COGNITION AND THE DEVELOPMENT OF SOCIAL COGNITION IN THE DOMESTIC DOG (CANIS LUPUS FAMILIARIS)

by

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DEDICATION

To Marty, Acorn, and Sage for showing me the joy of simply being with dogs. And to Don for always believing in me.

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INTRODUCTION

This dissertation examines aspects of cognition in dogs. Cognition, broadly defined, refers to ways in which animals retain, process, and act on information taken in through the senses (Shettleworth 2001; Dukas 2004) and includes processes such as perception, learning, memory, and problem solving. Such processes play an important role in how animals make decisions in dealing with their physical and social environments (Shettleworth 2001). A special subset of cognition referred to as social cognition deals specifically with a wide range of social phenomena. Examples include cooperation in food retrieval (Hare et al. 2007), cooperation and competition during play (Bauer & Smuts 2007), recognition and categorization of conspecifics (Dittrich 1990), the development and maintenance of social relationships (de Waal 1991), deception in food storage (Dally et al. 2005; Leaver et at. 2007), knowing about what other conspecifics can and cannot see (Hare et al. 2001) or hear (Santos et al. 2006), understanding of third-party relationships (Engh et al. 2005), and individual recognition (Seyfarth et al. 2005; Holekamp et at. 2007).

In recent times, scientific interest in animal cognition has exploded, but this was not always the case. In the 1600's Rene Descartes, one of the most influential Western philosophers of the past few centuries, built a rigid and long-lasting divide between human beings and other species. According to Descartes, language and the consciousness and mental processes that they engendered were uniquely human attributes. He wrote that not only "do the beasts have less reason than men, but they have no reason at all" (Descartes 1637, p. 45). To Descartes, animals were unconscious automata—biological robots with no capacity for thought or feeling.

In the mid-nineteenth century, Darwinian evolutionary theory and the notion of a continuum among organic life, including mental processes, began to slowly erode the barrier that had been set up between humans and other living beings. In the *Descent of Man,* Darwin (1871, p. 494) wrote that "…the difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind." Darwin emphasized the comparative method and examined similarities and differences among species to gain an understanding of evolutionary relationships.

The comparative method is especially important in the study of animal cognition because it allows us to compare cognitive abilities across a variety of taxonomic groups and gain insight into the selective forces responsible for specific behavioral traits. Studies of cognitive processes in non-human species have focused on primates, but recent research has revealed that other species, including crows (Emery & Clayton 2004), parrots (Pepperberg 2006), and dolphins (Mercado et al. 1998) also have highly developed cognitive skills.

The social complexity hypothesis predicts that animals living in highly social environments may have evolved special cognitive processing abilities to address the complexities associated with group living (Byrne & Whiten 1988; Bond et al. 2003; Emery et al. 2007). Primates, dolphins, and a variety of bird species live in demanding social environments, but so do many of the social carnivores. However, with the possible exception of spotted hyenas (Holekamp & Smale 1991; Engh et al. 2005), very little is known about the cognitive abilities of social carnivores (e.g., lions, wolves, and domestic dogs).

Why study cognition in domestic dogs? Both genetically and behaviorally the domestic dog is very similar to its direct wild ancestor the gray wolf (*Canis lupus*). Domestication is believed to have occurred between 14,000 (Olsen 1985) and 100,000 years ago (Vila et al. 1997; Savolainen et al. 2002). Molecular genetic analyses by Robert Wayne and his associates at UCLA suggest that dogs are essentially domesticated wolves with only minor genetic modifications that affect developmental rates and timing (Wayne 1993). Wolves are highly social animals. They live in multigenerational family units; they have a fairly long developmental period before becoming independent; group members recognize each other individually; and individuals cooperate as well as compete for access to limited resources. Dogs share at least 80% of all behaviors reported for wolves (with breed variations), including similar play signals, greeting rituals, and body postures and facial expressions used to signal dominance and appeasement (Schenkel 1967; Abrantes 1997; Smuts et al. in preparation). Additionally, the dog presents us with an exceptional and unusual opportunity to study behavior in a domestic animal whose direct ancestor still exists in the wild, in contrast to some other domesticated animals, such as horses and cattle.

The current research trend is to use the domestic dog as a model in which to study human social and cognitive evolution (Miklósi et al. 2004; Hare & Tomasello 2005). Dogs are especially well-suited for this purpose because having evolved in close association with human groups, they underwent selection for functionally similar social skills (Miklósi et al. 2007). These skills may be more flexible and “human-like” than those of some species more closely related phylogenetically to humans (e.g., chimpanzees, bonobos) (Hare & Tomasello 2005). For example, dogs (including puppies) are inherently more skilled than chimpanzees (and wolves) at using human communicative gestures (e.g., pointing and gaze following) to find hidden food (Miklósi et al. 1998; Hare et al. 2002). Such findings suggest that dogs’ social skills represent a case of convergent evolution with humans. The overlap in social communication between dogs and humans has led some researchers to propose that the behavior of domestic dogs may provide insight into the social behavior of early hominids, including attachment, social learning, rule following, and information sharing—behaviors that may have formed the basis of later complex interactions (Csányi 2000; Miklósi et al. 2007).

Looking to dog behavior in order to understand how different selective pressures influence cognition has at least one problem. The current research emphasis has been on human-dog interactions with very little effort directed towards understanding how dogs interact with one another. If we are going to use dogs to help us understand social and cognitive evolution then we need to learn more about their cognitive abilities in general (see Chapter One) and the development and patterns of dog-to-dog social interactions more specifically (e.g., social cognition) (see Chapter’s Two and Three). Much of what has been written about dog behavior comes from the popular literature and lacks firm empirical support. Information on the cognitive abilities of dogs, including the development of behaviors in the social-conspecific domain, will provide important data for comparing the evolution of traits both within and across phylogenetic groups. Dogs are ideal subjects for such comparative work because of their prevalence, and their adaptation to living with humans makes them especially easy to study.

In Chapter One, we examine the performance of dogs at quantity-judgment tasks. Research in this area compares numerical abilities of animals across a large variety of species and attempts to understand the mechanisms underlying such abilities. For example, do animals represent number or quantity exactly, or do they use an approximation? Apes such as chimpanzees and orangutans appear to represent number or quantity approximately (Dooley & Gill 1977; Call 2000), while humans appear to represent small numbers (< 3 or 4) exactly and large numbers approximately (Xu & Spelke 2000; Feigenson et al. 2002). Most research in this area has traditionally used primates. Expanding the scope of comparative work beyond primate species will allow us to draw inferences about the circumstances selecting for different kinds of numerical competence.

Chimpanzees and orangutans possess a sophisticated "number's sense". Both can form mental representations of quantity and can mentally combine quantities together to make optimal foraging decisions (Call 2000; Beran 2004). Having a sense of quantity or number can also benefit animals in other ways—for example, by knowing which environments have the most members of the opposite sex (mating opportunities) or the least number of predators. During the formation of coalitions, when two or more individuals can vanquish a single individual or a large group has an advantage over a small group, individuals who are able to keep track of number, even in a relative sense, will have a competitive advantage. Coalitions are especially relevant in wolf society where rank reversals can result (Zimen 1981).

Studies examining numerical abilities in the dog are important to understanding cognitive abilities in domestic animals. In nearly all species of domestic animals, the brain-size to body-size ratio is smaller than it is in the wild progenitors. This finding has led some researchers to suggest that the process of domestication reduced selection for complex cognitive skills in dogs (Frank & Frank 1983, 1985). Research on the ability of dogs to judge quantities under a variety of conditions will elucidate whether or not a domesticated animal can demonstrate advanced numerical abilities, and it will allow us to compare the results for dogs with other non-domesticated species that show complex cognitive abilities (e.g., chimpanzees and orangutans).

