensing, 1987; Zimen, 1978.)

Mech (1999) suggests that the linear hierarchies reported in captive wolves are due to unnatural social conditions in which unrelated wolves are forced to group together and are unable to disperse. He proposes that wild wolf packs are better described as families with male and female parents who guide the activities of the group than in terms of linear dominance hierarchies. Studies of captive wolves show an increase in levels of aggression and a decrease in levels of play during the mating season (Cordoni, 2009; Derix et al., 1993; Mech, 1970; Zimen, 1976; 1978) suggesting that wolf societies become more despotic as competitive pressures rise. Mech's (1999) argument, however, was based on observations of a single wolf pack during the summer season, when mating

competition is reduced, and it is not clear how much this applies to other wild populations. In Yellowstone, packs tend to be much larger than the pack Mech studied, and may contain more unrelated individuals (Vonholdt et al., 2008), and may be characterized by more despotic hierarchies (Smith et al., 2001), although data is scarce. In summary, data suggest that wolves have a relatively tolerant dominance style, especially during the summer months, but friendly relationships among wolves that are completely egalitarian with no discernable bias of power remain undescribed.

In most feral dog societies, food distribution and mating opportunities are less skewed than in wolf societies (Boitani et al., 1995; Pal, 2003). Theoretically, these social factors would favor more egalitarian relationships. A recent study of dominance in one free-ranging group of dogs living on the outskirts of suburban Rome found that dominance relationships were unable to be determined in 28% of the relationships in the group, but affiliative behaviors other than muzzle licks were not reported, so it is unclear if these pairs of dogs without discernable dominance relationships had friendly, egalitarian relationships or avoidance relationships. While egalitarianism (i.e. no discernable dominance) appears to be rare in nonhuman species, it is thought to be a core feature of human sociality (Kaplan et al., 2009). It is possible that over the course of domestication humans have selectively bred dogs that form social relationships similar to the ones we form with one another (Hare & Tomasello, 2005).

It is likely that the relaxed social environment for pet dogs at dog daycare where no one is very hungry and females are never sexually receptive had an even larger influence on the occurrence of egalitarian relationships than the effects of domestication. The reduced coverage of dominance relationships in our study group (29%) compared to

the Italian feral group of dogs (72%) seems to support this hypothesis (Cafazzo et al., 2010). Frafjord (1993) compared agonistic relationships in “tame” foxes that were caught in the wild as pups and hand-reared in captivity by humans for up to 2 years with those in “wild” foxes that were caught in the wild as adults and kept in captivity for no more than 3 weeks. He found that tame foxes were more playful and less aggressive with one another than wild foxes, they lacked a distinct display for signaling dominance, and they employed “ignoring” and “evading” behaviors more often than overt aggression to resolve conflicts (Frafjord, 1993). Environment was the only difference between these two experimental groups.

Further, social learning may have a strong influence on the strategies that dogs employ to negotiate and resolve conflicts. A study of two species of macaques, highly despotic rhesus macaques and more tolerant and affiliative stumptail macaques, found that five months of cross-housing juvenile rhesus macaques in groups of stumptails led to significant increases in the tendency of the rhesus macaques to reconcile after conflicts (de Waal & Johanowicz, 1993). The acquired social tendencies persisted after the subjects were returned to all-rhesus social groups. Further, the rhesus did not seem to be merely mimicking the stumptails because they displayed “rhesus-typical” affiliative behaviors during reconciliations. The authors propose that the changes in the “social attitudes” of the rhesus macaques were influenced by social exposure to the “easygoing” stumptails. The oldest stumptail male was even observed “breaking up fights” between juvenile rhesus and stumptails (de Waal & Johanowicz, 1993). In our study group, tolerance was often rewarded with kibble and praise from humans, and aggression was prevented, interrupted and often punished with temporary or permanent eviction from the

social group. Further, many of the dogs in this study were socialized since puppyhood to behave affiliatively rather than aggressively towards other dogs.

The tolerant and friendly social attitude promoted by humans likely contributed to the occurrence of egalitarian relationships in this group of pet dogs. Studies of affiliation, aggression, and dominance relationships among human children in school settings show that between the ages of two and four years, aggression in social conflicts becomes less physical and more verbal (Dodge et al., 2006; Roseth et al., 2007). In preschool settings where physical aggression is highly discouraged by teachers, children may learn to use verbal rather than physical aggression in social conflicts which may incur less frequent and less severe consequences (Roseth et al., 2007). Studies also show that dominance among school children becomes less associated with aggression and more associated with affiliation over the course of development (Strayer, 1981). Similar to human school children, pet dogs at dog daycare may learn to use milder forms of aggression and to use affiliative rather than physical aggression to negotiate their relationships with other dogs through the consistent reinforcement of friendly and tolerant behavior and the punishment of aggressive behavior by humans.

In egalitarian relationships we found that play accounted for a greater proportion of total affiliation than in formal relationships. In a study of play among adult wolves in captivity, Cordoni (2009) found that wolves tended to play with close-ranking group members, and levels of play were significantly higher during the non-mating period when competitive pressures were reduced. In a comparative study of play in captive groups of bonobos and chimpanzees, Palagi (2006) found that bonobos played at higher rates and more roughly than chimpanzees. She also found that bonobos displayed play signals at

higher frequencies during especially rough play, but play signals in chimpanzees were not related to the roughness of play. Dogs are also reported to use play signals more frequently during especially rough play (Bekoff, 1995). Palagi (2006) suggests that the more frequent and rougher play in bonobos is related to their tendency to exhibit “egalitarianism” (based on the frequency of undecided conflicts and the species’ apparent lack of consistent formal submissive displays) more often than in chimpanzees. Thus, play may be an alternative strategy to agonism that animals use to balance competitive and cooperative pressures in social relationships (Cordini, 2009; Palagi, 2006).

We found that play was significantly correlated with other friendly contact, and that males and females played more frequently than same-sex pairs. In contrast, Cordini (2009) found that play distributions among captive wolves were not related to relationship quality measured by body contact and agonistic support frequencies, and that play was equally distributed among same and cross-sex pairs. She proposes that these patterns of play suggest that wolves use play to assess the abilities of potential competitors and gain hierarchical advantages rather than to strengthen social bonds. Mating competition was an important influence on relationships in Cordini’s (2009) group of captive wolves, even during the non-mating period, but this competitive factor was absent among our study dogs. It may be that play becomes more or less related to competition depending on the competitive pressures present in the dyadic relationship and in the social group. Play may be more closely associated with social bonds in relationships and in groups with relatively low levels of competition.

We found egalitarian relationships to be more common and levels of play and affiliation to be higher between males and females than between dogs of the same sex,

while aggression was more frequent in the latter (Chapter 1). These patterns support the notion that competition is more intense among same-sex animals than between the sexes (Derix et al., 1993; Roll & Unshelm, 1997; Zimen 1978) and that both affiliation and play strengthen social bonds and promote cooperation between potential mates.

We did not find any relationship between age difference and relationship style. Thus, age difference does not seem to influence which style of relationship a pair may form. But in established dominance relationships, the older dog was dominant in 91% of dyads (Chapter 1). We also found no relationship between size difference and relationship style, or between dyadic observation time and relationship style. These findings suggest that the egalitarian relationships described here truly lacked a dominance component and did not simply reflect relationships between two animals that were close in age, size, and competitive ability, who have not yet had the opportunity to establish an accepted asymmetry of power in the relationship.

Half of the pairs of dogs in the group had non-interactive relationships making this the most-common relationship type in the group. Although these pairs did not exchange friendly or agonistic behaviors, it was not uncommon for them to sniff each other without making contact. It is unclear whether there was an accepted bias of power in these relationships. They could result from one dog staying out of the way of another because the other is dominant or from mutual avoidance. Unfortunately, our analyses did not reveal any significant results to provide further insight into the effects of sex, age or size on these relationships. The amount of time observed in the group together also did not significantly affect relationship style and some pairs spent over 200 observation hours

and never interacted at all. Still, non-interactive relationships might become less common as pairs of dogs spent more and more time together.