In Chapter One, we replicate a study (with some modifications) originally conducted on captive orangutans (Call 2000) designed to test their ability at various quantity-judgment tasks. Specifically, we examine the perceptual and cognitive abilities of domestic dogs to choose the larger versus smaller quantity of food in two experiments. In experiment 1, we investigated the ability of 29 dogs to discriminate between two quantities of food presented in eight different combinations. We presented the choices simultaneously, and they were visually available to the subjects at the time of choice. In experiment 2, we tested two dogs from experiment 1 under three conditions. In condition 1, we used similar methods from experiment 1 and tested the dogs multiple times on the eight combinations from experiment 1 plus one additional combination. In conditions 2 and 3, the food was visually unavailable to the subjects at the time of choice, but in condition 2, food choices were viewed simultaneously before being made visually unavailable, and in condition 3, they were viewed successively. In these last two conditions, and especially in condition 3, the dogs had to keep track of quantities mentally in order to choose optimally. If dogs perform better as the distance between quantities increases, this would suggest that dogs, like some species of apes (see above), use an approximate mechanism of number or quantity representation rather than represent number exactly.

In Chapter's Two and Three, we turn our attention to cognition in the social domain and examine the development of social relationships among littermates of domestic dogs. Our findings are based on video data collected from four litters comprised of various breeds and breed mixes. Data collection occurred when the puppies were between 3 and 40 weeks of age, but collection times varied by litter.

Why study the *development* of social behavior? A complete understanding of a behavior involves taking four perspectives, one of which is developmental (Tinbergen 1963). The other three include causation, adaptation, and phylogeny. Addressing questions related to the ontogeny of social interaction is critical to understanding and evaluating adult social behavior (Bekoff 1972), and a developmental approach will also suggest functional explanations for social behaviors observed in adults (Tinbergen 1951).

In young domestic dogs virtually all intraspecific social interactions occur in the context of play, so we used play as a vehicle in which to understand the development of social relationships. Social play is especially relevant to the study of social cognition because it involves unpredictable movement patterns and sequences of behaviors that often change quickly. As a result, partners must rapidly assess and reassess their partner's intentions in order for play to continue (Bekoff 1999; Spinka et al. 2001). Additionally play offers a balance between cooperation and competition (Bauer & Smuts 2007). Animals must agree on certain ground rules (e.g., inhibited biting) in order for play to occur, and through play, animals can practice agonistic behaviors that can be used outside of play in a more serious context (Bekoff 1998, Bekoff & Allen 1999).

In Chapter Two, we focus on dyadic play and look at the formation of play partner preferences, diversity in choice of play partners, and the stability of play-partner preferences across time. To our knowledge, only one other study has examined the development of individual play partner preferences in any mammal (Thompson 1996, 1998), and our study is the first to describe and quantify it in any canid species. We measured offense (e.g., chasing, forcing a partner to the ground, etc.) and self-handicapping (e.g., voluntarily placing oneself in a disadvantaged or compromised position) behaviors during play, and we examined relationships between play initiations, offense behaviors, self-handicapping, and play signaling and how these relationships varied by sex. We also determined whether play conformed to 50–50 symmetry of roles between partners, which some researchers claim is necessary to sustain play (Aldis 1975; Pellis & Pellis 1998). Lastly, we examined continuity in the development of individual play behaviors (e.g., chasing, mounting, biting and shaking, etc.) across litters and time periods. For example, do individual play behaviors show up at approximately the same time during development across different litters regardless of breed or variety?

In 1999 Bekoff wrote that “There are very few data that are concerned with self-handicapping … in play.” This is still true today. With the exception of one other study on adult domestic dogs (Bauer & Smuts 2007), this is the only study in dogs that examined self-handicapping in play and the first study to examine the behavior among littermates. Results from Chapter Two allow us to compare our findings in puppies with similar data obtained on adult domestic dogs (see work by Bauer & Smuts 2007). Such a longitudinal comparison can shed light on the development, maintenance, and possible function of self-handicapping and other play behaviors (e.g., offense behaviors and play signaling) in a domestic species over the lifespan.

In Chapter Three we study triadic interactions and the role of third-party interventions in dyadic play between littermates of domestic dogs. Third-party interventions occur when an animal becomes involved in an ongoing aggressive or competitive encounter between conspecifics; sometimes the one intervening takes sides by supporting one party or the other (de Waal & Harcourt 1992). Interventions also occur in other contexts besides aggression, such as during social grooming, sexual contact, and play (Schilder 1990; Keil & Sambraus 1998); however, most of the research has focused on interventions in competitive encounters. Triadic interactions are especially important to the study of animal cognition because attending to the behavior of two conspecifics rather than one significantly increases the complexity of the encounter, making it more cognitively demanding (Whiten & Bryne 1988).

Most of the research on interventions has been conducted on primates, starting in the 1950's (Kawai 1958; Kummer 1957) and continuing up through the current day (Cheney 1977; Silk 1992; Roeder et al. 2002; van Schaik et al. 2004; Range 2006; Schino et al. 2007). Intervention behavior has also been studied, but to a lesser extent, in species other than primates such as dolphins (Connor et al. 1992), zebras (Schilder 1990), and goats (Keil & Sambraus 1998).

With the exceptions of spotted hyenas (Zabel et al. 1992; Engh et al. 2000) and African wild dogs (de Villiers et al. 2003), the study of intervention behavior in social carnivores is sorely lacking. There is almost no information on the specifics of intervention behavior in wolves; however, the little data that do exist suggest that interventions are an important component of wolf society. For example, wolves may use interventions to secure mating opportunities (Derix et al. 1993), develop alliances with pack members (Zimen 1975), and also to restructure rank relationships (Zimen 1981).

Why study intervention behavior in domestic dogs? Much of the previous research on intervention behavior has focused on how interventions influence rank relations among female primates, but very little data exist on the development of intervention behavior in juvenile animals in any species (Prud'homme & Chapais 1996). Our research addresses this gap by examining the role that interventions play in the development of social relationships among domestic dog littermates.

We examined interventions during play as opposed to actual fighting because we never observed fights within our litters. Play is thought to provide competitive training for puppies because they are able to practice both offense and defense behaviors, and many of the behaviors used during play are also seen during real fighting in adults (e.g., biting, jumping on top of another). However, in play, behaviors are often handicapped (e.g., not biting too hard), and movements are often punctuated with play signals to help maintain a play mood.

In Chapter Three, we examine whether interveners are more likely to join the winner (e.g., the dog directing offense behaviors, also called "winner support") or the loser (e.g., the dog receiving offense behaviors, also called "loser support") of an ongoing dyadic encounter. This area of research has received considerable attention in the non-human intervention literature. In most cases, interveners support the winner (Nishida 1983; Hemelrijk 1994; Chapais 1996, Watts 1997; Vervaecke et al. 2000). This can be the least risky option, especially if the aggressor is likely to redirect offense behaviors towards the intervener if targeted.

We also test two hypotheses concerning why animals might intervene. The first hypothesis suggests that animals intervene and selectively provide support to those who also support them (de Waal & Lutteral 1988, de Waal 1992). The second hypothesis suggests that interventions are opportunistic in nature and present a low-cost mean to target and potentially subordinate a conspecific (Chapais 1996; Prud'homme & Chapais 1996).

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CHAPTER 1

QUANTITY-BASED JUDGMENTS IN THE DOMESTIC DOG (CANIS LUPUS FAMILIARIS)

INTRODUCTION

Animals that are able to judge quantities or amounts, even in a relative sense, should be at an advantage in determining which environments have the least number of predators or competitors, the most reproductive partners, and the largest amount of food resources (Dehaene 1997). Natural selection should favor optimal decision-making, but animals must first compare in order to optimize. Previous research has shown that children (Huntley-Fenner & Cannon 2000), infants (Feigenson et al. 2002), and variety of non-human animals such as dolphins (Kilian et al. 2003), monkeys (Hauser et al. 2000), apes (Rumbaugh et al. 1987; Boysen & Bernston 1995; Dooley & Gill 1997; Call 2000), rats (Meck & Church 1983), birds (Pepperberg 1987), and raccoons (Davis 1984) can discriminate between the quantities of various objects in their environments.

In some studies, researchers train or condition animals to make quantity comparisons. For example, rats learned to press 1 of 2 levers to distinguish 2 flashes of light from 4 flashes (Meck & Church 1983). Likewise, raccoons learned to select a transparent cube containing 3 grapes and ignore those cubes containing 2 or 4 grapes in order to receive a reward (Davis 1984). After years of training, an African grey parrot (*Psittacus erithacus*) could correctly identify the number of red keys present when researchers presented him with a group of objects containing red keys, green keys, red toys, and green toys (Pepperberg 1987).

Independent of training, selection should favor the natural development of such decision-making abilities in a number of ecological and social situations, including those involving parental investment, feeding competition, and intra- or inter-group aggression (Hauser 2003). For example, in the American coot (*Fulica americana*), an aquatic bird subject to conspecific brood parasitism, the number of eggs a female lays is directly related to the number or surface area of eggs already present in the nest. Females respond to their own eggs in a nest but ignore the number of parasitic eggs when regulating clutch size (Lyon 2003). Similarly, to maximize energetic rates of return, animals must make decisions between which patches of food to forage in (Stephens & Krebs 1986). Experiments using playbacks of conspecific calls in African lions (McComb et al. 1994), chimpanzees (Wilson et al. 2001), howler monkeys (Kitchen 2004), and wolves (Harrington & Mech 1979) showed that decisions about whether to respond aggressively to competitors reflected the size of the home group relative to the group size of competitors.

In this study, we examined how domestic dogs (*Canis lupus familiaris*) respond to differences in quantity naturally, without explicit training for a desired response. Previous research on chimpanzees (Dooley & Gill 1977; Rumbaugh et al. 1987; Beran 2001, 2004) and orangutans (Call 2000) addressed their ability to distinguish between two different quantities of food. Dooley & Gill (1977) reported that Lana the chimpanzee was able distinguish the larger quantity of cereal pieces from the smaller quantity in most trials. Lana was tested on all combinations between 1 and 10, and she performed better when the numerical distance (difference between quantities) was large (e.g., 1 vs. 4 was easier than 3 vs. 4), the ratio between quantities was small (e.g., 2 vs. 3 was easier than 5 vs. 6), and when the total number of pieces in both arrays combined was small.

Three orangutans performed similarly. When tested on all quantity combinations between 1 and 6, in most trials they chose the larger quantity of cereal over the smaller quantity (Call 2000), and their performance was positively correlated with the numerical distance between the two quantities and negatively correlated with ratio between quantities. For Lana, both quantities of cereal were always visually available at the time of choice. However, for the orangutans, in some trials the cereal was visually available, but in other trials, the experimenter covered the quantities with an opaque lid after the animal had an opportunity to visually compare them. Orangutans performed equally well whether the cereal was visually available or concealed at the time of choice. For all trials in both the chimpanzee and orangutan experiments, the subjects were positively rewarded whether they chose the larger or the smaller quantities, because they got to consume the quantity selected.

The performances of Lana and the orangutans suggest analog representations of quantity ("mental magnitudes") (Moyer & Landauer 1967; Gallistel & Gelman 2000) subject to scalar variability. Scalar variability describes a representation of quantity in which the "noisiness" of the estimate (measured by the degree of variation in response across trials) is directly proportional to the size of the quantity being estimated (Gallistel & Gelman 2000). Discrimination between mental magnitudes that are subject to scalar variability follows Weber's law, which states that two magnitudes are more easily distinguished as the ratio between the smaller divided by the larger magnitude decreases. Weber's law (Dehaene et al. 1998; Gallistel & Gelman 2000) reflects distance and size effects as described above for the chimpanzee and orangutan studies. Many other studies of quantity estimation report results consistent with Weber's law, implying that magnitude representations of quantity are widespread in both humans and nonhuman animals (Beran 2001, 2004; Cordes et al. 2001; Hauser 2003; Lewis et al. 2005; Jordan & Brannon 2006a).

In many natural situations, such magnitude representations may allow sufficiently accurate estimates of quantity. For example, for group-living, territorial species, the ability to assess and compare group sizes would allow for optimal decision-making during territorial disputes. In several studies, researchers used conspecific playbacks (playing calls from 1–5 individuals simultaneously) to simulate rival groups of conspecifics (chimpanzees: Wilson et al. 2001; lions: McComb et al. 1994; howler monkeys: Kitchen 2004, and wolves: Harrington & Mech 1979). In all of these species, animals were more likely to respond to perceived threats when numeric odds were in their favor, indicating an ability to accurately infer relative group size within this numerical range. Evidence from actual intergroup encounters supports the hypothesis that small groups avoid larger groups. For example, in 13 aggressive incidents between a pack of free-ranging, domestic dogs living in the mountainous region of central Italy and smaller packs or an individual dog, the smaller group always withdrew before aggression became physical (Macdonald & Carr 1995).

The importance of territoriality among wolves (Meier et al. 1995; Smith & Ferguson 2005) and their descendants, free-ranging domestic dogs, suggests at least one context in which the ability to judge relative quantities could prove important to survival and reproductive success. Since hunting in these species often involves discriminating the group size of potential prey, quantity comparisons could also be important during foraging. In this study, we took advantage of the availability and tractability of domestic dogs to investigate their discrimination abilities. Previous research that measured dogs' looking time at expected (e.g., 1+1 = 2) versus unexpected outcomes (e.g., 1+1 = 1 and 1+1 = 3) showed that dogs looked longer at unexpected outcomes. Researchers suggested that dogs anticipated the outcome of the calculations and demonstrated a limited ability to count (West & Young 2002). In the current study, we tested a wider range of quantities than West & Young (2002) and employed methods similar to those used to investigate orangutans' abilities to distinguish between two quantities of food (Call 2000). We use the term "quantity" to signify amount without implying a reference to number or the ability to count (cf. Rumbaugh et al. 1987; Call 2000; Shumaker et al. 2001).

Our study had three main goals. First, we aimed to compare numerical performance in a quantity discrimination task by a carnivore to performances by nonhuman primates (previous studies on carnivores are lacking). Are dogs as skilled as nonhuman primates in discriminating small sets of quantities? Second, we wanted to determine whether the responses of dogs conformed to Weber's law, indicating a mental magnitude mechanism for quantity estimation. Based on studies of primates, we predicted that dogs would be more likely to choose the larger quantity when numerical distance between the two quantities was large, ratio was small, and total quantity being compared was small. Third, because the choices were visually available simultaneously in our original trials (e.g., experiment 1, conditions 1 and 2 of experiment 2, below), dogs could discriminate quantity based on perceptual cues alone. Therefore, to investigate the possibility that dogs can form and remember mental representations of quantity, we conducted preliminary tests requiring two subjects to choose between quantities that were visually available successively (condition 3 of experiment 2). We predicted that dogs, like orangutans tested under similar conditions (Call 2000), would choose the larger quantity regardless of whether or not the food was visually available at the time of choice.

EXPERIMENT 1

In experiment 1, we tested whether dogs overall (data combined for multiple subjects) could discriminate the larger from the smaller quantity of food when presented with the following 8 combinations: 1 vs. 4, 1 vs. 3, 2 vs. 5, 1 vs. 2, 2 vs. 4, 3 vs. 5, 2 vs. 3, and 3 vs. 4. Results from a pilot study conducted prior to experiment 1 showed that all 12 adult dogs tested on the single quantity combination of 1 vs. 5 could discriminate the larger quantity over the smaller quantity.