Agonistic relationships that lacked friendly interactions were characterized by threats from dominants triggered by the intolerance of proximity with subsequent deference from subordinates, and appear to be cases of non-interactive relationships that also include accepted bias of power. Recently, Cafazzo et al. (2010) reported a linear dominance hierarchy in a group of feral dogs living in suburban Rome. However, coverage of dominance relationships within the group of feral dogs (72%) was lower than has been reported for captive wolves (98%) (van Hoof & Wensing, 1987). In a study of three groups in this Italian feral population, Bonanni et al. (2010a) identified two dominance styles among the dogs: formal dominance included submissive affiliative behavior on the part of the subordinate, and agonistic dominance included non-affiliative submission (e.g. averted gaze, retreats, low posture, passive submission). The authors found that these two dominance styles were correlated with one another, but also differed in terms of the affiliative or agonistic nature of the relationship. Dogs that received high levels of affiliative submission were more likely to initiate group movements and be followed than both low-ranking dogs and dogs that received high levels of agonistic submission (Bonanni et al., 2010a). Thus, in free-ranging situations, tolerant and affiliative dominants appear to be more successful group leaders than dominants who primarily use agonism to establish their hierarchical positions.

In conclusion, affiliation among pet dogs in the dog daycare social environment is intricately associated with aggression, dominance, and egalitarianism in social relationships. Affiliation was directed up the hierarchy and dogs appear to use muzzle

licking as a formal submissive signal (Chapter 1). These characteristics are associated with despotic societies (Van Schaik, 1989), yet close and equitable relationships that appear to have no bias of power also appear to be common among pet dogs. Friendly, egalitarian relationships were more common between males and females but were also present in some same-sex pairs. Some dogs appear to be more “status-conscious” than others (Chapter 1), but most dogs formed both formal and egalitarian relationships. Regardless of whether the relationship contained an established dominant, affiliation and play were associated with one another, but affiliation was more equitable in pairs without a discernable power bias. In egalitarian relationships, dogs may also use play instead of agonism to balance competitive and cooperative pressures in social relationships. The tolerant dominance style and egalitarian nature of many relationships among these pet dogs were likely influenced by the effects of domestication, reduced levels of competition for food and mates, and a relaxed social attitude promoted by human intervention and supervision of interactions between dogs. To evaluate these ideas, we require studies of social relationships in dogs under a variety of different social, reproductive and ecological conditions.

Table 2-1. Ethogram of affiliative behaviors

Behavior	Description
Nose Nudge	<i>A uses the tip of her nose to gently nudge R's mouth, head, or body.</i>
Muzzle Lick	<i>A licks R's nose, lips, and/or chin.</i>
Nuzzle/Rub On	<i>A rubs or presses his face, head, or body on R's body.</i>
Nibble	<i>A uses her front teeth to rapidly nibble on R's coat.</i>
Genital Lick	<i>A licks R's genitals and/or anus.</i>
Coat Lick	<i>A licks anywhere on R's body other than the muzzle or ano-genital area.</i>

Adapted from van Hoof & Wensing (1987) and Handelman (2008)

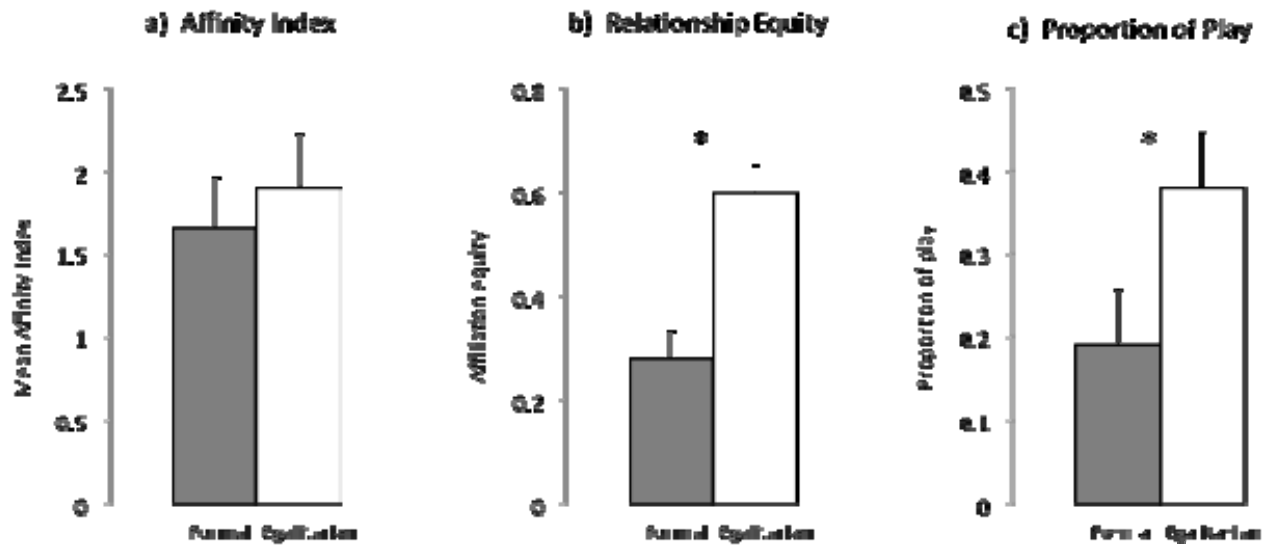
Table 2-2. Four relationship styles in domestic dogs

Relationship Style	Number and percentage of dyads
Formal Dominance 1-way Submission + Affiliation	61 (22%)
Egalitarian 2-way or No Submission + Affiliation	58 (21%)
Non-interactive No Submission + No Affiliation	137 (50%)
Agonistic Dominance 1-way Submission + No Affiliation	20 (7%)

Table 2-3. Directional consistency and coverage of affiliative behaviors

Relationship Style	Number and percentage of dyads
Formal Dominance- 1-way Submission + Affiliation	61 (22%)
Egalitarian 2-way or No Submission + Affiliation	58 (21%)
Non-Interactive No Submission + No Affiliation	137 (50%)
Agonistic Dominance 1-way Submission + No Affiliation	20 (7%)

Figure 2-1. Affinity, equity and play in formal vs. egalitarian relationships



- a) Mean affinity index + s.e. (LMM: $F_{1,117} = 0.03$, $P = 0.866$)
- b) Relationship equity + s.e. (LMM: $F_{1,117} = 11.77$, $P = 0.001$)
- c) Proportion of play to total affiliation index (LMM: $F_{1,117} = 7.76$, $P = 0.007$)

CHAPTER 3

THIRD-PARTY INTERVENTIONS DURING PLAY AMONG DOMESTIC DOGS

INTRODUCTION

In Chapters 1 and 2 we investigated the nature of and association between dominance and affiliation in a group of 24 pet dogs that socialize regularly at a dog daycare facility. Our findings suggest that dogs employ various combinations of agonism, affiliation, and play to negotiate their social relationships with other dogs. In addition to dyadic social interactions, we also observed numerous instances of dogs intervening in ongoing play between two other dogs. In this chapter, we propose 2 alternative hypotheses about the proximate benefits of third-party interventions during play in the negotiation of social relationships among the study dogs.