Methods

<u>Subjects</u>

The 29 dogs used in the study were pets recruited from veterinarian offices, a local dog club, friends, neighbors, and people affiliated with the study. Of the 29 subjects, 18 were female and 11 male; 17 were purebred and 12 mixed breeds. Ages ranged from 1 to 12 years. Testing was conducted between June 2003 and August 2003.

Procedure

We tested all dogs individually. Each dog's owner brought his or her dog into the testing room, and the dog had 5 min to explore the testing environment. Prior to trial 1, the experimenter fed the dog a piece of hotdog—the food used in the experiments. We wanted to be sure that the dog liked the food and was motivated to obtain it before proceeding. To increase motivation, we asked owners to refrain from feeding their dogs just prior to testing. All subjects were motivated by hotdogs.

In preparation for testing, the owner took the dog to a marked location. The owner positioned the dog into place, usually by gently holding the dog from behind. A few dogs maintained a sit and stay without aid, in which case the owner stood behind the dog. While the dog waited in place, the experimenter baited two plates outside of the dog's view. The experimenter randomly dropped a set number of hotdog pieces onto each plate, depending on the quantity combination being tested, making no attempt to arrange the pieces into a consistent pattern. Plate construction was blue plastic with a 19 cm diameter, and each piece of food was 1/8th of a standard hotdog.

After baiting, the experimenter covered each plate with an opaque lid (Fig. 1a, step 1). Hare et al. (2002) reported that dogs could follow a human gaze to locate hidden food, so the experimenter wore dark sunglasses to avoid inadvertently cueing the dog with her eyes. Visual cueing by the owners was unlikely because they stood behind the dog. However, as an extra precaution, we asked owners to refrain from looking at the plates and instead focus their attention straight ahead at the wall in front of them. The experimenter approached the dog and put both plates down on the ground at the same time in front of the subject. The plates were set 1.2 m apart with the midpoint between them 1 m directly in front of the dog. The experimenter uncovered both plates at the same time (Fig 1a, step 2) and simultaneously tapped lightly on the edge of each plate in order to get the dog to look at both plates. Once the dog had visually examined both quantities, the experimenter waited 5 s and then said “okay”, which meant that the owner could release the dog to choose (Fig 1a, step 3). The dog chose by going over to the plate and eating the hotdogs from that plate. As the dog was eating, the experimenter quickly removed the un-chosen plate from the dog’s access. We provided no additional reinforcement.

We tested each of the 29 dogs once on each of the 8 quantity combinations over 4 sessions, with 2 trials per session. Successive sessions for each subject were separated by a minimum of two days. We also wanted to test for a learning effect across sessions, so we randomly selected 14 of the dogs to begin testing with what we called the “small ratio group” and end their testing with the “large ratio group.” The remaining dogs began with the “large ratio group” and ended with the “small ratio group”. Ratio was simply the smaller quantity in the comparison divided by the larger quantity (e.g., 1 vs. 4 combination had a ratio of 0.25). We included combinations 1 vs. 4, 1 vs. 3, 2 vs. 5, and 1 vs. 2 in the small ratio group and combinations 2 vs. 4, 3 vs. 5, 2 vs. 3, and 3 vs. 4 in the large ratio group. Although the combinations 1 vs. 2 and 2 vs. 4 had the same ratio (i.e., 0.50), we assigned one combination to the small ratio group (1 vs. 2) and the other to the large ratio group (2 vs. 4) to equate sample sizes across groups. We assigned dogs to each ratio group in a counterbalanced manner. We counterbalanced the left-right presentation of quantities across trials for each combination and randomly assigned the order of presentation within each group.

Data analysis

For statistical analyses in all experiments, alpha was set at 0.05 for rejection of the null hypothesis. Statistical tests were conducted using SPSS® version 11.5 and SAS® version 8.1. Tests are one-tailed for all directional predictions: 1) dogs would choose the larger quantity more often than the smaller quantity and 2) their performance (the percentage of times, out of 8 trials, that the dog chose the larger over the smaller quantity) would improve as the numerical distance between quantities (the larger minus the smaller quantity) being compared increased and as the ratio between quantities (defined previously) and the total quantity (the larger plus the smaller quantity) decreased. Results from our pilot study and research on human children and nonhuman animals support these directional predictions (Dooley & Gill 1977; Boysen & Bernston 1995; Call 2000; Huntley-Fenner & Cannon 2000; Feigenson et al. 2002). For all parametric statistics, the assumptions of homogeneity and normality were met.

We used a GEE (generalized estimating equation) model to test whether the dogs' ability to choose the larger quantity varied with 1) ratio between quantities, 2) numerical distance between quantities, and 3) total quantity of hotdogs available at the time of choice. The GEE model is appropriate for use here because it extends the GLM (general linear model) algorithm to accommodate correlated observations within subjects, and it allows for comparison across subjects (Diggle et al. 1994; Hardin & Hilbe 2002).

To test whether dogs chose the larger quantity significantly more often than the smaller quantity in each of the 8 individual combinations (see above), we conducted binomial tests and compared the numbers of dogs choosing the larger and smaller quantities within each combination.

Results and Discussion

Of the 29 dogs tested, three never finished with the testing, and we excluded them from the analyses. Eight dogs exhibited a laterality bias, going to the same side on every single trial regardless of the quantity presentation. We excluded them as well, which left 18 dogs for data analysis. Of the 18 subjects, 12 were female and 6 male; 10 were purebred and 8 mixed breeds. Fifteen out of the 18 remaining dogs (83%) chose the larger quantity more often than the smaller quantity across the 8 trials (sign test, $P < 0.0001$); two chose the larger and smaller quantities equally often, and one chose the smaller quantity more often. There was no effect of age (Pearson correlation, $r = -0.163$, $P = 0.518$, $n = 18$) or sex (independent sample *t*-test, $t(16) = 0.230$, $P = 0.821$, $n_{\text{female}} = 12$, $n_{\text{male}} = 6$) on performance. Males chose the larger plate 73% of the time, and females 71% of the time.

We found no learning effect across trials. Dogs that started or ended with the smaller ratios got an equal percentage (75%) of the small ratio trials correct (independent sample *t*-test, $t(16) = 0.00$, $P = 1.000$, $n_{\text{female}} = 12$, $n_{\text{male}} = 6$). Likewise, there was no significant difference in the percentage correct between the dogs that started with (73% correct) or ended with (59% correct) the large ratio trials (independent sample *t*-test, $t(16) = 0.971$, $P = 0.346$, $n_{\text{started}} = 8$, $n_{\text{ended}} = 10$).

Dogs as a group followed Weber's law: they were more likely to choose the larger quantity when the ratio between quantity combinations was small (GEE, $Z = -2.69$, $P =$

0.007, *n* = 18) (Fig. 2) and when the numerical distance between quantity combinations was large (GEE, *Z* = 2.86, *P* = 0.004, *n* = 18) (Fig. 3). Previous research obtained similar results for orangutans (Call 2000) and chimpanzees (Dooley & Gill 1977) when tested under similar conditions. There was no significant relationship between total quantity and the dogs' overall performance (GEE, *Z* = 0.29, *P* = 0.769, *n* = 18). Again, similar results were obtained for orangutans (Call 2000) but not for Lana the chimpanzee, who was more likely to choose the larger quantity when total quantity available at the time of choice was small (Dooley & Gill 1977). However, the chimpanzee data contained a wider range of total quantity values compared to this study and the orangutan study. This difference may account, at least in part, for the discrepancy in total quantity results among the studies.