Interventions During Aggression

Studies of third-party interventions reveal that animals employ socially complex strategies to balance competition and cooperation in social relationships (Chapais, 1996; de Waal & Harcourt, 1992; Engh et al., 2005; Flack et al., 2005). The most common type of third-party intervention addressed in the ethological literature is that of an ongoing aggressive encounter between two animals (A & B) in which a third-party (C) intervenes and aggressively targets one animal (A), thereby providing support for the recipient (B). In this chapter, we will refer to interveners as “C,” targets as “A” and recipients as “B”

(Figure 3-1). These types of interventions have been termed ‘agonistic interventions,’ ‘aiding behavior,’ ‘agonistic support,’ and ‘coalitions;’ long-term supportive relationships between two animals are termed ‘alliances’ (de Waal & Harcourt, 1992). Agonistic interventions have been described in a wide array of taxa including nonhuman primates (Chapais, 1996, de Waal, 1992; Hemelrijk & Ek, 1991; Hunte & Horrocks, 1987; Nishida, 1983; Noe & Sluifjter, 1995; Pereira, 1989; Prud’homme & Chapais, 1996; Silk et al., 2004; Vervaecke et al., 2000; Watts, 1997; 2002; Widdig et al., 2000), social carnivores (de Villers et al., 2003; Engh et al., 2000; 2005; Zabel et al., 1992), dolphins (Connor et al., 1992), ungulates (Jennings et al., 2009), and human children (Grammer, 1992). They appear to provide interveners with immediate or delayed competitive and hierarchical advantages within social groups (de Waal & Harcourt, 1992). Agonistic interventions tend to be ‘low-risk’ and typically support the existing dominance hierarchy. For example, high-ranking animals tend to intervene at higher rates than lower-ranking animals, and interveners tend to join the higher-ranking of the original opponents in targeting the lower-ranking animal and usually target animals that are lower-ranking than themselves (Chapais, 1996; de Villers et al., 2003; Engh et al., 2005; Hunte & Horrocks, 1987; Nishida, 1983; Noe & Sluifjter, 1995; Prud’homme & Chapais, 1996; Silk et al., 2004; Widdig et al., 2000; Zabel et al., 1992). Animals are believed to use interventions to maneuver for position in the social hierarchy and to build alliances with close associates who may reciprocate support in the future (de Villers et al., 2003; de Waal & Harcourt, 1992; Hemelrijk & Ek, 1991). Coalitionary support between two lower-ranking animals can occasionally cause the target to fall in rank (de Villers et al., 2003; de Waal & Harcourt, 1992; Jenks, 1988; Zabel et al., 1992; Zimen, 1978), but this

appears to be rare. In addition to gaining personal hierarchical advantages, animals also appear to use interventions to help kin and unrelated “friends” gain hierarchical advantages by targeting their opponents (Chapais, 1996; de Villers et al., 2003; de Waal & Harcourt, 1992; Engh et al., 2000; 2005). Agonistic support seems to be an important component of close social bonds among many primates (Silk et al., 2010; Vervaecke et al., 2000; Watts, 2002), and it seems to be the primary mechanism of matrilineal rank inheritance in Old World monkeys and spotted hyenas (Chapais, 1996; Hunte & Horrocks, 1987; Eng et al., 2000; 2005).

Interveners can also be impartial during ongoing aggression, positioning themselves in between two opponents (i.e. interpositions) or displaying threatening or affiliative behaviors at both opponents without taking sides (Flack et al., 2005; Roeder et al., 2002; Petit & Theirry, 2000; Tajima & Kurtori, 2010; Watts 1997). These types of interventions are less common than those in which one opponent is targeted and the other supported (Flack et al., 2005). They have been termed ‘peaceful’ ‘neutral’ ‘non-aggressive’ and ‘policing’ interventions in the literature (Flack et al., 2005). Animals may benefit from neutral interventions by protecting one social partner from harm without damaging the relationship with the other (Petit & Theirry, 2000; Tajima & Kurtori, 2010; Schilder, 1990). Animals appear to use peaceful interventions to halt aggression directed at offspring or other kin (Petit & Theirry, 2000; Tajima & Kurtori, 2010), and also to temper aggression between valuable social partners. For instance, male gorillas and zebras have been observed to halt aggression between their harem females (Schilder, 1990; Watts, 1997).

Interventions During Affiliation

Third-party interventions can also occur during ongoing affiliation between two other group members (de Waal, 1982; Rivero & Colmenares, 1984; van Dierendonck et al., 2009; Ward et al., 2009). A study of interventions in a captive group of mares and geldings found that horses were significantly more likely to intervene in allogrooming or playful interactions that involved a preferred social partner. Horses tended to ‘take over’ the affiliative interaction with their most preferred partners. A study of interventions during play among juvenile baboons described third-parties joining ongoing play bouts and instances of ‘protection play,’ in which an intervener protected one participant from the play actions of another (Rivero & Colmenares, 1984a). Chimpanzees and bonobos have been observed breaking up grooming bouts between two other individuals; such interactions have been called ‘separating interventions’ (Boose et al., 2009; de Waal, 1982). Friendships and alliances with certain social partners can provide animals with several fitness enhancing benefits such as access to food and mates, protection from hostile conspecifics, reduced stress, and longer life-spans (Aureli et al., 2002; de Waal, 1982; Palombit et al., 1997; Rivero & Colmenares, 1984a). Interventions during dyadic affiliative interactions may function to maintain valuable social relationships and to compete with other group members for valuable social partners (de Waal, 1982; Rivero & Colmenares, 1984b; van Dierendonck et al., 2009). In a study of third party interventions during play in litters of puppies, Ward et al. (2009) found that interveners tended to target the puppy that was in the losing position at the time of the intervention. The puppies did not preferentially target or support their preferred playmates and did not show reciprocity in support during play. Aggressive fights and submission were not observed in the litters,

and the authors propose that puppies use play interventions opportunistically to practice aggressive behaviors and/or aid in the formation of dominance relationships (Ward et al., 2009).

Interventions During Play among Adult Dogs

Interventions during play occur quite frequently in groups of adult dogs at dog daycares and dog parks (personal observations). To our knowledge third-party interventions during play have not been investigated among adult dogs. In addition to the developmental benefits that play-fighting can provide for young animals, play is also likely to provide immediate benefits to adult animals as they balance cooperation and competition with group members in their daily lives (Chapter 2; Cordoni, 2009; Drea et al, 1996; Palagi, 2006; Palagi et al., 2004; Pellis et al., 2005). During play fights, animals compete to ‘win’ the interaction by biting, chasing, pushing, tackling, and pinning each other to the ground, as they do during aggressive interactions (Bauer & Smuts, 2007; Bekoff, 1974; Biben, 1998; Fagen 1981; Palagi, 2006; Palagi et al., 2004; Paquette, 1994; Pellis et al. 2005). Social play may allow individuals to improve their competitive abilities, assess their own abilities relative to others, and to establish, maintain or test dominance relationships without the risk of serious aggression (Bauer & Smuts, 2007; Drea et al., 1996; Pellis et al., 2005; Ward et al., 2009; Zimen, 1978).

Play-fighting also contains cooperative elements that distinguish it from real fighting, including relaxed body postures/facial expressions, special play signals to communicate playful intent, self-handicapping (voluntarily using less than full force or putting oneself in a vulnerable position), and role reversal (subordinates assuming

winning or dominant roles) (Bauer & Smuts, 2007; Bekoff, 1974; Biben, 1998; Fagen, 1981; Pellis et al. 2005; Spinka et al. 2000). Play is thought to contribute to social bonding and cooperation in close social relationships (Bekoff, 1974, 1995, 2001; Drea et al., 1996). Aggression tends to decrease between animals that regularly play together (Bekoff, 1974; 1995; Drea et al., 1996). Repeated bouts of mutual dyadic play-fighting that do not lead to aggression may help establish trust between playmates (Bekoff, 2001). Play may also aid in the coordination of movements between frequent play partners, particularly important for cooperative hunters (Bekoff, 1974; Ward et al., 2009; Zabel et al., 1992). Bekoff (2001) proposes that play-fighting may have played a role in the evolution of morality, contributing to the formation of cooperative social rules. Both partners must willingly participate for mutual play to occur. If an animal does not follow the social rules of play (e.g. self-handicapping & play signaling), they may find themselves with no willing play partners and therefore have fewer opportunities than “rule-abiding” counterparts to practice competitive behaviors, establish dominance relationships and to build valuable social bonds (Bekoff, 1995; Pellis et al., 2005).

Interventions during play appear to increase arousal levels in groups of dogs, and can lead to defensive aggression from the dog that is the target of play attacks from multiple dogs (personal observations). At the dog daycare facility where the present study was conducted, human supervisors were trained to prevent and interrupt many interactions between multiple dogs, especially if the play was particularly rough or vigorous. Interventions during play were thus prevented and interrupted several times an hour. Despite human interruptions, we observed 193 third-party interventions during play among the study dogs. When a dog intervened during ongoing play, they directed an

offensive play-fighting behavior (*playful interventions*), an affiliative behavior (*affiliative interventions*), or an aggressive behavior at the target (*aggressive interventions*) (Table 3-1).

Hypotheses & Predictions

Based on the competitive and cooperative nature of play in adult animals, we formulated two alternative hypotheses about the proximate benefits of interventions during play among dogs. The ‘competitive advantage’ hypothesis proposes that dogs intervene during play to practice fighting and to gain competitive and hierarchical advantages in social groups. The ‘valuable relationships’ hypothesis proposes that dogs intervene during play to maintain and compete for relationships with preferred social partners. These hypotheses are not mutually exclusive, but they predict different patterns interventions during play.

If dogs use interventions during play to practice fighting and gain competitive advantages, we expect to find the following patterns of interventions during play: 1) rank will be positively correlated with individual intervention rate, 2) interveners will target the lower-ranking dog in the original dyad ($B > A$) more often than the higher-ranking dog, 3) interveners will target dogs who are lower-ranking than themselves ($C > A$) more often than dogs who are higher-ranking than themselves, and 4) interveners will support their preferred partners during play by targeting their opponents more often than they will target their preferred partners.

If dogs use interventions during play to maintain and compete for valuable relationships, we expect to find the following patterns of interventions during play: 1)

rank will not influence interventions during play, 2) interveners will target their preferred partners during play more often than they will support them by targeting their opponents, and 3) interveners will play with targets more often than recipients immediately following interventions.

If the patterns of interventions during play more closely follow the predictions of the competitive advantage hypothesis, it will suggest that play in dogs mainly serves to assess the competitive abilities and compete with group members. If the patterns of interventions more closely follow the predictions of the valuable relationships hypothesis, it will suggest that dogs use play mainly to promote, protect, and compete for social partners. To evaluate these two hypotheses, we investigated the effects of rank and individual variation on intervention rates, the effects of rank relationships between interveners, targets and recipients on intervention targets, the effects of play partner preferences on targets/supports during play, and the outcomes of the interventions.

METHODS

Subjects & Behavioral Observations

Interventions were recorded among 24 dogs that socialize regularly at a dog daycare facility in Evanston, IL. Observations took place several days per week for a total of 90 days distributed over the course of one year. Refer to Chapter 1 for a detailed description of the housing conditions, observational methods, study subjects, and degree of human influence on the dogs' behavior. An *intervention* occurred when dog A and B were engaged in dyadic play and dog C intervened and *targeted* one of the players by directing playful, affiliative, or aggressive behavior at him, consequently *supporting* the

dog that was *not* targeted (‘non-target’ or ‘recipient’) (Figure 3-1). The term *support* is not meant to imply any intentionality on the part of the dogs but is used here for ease of comparison with other intervention studies.

Playful behaviors used to intervene included *play bite, nose jab, body slam, push, tackle, mount, and chin-over*. *Affiliative* behaviors included *lick, nuzzle/rub on, nibble, and nose nudge* (see Chapter 2 for behavioral definitions). The behaviors we classified as *playful* were ‘offensive’ or ‘attack-like’ behaviors (Bauer & Smuts, 2007; Ward et al., 2009), while the affiliative behaviors were more cooperative than competitive in form. Mounts and chin-overs were closely associated with both play and affiliation (Chapter 2) but were categorized as playful rather than affiliative behaviors in this study because they appear to give the actor a physical advantage over the recipient. Aggressive behaviors included threats (Chapter 1) and non-playful bites. A bite was considered non-playful if it triggered a yelp or defensive aggression from the recipient. No bites resulted in injuries among the study dogs.

Dominance Rank

We found a significantly linear hierarchy among the dogs based on the actor/receiver matrix of total submission ($h' = 0.258, P = 0.014$) (see Chapter 1 for detailed behavioral analysis of dominance relationships in this group of dogs). We used the procedure proposed by de Vries (1998) to reorder the dogs in the dominance order most consistent with a linear hierarchy (MatMan 1.1). Dogs were ranked from highest (1) to lowest (24) to assess the effects of rank on interventions.

Partner Preferences

To measure partner preferences among the dogs, we used the number of minutes spent playing and the frequency of affiliative behaviors to compute a composite index of affiliation preference for each dog with every other dog. A partner preference index (PP_{ab}) was calculated as follows (adapted from Ward et al., 2009 & Thompson, 1996):

$$PP_{ab} = \frac{I_{ab}}{I_a}$$

where I_{ab} is the rate of affiliation between a and b (calculated by dividing the number of minutes that a and b spent playing and the number of affiliative behaviors they exchanged, by the number of hours that the dyad was present in the study group), I_a is a 's average rate of affiliation with the 23 study dogs. The partner preference indices were used to construct an actor/receiver matrix where a 's preference for b is different from b 's preference for a . In this group, social preference scores ranged from 0 indicating no affiliation between a and b , to 20.2 indicating that a affiliated with b at a rate 20.2 times higher than she affiliated with all 23 dogs on average. PP scores higher than 2 were considered strong preferences (Thompson, 1996).

For ease of discussion, we will refer to preferred partners among the dogs as "friends," but we do not assume that the social relationships among temporary groups of pet dogs are the same as the long-term, reciprocal social bonds that have been described among kin and non-kin in primate species (Mitani, 2009; Silk et al., 2010; Smuts, 1985). Rather, we aim to use our data to foster a comparison of affiliative relationships in dogs with those in other species and to discuss the applicability of these terms to the relationships that domestic dogs form with one another.

Statistical Analyses

To test whether individual rank influenced intervention rates, we used Spearman's rank correlations. To determine whether interveners targeted the higher-ranking dog ($A > B$) or the lower-ranking dogs ($B > A$) more often during playful and affiliative interventions, we performed generalized estimating equations (GEEs) to determine if each dog's proportion of $A > B$ targets was significantly different from 0.5 (SAS 9.4). For the other analyses of playful and affiliative interventions, we used rowwise matrix correlation tests and present Kendall's K_r statistics (MatMan 1.1). Rowwise matrix correlation tests permute rows and columns in a matrix independently to control for individual differences in behavioral tendencies (de Vries, 1993; Hemelrijk, 1990). Each dyad spent a different amount of time present in the study group together. The matrices of targets and supports were therefore corrected for variation in the opportunity for each dog to target or support another dog by dividing the frequency matrices by a matrix of dyadic observation hours. To determine whether interveners targeted dogs that were higher-ranking ($A > C$) or lower-ranking ($C > A$) than themselves, the 'target' matrix was correlated with a matrix of 'relative rank of target' (1 = higher-ranking than intervener ($A > C$), 0 = lower-ranking than intervener ($C > A$)). To determine whether interveners tended to target or support their preferred partners during playful and affiliative interventions, the 'target' and 'support' matrices were correlated with the matrix of partner preference scores. For all statistical analyses, two-tailed probabilities are reported. Results were considered statistically significant at probabilities less than or equal to 0.05. Only seven aggressive interventions during play were recorded among the dogs, so we

were unable to perform statistical analyses on these types of interventions during play. Instead, we will describe the contexts of the aggressive interventions and the relationships between the dogs involved.

RESULTS

Rank and Individual Intervention Rates

Playful interventions were the most common type of intervention and were displayed by 16 dogs (67%). We observed a total of 41 affiliative interventions by 6 dogs (25%). We observed a total of 7 aggressive interventions during play by 2 dogs (8%) (Table 3-1). Rank was not significantly correlated with individual intervention rates (Spearman's rank correlation; $r_s = -0.228$, $N = 24$, $P = 0.271$). There was a large amount of variation in the individual dogs' tendencies to intervene. We will use two lower case initials to refer to males and two upper-case initials to refer to females (see Chapter 1, Table 1-2 for detailed information on the individual study subjects). Three dogs (wa, LH and bn) were responsible for 136 (70%) of the 193 interventions among the study dogs (Figure 3-2): wa displayed 48 playful interventions, 22 affiliative interventions, and 5 aggressive interventions; LH displayed 30 playful interventions, 7 affiliative interventions, and 2 aggressive interventions; bn displayed 15 playful interventions and 7 affiliative interventions. LH and wa were mid-ranking dogs, bn was the lowest-ranking male, and all three dogs had a large number of established dominance relationships compared to most of the study dogs (15, 12, and 15 respectively). Bn was subordinate in all of his known dominance relationships, while wa and LH were dominant in most of

their known dominance relationships. Individual rank did not predict intervention rates providing no support for the competitive advantage hypothesis.