Finally, we examined the ability of dogs to discriminate the larger from the smaller quantity within each of the 8 individual quantity combinations. Dogs as a group chose the larger quantity significantly more often than the smaller quantity for all combinations except those that differed by 1 piece (binomial test, 1 vs. 4: *P* = 0.001; 1 vs. 3: *P* = 0.048; 2 vs. 5: *P* = 0.048; 1 vs. 2: *P* = 0.240; 2 vs. 4: *P* = 0.004; 3 vs. 5: *P* = 0.015; 2 vs. 3: *P* = 0.240; 3 vs. 4: *P* = 0.407; *n* = 18 for each combination). Our findings parallel the data obtained for orangutans when tested under very similar experimental conditions. Although Call (2000) did not statistically examine the performance of orangutans within each quantity combination, the data he presented (Table 2, p. 139) enabled us to do so. He tested each subject 12 times in each quantity combination, and using his data, we calculated that two of the three orangutans did not discriminate above chance between 1 vs. 2 and 2 vs. 3, and one orangutan did not discriminate between 3 vs. 4 (binomial test, $P > 0.05$), similar to the dogs in the current study.

EXPERIMENT 2

In experiment 2, we examined, in greater depth, the abilities of two dogs from experiment 1. Experiment 2 consisted of three conditions that were presented successively. Progression from one condition to the next was dependent upon successful performance in the previous condition.

In condition 1, we verified the generality of the results from experiment 1, and in conditions 2 and 3 we tested to see if dogs could still choose the larger quantity when the food was visually unavailable at the time of choice. In conditions 1 and 2, the dogs could rely strictly on perceptual cues to choose the larger quantity, but success in condition 3 required some mental representation of quantity in order to choose optimally. For all three conditions, we tested the dogs multiple times on the 8 combinations from experiment 1, and we also tested them on two additional combinations, 1 vs. 1 and 1 vs. 5. We included the 1 vs. 1 condition to see if a side preference might develop in a setup where the dogs would do equally well by choosing either plate. Condition 2 and 3 tests presented a potentially more difficult challenge for the dogs, so we added a combination (1 vs. 5) that, according to Weber's law and the results from our pilot study (see experiment 1), should be relatively easy for them to discriminate. We also included the 1 vs. 5 combination in condition 1 to make it directly comparable to conditions 2 and 3.

Methods

Subjects

One of the dogs, Marty, an 8-year old Labrador retriever, chose the larger quantity in 7 out of 8 trials in experiment 1; he missed only the 3 vs. 4 combination. The second dog, Acorn, a 5-year old Doberman pincher, chose the larger quantity in all 8 trials. Testing was conducted between August 2003 and January 2004.

Procedure

Condition 1: open. The setup was nearly identical to that of experiment 1 (Fig. 1a), with some exceptions. First, we gave each dog 4 warm-up trials using 1 vs. 0 just prior to a session. If the dog chose the quantity of 1 in all 4 trials, we preceded to testing. If not, we gave 2 additional warm-up trials. We used warm-up trials as a pretest to screen for laterality preferences. We did not anticipate laterality preferences in experiment 1 and, therefore, did not screen for them. Second, we presented all 10 combinations in a single session. We randomized the order of presentation within sessions, and counterbalanced trials for side within sessions. Third, we tested Marty and Acorn 11 times in each quantity combination over the course of the experiment. Lastly, because we tested the two dogs numerous times within a session, we used smaller pieces of hotdogs to prevent them from becoming satiated early on, and we positioned the dogs slightly closer to the plates, so that they could more easily view the smaller individual pieces. Each piece of food was 1/16th a standard hotdog; the plates were 1 m apart with the midpoint between the plates being 0.8 m directly in front of the subject.

Condition 2: simultaneous closed. The procedure and quantity combinations were the same as in condition 1 except the hotdogs were not visually accessible to the dogs at the time of choice. After the experimenter presented both plates (Fig. 1b, step 1), she uncovered them simultaneously and allowed the dog to examine the two quantities (Fig. 1b, step 2). She waited 5 s, re-covered the plates, and then waited an additional 3 s before releasing the dog to choose (Fig. 1b, step 3).

Condition 3: successive closed. The setup and quantity combinations were the same as in conditions 1 and 2 with one exception. After baiting both plates and placing them on the ground in front of the dog (Fig. 1c, step 1), the experimenter first uncovered the plate on her right and waited until the dog examined the quantity for 5 s before placing the cover back on the plate (Fig. 1c, step 2). Next, she uncovered the plate to her left and waited until the dog examined that quantity for 5 s before covering the plate (Fig. 1c, step 3). After both plates were covered, she waited an additional 3 s before releasing the dog to choose (Fig. 1c, step 4).

Results and Discussion

For all conditions, both dogs chose the larger quantity significantly above chance for all trials combined (binomial test, Marty: condition 1, 92% of trials, condition 2, 88%, condition 3, 84%, $P < 0.001$ for all, $n = 99$ for each condition; Acorn: condition 1, 93% of trials, $P < 0.0001$, condition 2, 65%, $P = 0.002$, condition 3, 64%, $P = 0.005$, $n = 99$ for conditions 1 and 3 and $n = 98$ for condition 2 [Acorn refused to choose in one trial]).

In conditions 1 and 2, Marty was more likely to select the larger quantity when the numerical distance between quantities was large and the ratio between quantities was small. Ratio and numerical distance were not significantly correlated with the percentage of correct trials in condition 3, and total quantity was not significant in any of the conditions (Table 1).

In condition 1, Acorn performed better when the ratio between quantities was small and the total quantity large. Ratio, numerical distance, and total quantity were not significantly related to performance in conditions 2 and 3, and numerical distance was not significant in condition 1 (Table 1).

Neither Marty nor Acorn showed a side preference in the 1 vs. 1 combination (binomial test, $P > 0.05$ for both dogs in each condition, $n = 11$ for each dog and condition), and with one exception (i.e., Marty in condition 2, $\chi^2 = 4.18$, $df = 1$, $P = 0.041$), the dogs' success choosing the larger quantity did not differ significantly between the first 4 and last 4 testing sessions (condition 1, Fisher's exact test; conditions 2 and 3, Pearson chi-square test; $P > 0.05$ for both dogs in each condition with the one exception [see above]).

In condition 1, which is most comparable to experiment 1, the effects of ratio on performance for Marty and Acorn and the effect of numerical distance on performance for Marty are similar to what we found for the dogs as a whole in experiment 1. The finding that Acorn's performance was not related to numerical distance in condition 1 may have resulted from a ceiling effect that masked the distance effect for her. Such distance effects might become apparent if a larger range of quantity combinations are used. The results for individual quantity combinations varied with condition (Table 2), but neither dog chose the larger quantity in the 3 vs. 4 combination under any condition in experiment 2 (and dogs were unsuccessful at it in experiment 1), further suggesting a ratio effect.

Control Tests

In experiments 1 and 2, we showed that dogs could discriminate based on quantity, but we do not know whether dogs were basing their decisions on number or some other parameter that varies with number such as surface area or volume. However, we can eliminate two other potentially confounding cues that could have affected the dogs' decision-making: 1) olfaction and 2) experimenter effects.

A dog's sense of smell is extremely sensitive (McCartney 1968; Passe and Walker 1985), serving to enhance social recognition (Fox 1971; Hepper 1986) and aiding in the identification and receptivity of potential mates (Beach et al. 1983). To address the possibility that choices were based on olfaction, we tested Marty and Acorn ten times on the quantity combination of 1 vs. 5. The experimental setup was nearly identical to that of experiment 1 except instead of plates, we placed hotdog pieces in opaque bowls that were open at the top and tall enough so that the dogs could not see inside of the bowls. We hypothesized that if dogs were basing their choice on smell, they should go to the bowl containing 5 pieces in most of the trials. However, Marty chose the bowl containing 5 pieces in 50% of trials and Acorn chose the bowl containing 5 pieces in 60% of trials (binomial test, $P = 1.000$ for both dogs, $n = 10$ for each dog).