Rank Relationships Between Interveners, Targets, and Recipients

Interveners did not playfully target the lower-ranking dog ($B > A$, 73 times) more or less often than the higher-ranking dog ($A > B$, 72 times) in the original dyad (GEE: $Z = -0.03$, $P = 0.978$). Interveners showed no tendency to playfully target dogs that were higher-ranking ($A > C$, 70 times) or lower-ranking ($C > A$, 75 times) than themselves (rowwise matrix test: $K_r = -36$, $P = 0.696$) (Figure 3-3a). Interveners affiliatively targeted the higher-ranking dog ($A > B$, 33 times) significantly more often than the lower-ranking dog ($B > A$, 8 times) in the original dyad (GEE: $Z = 4.22$, $P < 0.0001$). Interveners affiliatively targeted dogs that were higher-ranking than themselves ($A > C$, 32 times) significantly more often than they targeted dogs that were lower-ranking than themselves ($C > A$, 9 times) (rowwise matrix test: $K_r = 79$, $P = 0.047$) (Figure 3-3b). These patterns provide more support for the valuable relationship hypothesis than the competitive advantage hypothesis.

Partner Preferences

Interveners tended to target dogs for whom they had strong partner preferences (rowwise matrix test: $K_r = 591$, $P = 0.001$). The correlation between playful supports during play and partner preferences trended towards significance (rowwise matrix test: $K_r = 160$, $P = 0.054$). Affiliative targets were significantly correlated with partner preferences (rowwise matrix test: $K_r = 194$, $P = 0.001$). No correlation was found

between affiliative supports and partner preferences (rowwise matrix test: $K_r = -35$, $P = 0.455$). These results provide more support for the valuable relationship hypothesis than the competitive advantage hypothesis.

Intervention Outcomes

Thirty-three (17%) interventions during play were interrupted by human supervisors. When humans did not interrupt, the intervener played with the target (C & A) after 103 interventions (64%), the original dyad continued playing (A & B) after 48 interventions (30%), and the interaction ended after 9 interventions (6%). Playful and affiliative interventions never resulted in social interaction between the intervener and recipient (C & B) (Figure 3-4). The interventions that were interrupted by humans often included mild defensive aggression on the part of the target or other subtle signs that the target was uncomfortable with the social interaction. For example, in response to an intervention the target may quickly spin around with her raised hackles and show her teeth or snap at the intervener. Raised hackles, lip curls and snapping is also observed during play that has no signs of aggression (Bauer & Smuts, 2007; Ward et al., 2008; 2009; personal observations), and at times it was difficult for human observers to distinguish play from actual aggression. At these times, humans interrupted and redirected the dogs using verbal cues and pieces of kibble. In addition to the interventions that were interrupted by humans, an immeasurable number of interventions were also prevented by human supervisors trained to prevent aggression and particularly rough play among the dogs.

Interveners tended to play with the dogs they targeted, providing support for the valuable relationships hypothesis.

Aggressive Interventions

Two dogs (wa and LH) were responsible for the seven aggressive interventions during play. All five of wa's targets were male, lower-ranking than the recipients ($B > A$) and himself ($C > A$). Wa had weak to zero preference scores for his targets, and the aggressive interventions occurred while the targets were playing with two of his preferred partners. Two occurred when the target was playing with cd (wa's preference for cd = 8.5), and three occurred while the target was playing with LA (wa's preference for LA = 2.4). Twice, LH aggressively targeted females with whom she had zero preference scores. Once, the target was lower-ranking than the recipient ($B > A$), and once the target was higher-ranking than the recipient ($A > B$). Both times, LH was higher-ranking than her targets ($C > A$) (Figure 3-3c). One occurred while the target was playing with MD, one of LH's preferred partners (LH's preference for MD = 2.7). On the other occasion, LH had zero preference scores for both dogs in the original dyad. Over all, aggressive interventions during play were rare, but the few that occurred were directed at the play-partners of the intervener's friends, providing support for the valuable relationship hypothesis.

DISCUSSION

The patterns of interventions during play in this group suggest that dogs use interventions during play to maintain and protect close social relationships more than to

practice fighting, gain a competitive advantage over other group members, or to support their friends during play fights. Higher-ranking dogs were not more likely to intervene than lower-ranking dogs. In fact, the lowest-ranking male had the highest intervention rate of all the dogs (Figure 3-2). The three dogs responsible for the majority of the interventions (wa, LH, and bn) did appear to be “status-conscious” (i.e. each had a high number of known dominance relationships in the group when compared to the other dogs) (see Chapter 1, Table 1-2). However, their high number of dominance relationships and intervention rates are likely to be a result of personality differences. These three dogs interacted at higher rates than most in the group (unpublished data), indicating a greater motivation to strengthen and protect valuable social relationships. The ‘competitive advantage’ hypothesis predicts that interveners will target the lower-ranking dog in the original dyad (supporting the higher-ranking dog) and target dogs lower-ranking than themselves. In this study, rank relationships did not appear to influence the patterns of playful interventions. Rank did influence affiliative interventions, but interveners targeted higher-ranking dogs more often than lower-ranking dogs. Intervenors targeted their friends during play, most often leading to the intervener playing with the target. Intervenors and recipients never played immediately following interventions. Affiliative interventions seem to be a way of ‘kissing up’ to higher-ranking dogs in order to initiate play. Targets during play were significantly correlated with partner preferences, and the correlation between supports and partner preferences was nearly significant. Intervenors both targeted and supported their friends, most likely due to overlapping social networks (“social cliques”) among the dogs, rather than a motivation to help their friends win during play. For example, wa, LH, LA, and CH all had relatively strong preferences for

one another, and each dog both targeted and supported one another during play. A similar study of play interventions in litters of puppies found no relationship between playful targets/supports and partner preferences (Ward et al., 2009). This contrast is likely due to the greater variation in partner preferences and degrees of familiarity in our study group than than in the litters. Within a litter, all the puppies are related and extremely familiar with all of their littermates. This is not the case at dog daycare. Some pairs of dogs are more familiar than others, and many pairs do not affiliate at all (Chapter 2). Interventions were often prevented and interrupted by human supervisors because they can lead to defensive aggression from the target. Targeting a dog that is already being targeted by another dog can be somewhat of a “risky” tactic, even during play. It puts the target in a highly vulnerable position, and playful interventions without defensive aggression are likely to require a certain level of trust between the intervener and the target. Perhaps a friend of the intervener is more likely to forgive precarious play moves than a dog less familiar with the intervener; that is, neither misinterpret nor retaliate against them. Role-reversals are commonly observed during play, but dominants still assume the winning role more often than do subordinates (Bauer & Smuts, 2007). The rules of play-fighting may be more lenient in stronger relationships, allowing close friends to practice particularly rough play moves and "bend the rules" a little.

Only two dogs were observed directing an aggressive behavior at one of two dogs that were engaged in play. These aggressive interventions did appear to follow the predictions of the ‘competitive advantage’ hypothesis. Interveners tended to target the lower-ranking dog in the original dyad and always targeted dogs lower-ranking than themselves. One aggressive intervention during play was directed at two lower-ranking

dogs that were not friends of the intervener. However in 6 of the 7 interventions, interveners aggressively targeted dogs that were playing with their friends. Even when the dogs appear to be using play to compete, they seem to be competing for social partners rather than social status. However, it is quite possible that valuable social partners can indirectly lead to status-related and other benefits for the dogs as they do for other social mammals (Silk, 2007). This is where the 'valuable relationships' and 'competitive advantage' hypotheses intersect.

Concluding Considerations

The current study offers novel evidence for distinctions between the patterns of play versus aggression, but this study was conducted on neutered, unrelated pet dogs who did not need to compete for food or mates. Further, the group appears to have relaxed dominance relationships compared to free-ranging domestic dogs (Chapters 1 & 2), and results should be interpreted with this consideration. Other comparisons between wolves and dogs report very few, if any, differences in the play behavior of these species (Bekoff, 1974, 1995; Cordoni, 2009; Frank & Frank, 1982). Without further study we cannot conclude if the differences in interventions between wild mammals during aggression and domestic dogs during play are due to fundamental differences between aggression and play or wild animals and neutered pet dogs.

Cordoni (2009) found that play among captive wolves was more frequent between those who were close in rank, and that play was not correlated with other affiliative behavior associated with close social bonds. Zimen (1978) describes an account of a juvenile wolf falling in status after being repeatedly targeted by multiple wolves during

play. Thus, at least in some contexts, the proximate benefits of play-fighting may be similar to the benefits of real fighting, namely to assess the competitive abilities of opponents and to maintain and test dominance relationships. The large amount of variation observed in play behavior among social mammals suggests that social play is likely to have different functions for different species, as well as for different age and sex classes within a species (Bekoff, 2001; Spinka et al., 2000). It is likely that play is more cooperative in groups with relaxed dominance styles and at times of low competitive pressures, and more closely resembles aggression in groups with stricter dominance hierarchies and at times of tension between group members.

Table 3-1. Types of interventions during play

Type	N	# of dogs	Behavior directed at target
Playful Intervention	145	16	Play bite, nose punch, body slam, jump on, nuzzle, stand over or mount
Affiliative Intervention	41	6	Lick, muzzle/rub on, nibble, or nose nudge
Aggressive Intervention	7	2	Threat or non-playful bite

Figure 3-1. Participants in third-party interventions

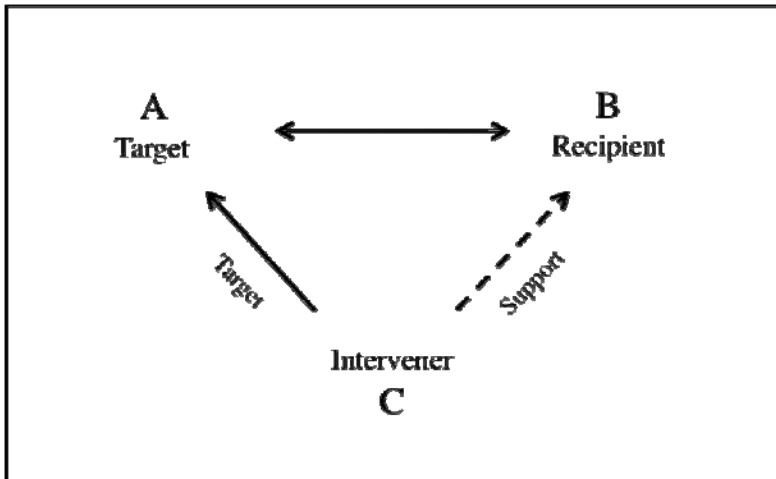


Figure 3-2. Individual intervention rates

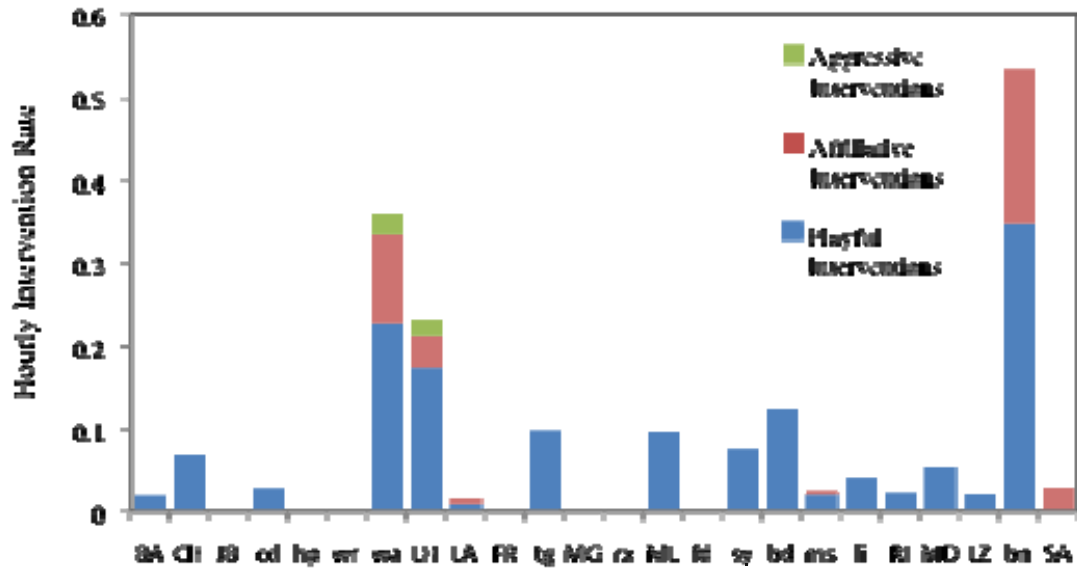
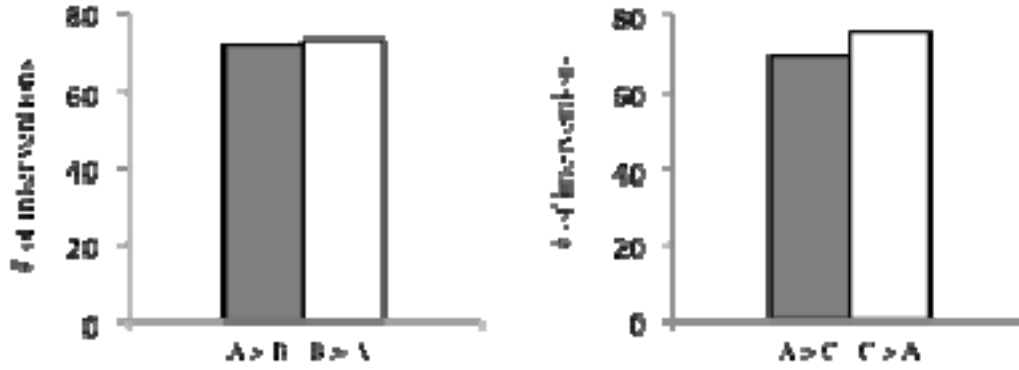
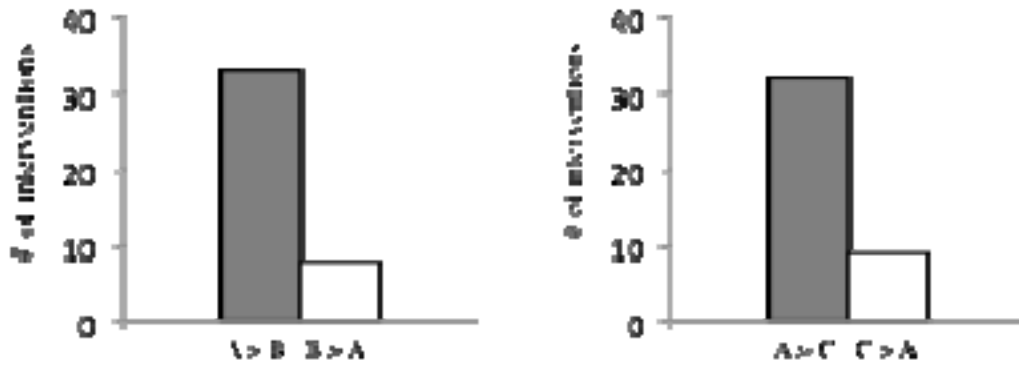


Figure 3-3. Rank relationships between interveners, targets and recipients.