A second alternative explanation for the dog's performance is that the experimenter, despite wearing sunglasses, somehow inadvertently provided cues that aided subjects in selecting the larger quantity (i.e., the Clever Hans effect). In both experiments 1 and 2, a single researcher was responsible for both baiting the plates and presenting them to the dogs. To test for the possibility that the experimenter knowing which plates contained the larger and smaller quantities may have affected the dogs' performance, we conducted additional trials with Marty and Acorn. For all trials, an assistant baited both plates and handed them to the experimenter already covered. For half the trials (randomly chosen), the assistant informed the experimenter which plate contained the greater number of pieces ("informed" trials), and for the remaining 6 trials, the experimenter was not informed which plate contained more ("blind trials"). When the experimenter was informed, she presented the plates as described in the setup for experiment 2, condition 1, and in the other half, the experimenter presented the plates from behind an opaque screen that prevented her from seeing the two quantities until after the dog chose, precluding inadvertent cueing (the assistant, in all trials, was not visible to the dog).

We tested Marty and Acorn on the quantity combinations 1 vs. 4, 1 vs. 3, and 3 vs. 5. We presented each combination 8 times over 2 sessions, with 12 trials per session. Quantity combinations and screen/no-screen trials were counterbalanced within each testing session. If the experimenter inadvertently influenced the subjects' ability to choose the larger quantity, then the dogs should have performed better on no-screen trials. They did not. Marty chose the larger quantity in 92% of trials and Acorn in 83% of trials (binomial test, Marty: $P < 0.001$; Acorn: $P = 0.001$; $n = 24$ for each dog), and their ability to choose the larger quantity was independent of trial type (binomial test, Marty: $P = 0.832$; Acorn: $P = 0.503$; $n = 24$ for each dog).

DISCUSSION

Our study had three primary goals. First, we examined the ability of dogs to discriminate between two quantities that differed in number and compared their performances to nonhuman primates. Pooling across all quantity conditions, dogs chose the larger quantity of food over the smaller quantity in all experiments. For all dogs in experiment 1 and Marty in conditions 1 and 2 (experiment 2), dogs chose the larger quantity most often when the numerical distance between quantities was large and ratio between quantities was small. These results parallel those obtained for orangutans (Call 2000) under testing conditions similar to those in experiments 1 and 2. In condition 1 (experiment 2), Acorn chose optimally when ratio between quantities and total quantity compared were small. Lana the chimpanzee was more likely to choose the larger quantity of food under these same two conditions (Dooley & Gill 1977). Overall, our results indicate that some dogs can perform on par with nonhuman primates in these particular tasks.

Second, we examined aspects of the mechanism responsible for quantity discrimination. Does the pattern of discrimination conform to an analog (magnitude) model of quantity representation, or do the results suggest an alternative explanation? The detrimental effect on performance of smaller numerical distances between quantities, larger ratios between quantities, and larger total quantities (i.e., for Acorn in condition 1) suggests that dogs rely on an approximate mechanism of quantity representation that conforms to Weber's law and fits an analog model (Gallistel & Gelman 2000). However, correlations between the subject's performance and numerical distance between quantities, ratio, and total quantity broke down for Acorn in condition 2 and for Marty in condition 3. Therefore, these later results do not conform to an analog model of representation. Nor do they resemble the results for orangutans (Call 2000), whose performance conformed to the predictions of Weber's law under all testing conditions, including those comparable to our conditions 2 and 3. Beran (2004) found a similar break-down effect with chimpanzees. Chimpanzees chose the larger quantity when presented with two and three sets of non-visible food items. Their decreased performance when sets were close in number and large in magnitude suggested an analog model of magnitude representation. However, when chimpanzees were given the more challenging task of choosing the larger of two sets after the experimenter removed two or three of the initially presented food items, ratio was no longer associated with performance, even though one of the two subjects still chose the larger quantity at levels above chance. Future work should explore the mechanisms responsible for outcomes in condition 2 and especially condition 3 (also see the discussion on mental representation below).

One commonly cited alternative to the analog model of quantity representation is the object file model (although there are other models, e.g., Siegler & Opfer 2003). In this model, performance is not subject to Weber's Law, but instead is limited by set size. Mental files are opened, one for each object in the set. This mechanism is precise, rather than approximate, representing quantity exactly up to a set size limit of approximately three or four (Hauser 2000, 2003; Feigenson et al. 2002). If dogs were using an object file model of quantity representation, we would have expected success at 1 vs. 2 and 2 vs. 3, but this was not typically the case (see experiment 1 and Table 2).

Our third goal for the study was to examine whether dogs could form mental representations of quantity, rather than rely strictly on perceptual cues to choose the larger quantity. In experiment 1 and experiment 2 (condition 1) , dogs were most likely using some perceptual mechanism (Rumbaugh et al. 1987) to approximate differences in quantities when both plates of food were visually available at the time of choice (Fig. 1a). In conditions 2 and 3 (Figs. 1b and 1c), the tasks were potentially more difficult because the food was visually unavailable at the time of choice. As the tasks became more difficult, individual performances decreased somewhat; however, both subjects performed above chance at selecting the larger quantity across all trials in both conditions. In condition 2 (Fig. 1b), Marty visually compared both quantities and then sometimes focused and held his attention on the plate containing more, so that even after the experimenter covered both plates, his gaze was fixed on his final choice. With this strategy, Marty could still choose the larger quantity using strictly perceptual cues. However, the successive presentation in condition 3 (Fig. 1c) made visual fixation impossible because subjects had to examine each plate in turn and form some mental representation of quantity, rather than rely solely on perceptual mechanisms (Call 2000) to choose optimally.

A number of studies have examined the ability of dogs to encode and maintain the spatial location of objects in working memory using a series of retention intervals. In one such study, dogs' working memory for locating hidden objects was very good up to 30 s and then gradually deteriorated up to 240 s, but even at 240 s, the subjects still performed above chance (Fiset et al. 2003). Other studies show that dogs can remember the spatial location of auditory information for up to 120 s (Kowalska 1995, 2000). Although these experiments examine how memory relates to spatial location rather than to quantity discrimination, the current study does contain a spatial component. The dogs in condition

3 (experiment 2) showed evidence of an ability to encode in memory which of the two locations contained the plate with more food. Future studies could examine the effects of increasing delays on the dog's performance in two-choice tasks like the ones used in conditions 2 and 3 (experiment 2).

The current study addressed the potential for dogs to judge differences in food quantity. The question remains whether quantification ability in dogs is context-specific or a more general mechanism—i.e., does the ability to quantify in a foraging context transfer to quantities in a social or territorial context? Research in this area is sparse. However, some experimental work suggests the existence of cross-modal transfer in quantification. For example, both human infants and rhesus monkeys (*Macaca mulatta*) were able to match the number of vocalizations they heard (i.e., auditory task) with the corresponding number of adult humans or monkeys (i.e., visual task) in 2 vs. 3 comparisons (Jordon et al. 2005; Jordan & Brannon 2006b). Likewise, adult humans approximated the difference between large sets of elements presented successively when one array consisted of dots on a screen and a second array consisted of auditory sequences, and their ability to discriminate decreased as the ratio between the two comparisons increased (Barth et al. 2006).

We demonstrated that domestic dogs can perform similarly to apes when required to judge relative quantities of food. Our study focused on what domestic dogs can do in general (experiment 1) and what two "high performing" dogs can do given increasingly demanding tasks (experiment 2), rather than on the potential for differences in quantification abilities among breeds. Dogs have descended from group-living wolves (Vilà et al. 1999), but we have since modified form and function to meet our requirements. The American Kennel Club classifies purebred dogs into 7 breed groups based on intended function (AKC 1992). The 10 purebred dogs in this study represented only 3 out of the 7 breed groups (1 working group dog, 3 herding dogs, and 6 sporting group dogs). Systematic investigation of breed differences in quantity judgment tasks could reveal relationships between specific cognitive abilities and "ecological niche" (i.e., the jobs the dogs were bred for) *within* species, as previously demonstrated in comparisons across species (Gould-Beierle 2000; Brodin 2005). For example, some herding dogs bred to keep track of livestock might naturally be more attentive to quantity differences than breeds bred primarily for chasing game or human companionship.