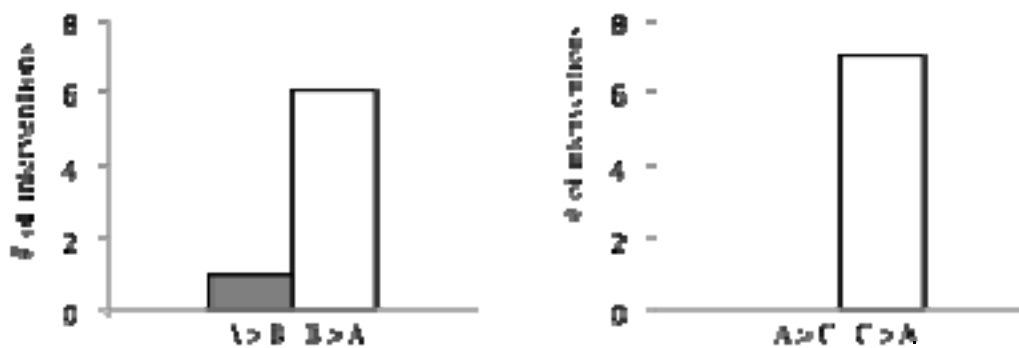
a) Playful Interventions



b) Affiliative Interventions



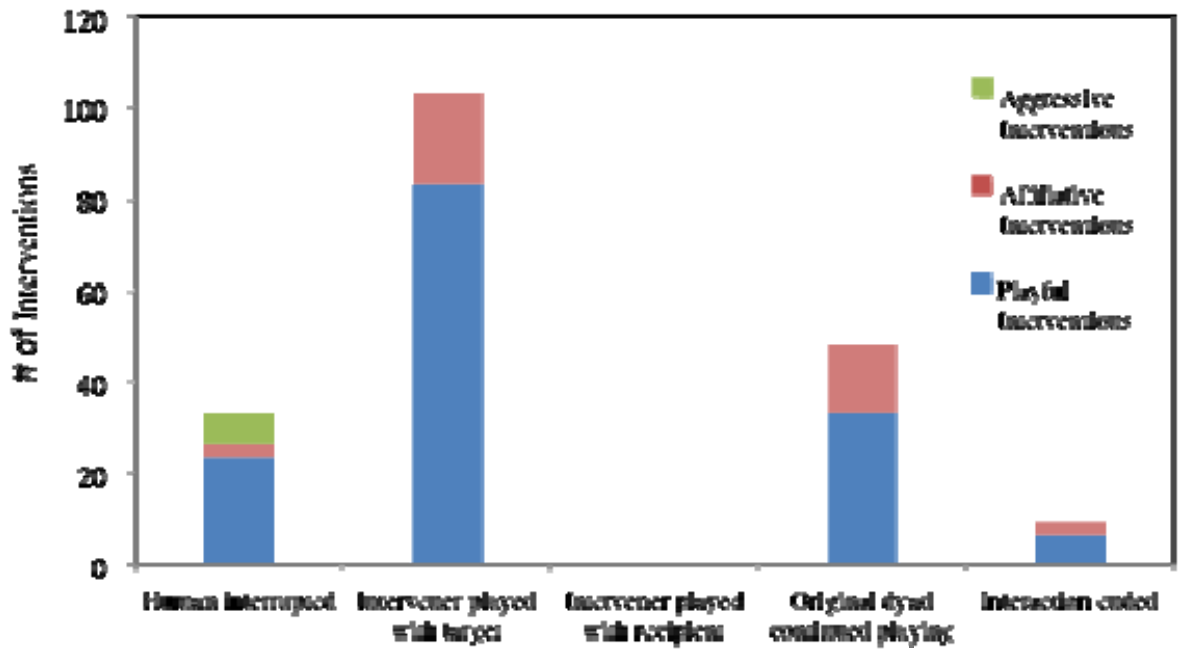
c) Aggressive Interventions



A > B: Target higher-ranking than recipient; B > A: Target lower-ranking than recipient

A > C: Target higher-ranking than intervener; C > A: Target higher-ranking than intervener

Figure 3-4. Intervention outcomes



CONCLUSION

Oxytocin is a feel-good, stress-relieving hormone that facilitates social bonding between mothers and offspring and is relevant to the attachments formed between humans and dogs (Nagasawa et al., 2009; Odendaal & Meintjes, 2003). Sharing affiliation and simply gazing at our beloved dogs triggers the release of oxytocin in our systems, and affiliative contact with humans results in increased levels of oxytocin for dogs as well (Nagasawa et al., 2009; Odendaal & Meintjes, 2003). When I first learned of the connection between oxytocin and our relationships with dogs, I understood my own personal and intellectual history better. I grew up in a household where pets easily outnumbered humans. When I took my first undergraduate course in primatology with John Mitani, at the University of Michigan, I quickly became fascinated with scientific investigations of animal behavior.

Since then, I have spent almost every day of my life observing, supervising, playing with and above all, sharing affiliation with my pets and hundreds of dogs at kennels and dog daycares where I was employed. In 2007, I opened my own dog daycare and training facility, Unleashed in Evanston™, where we conducted the research presented above. Opening up a successful business while writing a dissertation can be quite challenging and stressful at times, but the warm (likely oxytocin induced) feelings I

get each day playing and sharing affiliation with dogs make it all worthwhile. I am constantly surrounded by dogs eager to offer me licks, nuzzles, nibbles, and nose nudges, and I am delighted to offer affection in return.

My affection for dogs was not the only motivation behind my career choice, however. As I hope the above research conveys, I find the social relationships that dogs form with one another to be complex and fascinating. Writing these chapters has made me realize that I train dogs to resolve conflicts using egalitarian means every day. In fact, that fairly well sums up the task of supervising groups of dogs at daycare. I also aim to be dominant in most of my established social relationships with dogs in order to keep them safe, but I never use physical aggression. I may use a sharp verbal threat once in a while such as, “ah ah!” if a dog is about to steal my food or pee on my rug, but I truly do my best to make it in the dogs’ interest to follow my lead. I use positive reinforcement and more importantly, patience when I am working professionally with dogs. My family, friends and staff can corroborate that I dole out much more affection than most dog trainers. I am an infamous “baby talker” when I interact with dogs. Based on hundreds of informal experiments that I’ve conducted, baby talk nearly always gets a dog to wag his tail (It would be interesting to test whether high-pitched verbal nonsense from humans triggers oxytoxin release in dogs).

As I converse about dogs with clients, employees, friends, and family in my daily life, I find myself saying the same thing over and over, “Dog’s are just like kids.” My mom was an elementary school teacher for 30 years, and she and I have traded countless stories demonstrating the similarities between dogs and human children. In my puppy class I emphasize teaching puppies to tolerate frustration, to play calmly and politely with

other dogs, and to share possession of a toy when asked. Brief ‘time-outs’ from socializing with peers seem to be very effective behavior management tools and incentives to follow rules for both school children and daycare dogs who behave inappropriately (Kathy Trisko personal communication; personal observation).

You might empathize with my anthropomorphic sentiment after reading the following account describing the social life of one of the study subjects, Lily A. Lily has been attending daycare at Unleashed for over three years. Three days a week the “dog bus” (i.e. the author’s Honda Element) stops at Lily’s residence and brings her to daycare where she socializes with dogs from other households for the day. At daycare, she is taught by human supervisors to behave calmly and patiently, to pay attention when they call her name, to share toys, and to play nicely with others. Lily meets new dogs on a regular basis, but she has a few close friends at daycare with whom she prefers to interact. At daycare she has a strong preference for an older female dog named Charlie. Charlie is friendly and will occasionally engage in play with Lily, but Charlie is a little aloof and is not a frequent player. Lily plays often with a male dog named Wallaby. At times Wallaby appears to play too rough for Lily, because she occasionally refuses to play with him (i.e. tucks her tail, shows her teeth, and snaps). About once week she encounters another male dog, Logan. When she sees him, she usually initiates “flirty” play (i.e. slightly bouncy movements, erect posture, pricked ears facing out to the sides, a high quick tail wag, nose nudges and chin-overs). When Lily plays with Logan, his housemate, Muddy, occasionally intervenes targeting Logan and ends up playing with him. Lily socializes with a third male, Rex, at daycare and also in other social settings.

Their human owners are close friends. Lily and Rex occasionally spend the night at each others' respective homes, and visit the dog park together on the weekends.

Does this description sound similar to social life in another species? I propose that when dogs are immersed in extremely “human-like” social environments and socialized to obey “egalitarian” rules enforced by humans (i.e. friendly behavior is rewarded, aggression is punished, sharing is enforced by group leaders), the relationships that dogs form with each other appear to be quite “human-like.” In my search for literature on egalitarian relationship styles, I found several studies of dominance, affiliation and relationship styles in humans that appear to be relevant to our research on dogs. Neff & Harter (2003) examined three different relationship styles used by college students with their mothers, fathers, best friends, and romantic partners: ‘self-focused autonomy’ was associated with dominance, ‘other-focused connectedness’ was associated with subordination, and ‘mutuality’ with equality. Most students reported using all three relationship styles in different relationships and contexts, but mutuality was the most commonly reported relationship style. The authors cautioned against dichotomizing autonomy and connectedness “because the integration of these two concerns is more typical in relationships” (Neff & Harter, 2003; p. 81). Using factor analysis methods, Fischer (1981) identified four relationship styles reported by adolescents and young adults in their relationships with peers: “integrated (high friendly and high intimate), intimate (high intimate and low friendly), friendly (high friendly and low intimate) and uninvolved (low friendly and low intimate)” (p. 11). In preschool children, aggression becomes more verbal and less physical over the course of the school year (Roseth et al., 2007), and dominance becomes less associated with aggression and more associated with

affiliation over the course of development (Strayer, 1981). Comparisons of these studies with the research presented in the chapters above demonstrate similarities in social relationships that humans form with one another and those that we observed among the study dogs.

Recently there has been a surge of studies that report “human-like” social skills in dogs who appear to possess specialized social skills for attending to, learning from, and communicating with humans (see review in Topal et al., 2009a). For instance, dogs outperform chimps and wolves raised under similar conditions in tasks that require attention to human gestures; the performance of dogs is similar to that of human toddlers (Hare & Tomasello, 2005, Topal et al, 2009b). Topal et al. (2009a) proposed that socially, humans and dogs have shifted away chimpanzees and wolves and have converged towards one another over the course of evolution. The authors propose several similar aspects of sociality in human groups and in dog-human mixed groups (Topal et al., 2009a). Based on the research presented above and my anecdotal observations, I propose that several of these social characteristics are also present in groups of dogs.

Topal et al. (2009a) suggest that dogs have evolved the capacity to form close social attachments similar to those among humans. “Attachment” to specific individuals is distinguished from “social attraction” which is simply a tendency to have a fondness for group members, but “not as unique individuals” (Topal et al., 2009, p. 93). Our analyses of affiliative relationships in Chapter 2 and partner preferences in Chapter 3 revealed that dogs do not distribute affiliation equally among group members. In fact, some dogs showed strong preferences for particular individuals (e.g. PP scores ranged from 0-20, indicating that A affiliated with B at a rate 20 times greater than A affiliated

on average; Chapter 3), while most of the possible dyads in the group did not affiliate at all. Social attachments in human children and dogs (to humans) are often characterized by signs of anxiety and proximity seeking behaviors upon separation from the individual to whom they are attached (Topal et al., 1998). These observations suggest that dogs are capable of forming strong attachments to other dogs. For example, as a young girl my family adopted two adult huskies from an animal shelter named Ivan and Quila. True to his breed, Ivan was an escape artist and loved to roam. He was often missing for hours or even days at a time. Each time he escaped, Quila would howl incessantly until he returned. When Ivan died, she would howl every night for months. From that point on, she was glued to my mom's side until it was Quila's time to pass. At Unleashed, there are several pairs of dogs who attend the facility that reside in the same household who show signs of anxiety and proximity seeking (i.e. whining, barking, scratching at the gate, visually attending to the other through the fence) when they are separated into different play groups at the daycare facility. These anecdotal examples of social attachments suggest that dogs can form attachments with one another that are similar to the attachments they form with humans and those that humans form with one another.

Topal et al., (2009a) proposed that both humans and dogs have tendencies to follow "social rules" that allow for individuals to peacefully integrate into different groups with fluctuating membership and divergent rank orders. In Chapters 1 and 2, we proposed that dogs tend to follow a social rule to defer and "kiss-up to" older dogs. This social rule would facilitate the organization of social structures in groups with fluctuating membership without a need to assess relative competitive abilities among group members

to establish status. “Respect and defer to your elders” also appear to be social rules in human groups (Greve & Bjorklund, 2009) and wolf packs (Packard, 2003).

Topal et al (2009a) proposed that dogs and humans have predisposition towards social learning. Human toddlers and dogs but not chimps appear to imitate the behavior of human adults even when the functional outcome of the behavior is not clear (Horner & Whiten, 2005; Topal et al., 2009b). Lionel, a male yellow lab, had a quirky habit of attacking trees. He would be strolling along nonchalantly in the yard at daycare, when all of a sudden he would freeze and turn to stare at a tree. After a few seconds of intense staring he would lunge, growl and bite the tree ripping off large pieces of bark. After being present in the group with Lionel at daycare when he attacked trees, two other dogs, Janey and Wallaby, also began jumping up and biting on the tree. Their assaults on the tree didn't seem to have quite the ferocity that Lionel's had, however.

Topal et al (2009a) suggest that human groups and dog-human groups have a tendency towards emotional and behavioral synchronization. Another social rule among dogs seems to be: “react when other dogs react.” Such emotional contagion presents a challenge for dog daycare supervisors who work to keep arousal levels among the dogs as low as possible. On the first Tuesday of every month, the city of Evanston sounds an emergency broadcast test alarm from a tower near Unleashed triggering “group howls” among the dogs. A few dogs truly howl, others remain quiet, but most bark repeatedly. Some dogs seem to become better howlers over the course of time, or at least their vocalizations seem to become longer and more “howl-like.” (Watch videos of the group howls at: <http://www.facebook.com/pages/Evanston-IL/Unleashed-in-Evanston/310082186031>).

Topal et al. (2009a) argued that dogs and humans have shown increased sociality and decreased agonism compared to their wolf and ape relatives. In Chapters 1, 2 and 3, we presented evidence for decreased agonistic and competitive behavior compared to captive wolves (van Hoof & Wensing, 1987; Cordoni, 2009). However, it is impossible to determine to what extent this decrease in agonism was a result of human influence and environmental differences versus genetic modifications between dogs and wolves that have accumulated over the course of domestication. It is impossible to say how relationships would be expressed in a pack of neutered, well-fed wolves where the leader wolves punished aggression and rewarded tolerance and affiliation among pack members with food, as human supervisors did in our study group. Mech (1999) emphasizes the relaxed nature of dominance and high levels of affiliation and cooperation in a wild wolf pack. His observations occurred only during the summer when competitive pressures are relatively low, but it is quite feasible that wolves have the capacity to form both despotic and egalitarian relationships depending on the particular relationship and the social context. Both despotic and egalitarian relationships are also found in dogs (Chapter 2) and humans (Kaplan et al., 2009; Neff & Harter, 2003) (e.g. a military general and a private vs. best friends). A common factor of sociality in wolves, dogs, and humans may be the capacity for behavioral flexibility based on social context.

Wolves do not appear to attend to humans to the extent that that dogs do (Hare et al., 2002; Topal et al., 2009b), but there is no evidence suggesting that wolves do not possess “human-like” social skills when they interact with conspecific group members. Social similarities between humans and dogs listed in Topal et al (2009a) include high degrees of sociality, behavioral and emotional synchronization, social learning, social

rules, and complex social communication skills based on the anticipation of another's attention and behavior and mutual attention toward common goals. These social skills seem to be quite relevant for cooperative hunters and reminiscent of descriptions of wolf societies (Mech, 1970; 1999; Packard, 2003; Peterson et al., 2002; Zimen, 1978). Humans and dogs may have converged towards each other and away from chimpanzees and wolves, but it could be that humans have converged towards the wolf/dog social system. It may be more appropriate to say that humans have become more "wolf-like" over the course of our evolutionary history than to say that dogs have become more "human-like" (Schleidt & Shalter, 2003). Rather than humans selectively breeding for "human-like" social skills in dogs, I find it more plausible that dogs came equipped with the ancestral wolf's capacity for egalitarianism, social attachments and complex communication skills essential for survival and reproductive success. Perhaps it was dogs who taught humans the communicative and cooperative ways of the wolf.

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