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Table 1-1. Summary of results for two subjects from experiment 2 as a function of ratio between quantities, numerical distance, and total quantity

	Ratio		Numerical distance		Total Quantity	
Conditions	rho	*P*	rho	*P*	rho	*P*
Marty:						
1	**-0.875**	0.001	**0.633**	0.03	-0.397	0.15
2	**-0.699**	0.02	**0.612**	0.04	-0.209	0.30
3	-0.492	0.09	0.324	0.20	-0.426	0.13
Acorn:						
1	**-0.755**	0.01	0.377	0.16	**0.715**	0.02
2	-0.368	0.17	0.332	0.19	-0.151	0.35
3	-0.069	0.43	0.332	0.19	0.532	0.07

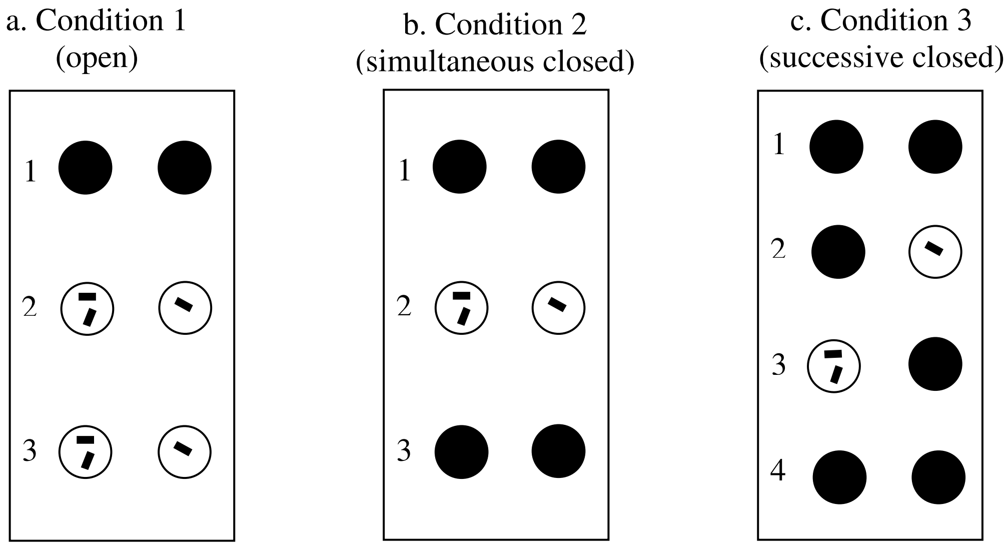
Spearman rho correlation coefficients a and associated *P* values from testing the relationship between the percentage of correct trials for each dog in 3 conditions of experiment 2 as a function of ratio between quantities, numerical distance and total quantity ($n = 99$ for each dog in each condition with one exception[b]). Condition 1 = open, Condition 2 = simultaneous closed, Condition 3 = successive closed. [a]one-tailed tests, significant rho ($P < 0.05$) in bold. [b]$n = 98$ for Acorn in condition 2; she refused to choose in one trial.

Table 1-2. Performance of two dogs from experiment 2 in each of nine individual quantity combinations

	Individual quantity combinations							
Conditions	1 vs. 5	1 vs. 4	1 vs. 3	2 vs. 5	1 vs. 2	2 vs. 4	3 vs. 5	2 vs. 3
Marty								
1	**<0.0005**	**<0.0005**	**<0.0005**	**<0.0005**	**<0.0005**	**0.01**	**0.01**	0.11
2	**<0.0005**	**0.01**	**<0.0005**	**<0.0005**	**0.03**	0.11	**0.03**	**0.01**
3	**<0.0005**	**0.01**	**<0.0005**	**0.03**	0.11	**0.03**	0.50	**<0.0005**
Acorn:								
1	**<0.0005**	**<0.0005**	**<0.0005**	**0.01**	**<0.0005**	**<0.0005**	**0.03**	**0.01**
2	**0.01**	0.27	0.11	0.50	0.50	0.11	0.50	0.11
3	0.11	0.11	0.50	0.50	0.50	0.27	0.11	0.50

Summary of results for individual quantity combinations for each dog in 3 conditions of experiment 2 ($n = 99$ for each dog and condition with one exception[a]). Condition 1 = open, Condition 2 = simultaneous closed, Condition 3 = successive closed. Numbers in table are P values[b] associated with one-tailed binomial tests. [a]$n = 98$ for Acorn in condition 2; she refused to choose in one trial of 3 vs. 4. [b]significant values ($P < 0.05$) in bold.

Figure 1-1. Procedures followed in experiments 1 and 2

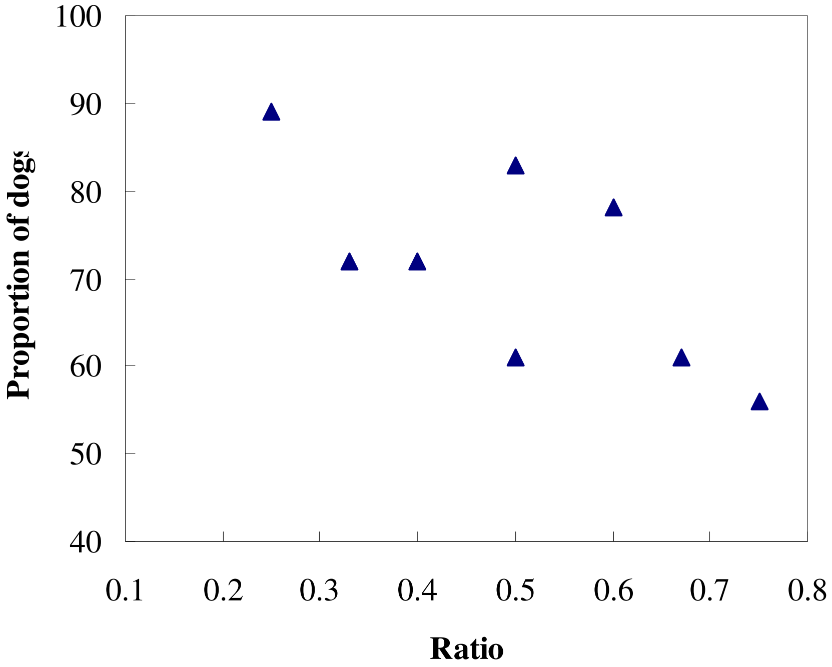

a. Condition 1
(open)

b. Condition 2
(simultaneous closed)

c. Condition 3
(successive closed)

Procedure followed in experiment 1 (open condition) and each of the three conditions in experiment 2 (modeled after Call 2000). Numbers next to plates refer to the steps of each procedure. See text for full description.

Figure 1-2. Results from experiment 1 as a function of ratio between quantities



Proportion of dogs selecting the larger quantity in experiment 1 as a function of ratio between quantities on two plates. Generalized estimating equation (GEE), $Z = -2.69$, $P = 0.007$, $n = 18$.

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CHAPTER 2

PARTNER PREFERENCES AND ASYMMETRIES IN SOCIAL PLAY AMONG DOMESTIC DOG (CANIS LUPUS FAMILIARIS) LITTERMATES

INTRODUCTION

Social play is play directed at a conspecific (Bekoff & Byers 1981; Fagen 1981; Bekoff 1984) and in canids includes behaviors such as chasing and play-fighting games, mounting behavior (i.e., mimicking copulatory behavior), and inhibited biting (Bekoff 1974; Burghardt 2005). In this study we videotaped social play within litters of domestic dogs (*Canis lupus familiaris*) to examine its role in the development of social relationships. We studied four litters of different breeds (one was a mixed-breed litter), and we continued observations on one litter for longer (40 weeks) than many previous studies have done. To our knowledge, this is the first study in domestic dogs to systematically compare numerous aspects of social play (such as play-partner preferences, role reversals, and self-handicapping) both across time and across different litters.

Hypotheses abound concerning the functions of social play (Burghardt 2005). Animals may play to learn valuable social skills (Biben 1998) or to strengthen (Bekoff 1984) or test social bonds (Zahavi 1976); as training for cognitive (Bekoff 1984; Spinka et al. 2001) or motor development (Byers 1998); to develop the emotional flexibility needed for dealing with unexpected situations (Spinka et al. 2001), or as a way to assess their own capabilities (Thompson 1998).

Some evidence indicates that mammals play more and initiate play more often with individuals they can dominate during play (Owens 1975; Biben 1986 & 1998). Even so, experiencing subordinate positions during play may also confer long-term benefits because individuals gain the opportunity to practice defensive strategies that could later be used during an actual fight. Also, individuals who consistently maintain a dominant position during play may find themselves at a loss for willing play partners (Biben 1998). Some researchers contend that in order for play to occur, both participants must win an equal proportion (50%) of play encounters. This is called the 50–50 rule. (Aldis 1975; Pellis & Pellis 1998). Individuals may balance the time spent in dominant and subordinate roles during play by self-handicapping and reversing roles. Self-handicapping occurs when individuals place themselves in disadvantaged positions or situations that could make them more vulnerable to attack by "opponents" (Fagen 1981; Bekoff & Allen 1998; Spinka et al. 2001; Bauer & Smuts 2007). For example, red-necked wallabies (*Macropus rufogriseus banksianus*) self-handicap when playing with younger partners by standing in a defensive, flat-footed posture and pawing rather than sparring (Watson & Croft 1996), thereby allowing younger partners to gain a competitive advantage. Role reversals occur when animals change dominant and subordinate positions during play-fighting (Biben 1998; Burghardt 2005) or when animals dominant outside of play assume subordinate roles during play (Bauer & Smuts 2007). In some cases, the opportunity to play may be more important than winning. For example, among squirrel monkeys (*Saimiri sciureus*) (Biben 1998) and hamadryas baboons (*Papio* *hamadryas hamadryas*) (Pereira & Preisser 1998), stronger individuals "soften" their play style as a mechanism to promote play relations when choice of play partners is restricted.

None of the above studies specifically quantified adherence to the 50–50 rule during play, with one exception. In that study among adult domestic dogs, subordinate members of play dyads actually self-handicapped more often than dominants, and dominance status outside of play predicted adoption of the dominant role during play-fighting (Bauer and Smuts 2007). The authors concluded that neither role reversals nor self-handicapping were necessary for play to occur but that, at least in some dyads, they probably did facilitate play.

Because social play often includes motor patterns used in predatory, mating, and agonistic contexts, play signals have evolved to help animals convey playful intentions (Bekoff & Allen 1998). For example, Bekoff (1995) found that among captive coyotes (*Canis latrans*), wolves (*Canis lupus*), and domestic dogs, the play bow signal was more likely to occur immediately preceding or following behaviors that could most easily be misinterpreted as real aggression, such as when an animal shook the head while biting another (Bekoff 1995). In adult domestic dogs, the individual within a dyad who showed more self-handicapping behavior also play signaled more often (Bauer & Smuts 2007).

For a given species, sex differences in play should be present whenever females and males differ in physical characteristics (e.g., body size), behavioral characteristics (e.g., involvement in hunting activity, intraspecific fighting, territorial defense), or social preferences (e.g., formation of strong bonds with same vs. opposite sex individuals) (Maestripieri and Ross 2004; Burghardt 2005). Among canids, males and females show little size dimorphism and engage in similar roles (Derix et al. 1993; McLeod & Fentress 1997), and some research has suggested no sex differences in play style (Bekoff 1974; Bauer & Smuts 2007). However, among infant domestic dogs, there have been reports of sex differences in play (Lund & Vestergaard 1998; Pal, in press).

In domestic dogs, social and sexual play (e.g., mounting) first emerge during the socialization period that begins at 3 weeks and ends at approximately 12 weeks of age (Freedman et al. 1961; Scott and Fuller 1965). During this time, puppies learn social skills and form bonds with other dogs (Lindsay 2000), and play-partner preferences may begin to form. Following the socialization period, the juvenile period lasts from approximately 12 weeks to 6 months or later (until sexual maturity) (Scott & Marston 1950; Scott & Fuller 1965). During this time, play continues to be common.

Some research suggests that in domestic and wild canids, play contributes to the formation of dominance relationships within litters (Scott & Fuller 1965, Bekoff 1972). However, no one, to our knowledge, has systematically quantified the development of dominance relations among littermates in wolves or domestic dogs during naturally occurring social interactions. In our study, virtually every intraspecific social interaction puppies had (other than resting in body contact or sniffing) occurred in the context of play. Therefore, we made no attempt to analyze dominance relationships *per se*, although we did examine role asymmetries during play (see below).

We examined the development of social relationships during play among littermates in three ways. First, we examined play-partner preferences in puppies, diversity in choice of partners, and the stability of preferences over time. Second, we examined asymmetries in social play. Specifically, we determined whether play conformed to the 50–50 rule; we examined the relationship between various play behaviors, including play initiations, “offense behaviors” (similar to “attacks and pursuits” in Bauer & Smuts 2007), self-handicapping, and play bows; and we determined whether play behaviors varied by sex. Lastly, we examined how the individual actions that comprised offense and self-handicapping behaviors varied by litter and time.

METHODS

Subjects

We observed four litters of domestic dogs (three purebred litters and one mixed-breed litter; Table 1). All dams lived in ordinary households and all puppies whelped naturally (no Cesarean births) at home. The dams suckled the puppies and weaned them prior to placement in permanent homes. Breeders supplemented nursing with solid foods starting around 4 weeks of age. Puppies from litters 2–4 remained sexually intact for the duration of the study. With the exception of one male, all of the puppies from litter 1 were spayed or neutered, starting at 21 weeks of age.

Data Collection

Data collection was divided into three time periods (Table 1) to approximately coincide with critical periods associated with the development of social behaviors (Scott & Fuller 1965) and also to equate data collected across litters. Time 1 included the socialization period, time 2, the late socialization and early juvenile period, and time 3, the later juvenile period.

For all litters, we observed puppies in the breeders' homes from 3 to 7–8 weeks of age (time period 1; see Table 1). During time 1, litters 1–3 were housed indoors in one-room enclosures approximately 7.2 m^2. Litters 2 and 3 also had free access to outdoor fenced areas 99 m^2 and 72 m^2 in size, respectively. Litter 4 was kenneled outdoors in a 4 m^2 enclosure, but data were collected in the adjacent yard, a 506 m^2 fenced area. For all litters, living areas were large enough to allow puppies to move and play freely.

During time period 2 (Table 1), owners of puppies from litters 1 and 2 brought them back to the breeders' homes once or twice a month and placed them together for a couple of hours in the outdoor enclosures described above (extended observations of litters 3 and 4 were not possible). This allowed us to collect longitudinal data on littermate play behavior starting at 10–11 weeks through 23 weeks of age. For litter 1, all six littermates attended four sessions. For litter 2, five puppies attended three sessions, and all six puppies came to the remaining session.

Finally, for litter 1, we continued once-a-month observations from 23–40 weeks of age (time period 3, Table 1) under the conditions described above. All littermates attended two sessions and five attended one session.

For litters 1–3 (hereafter referred to as 'focal litters') for all time periods that applied, we conducted 5-min focal samples on each puppy randomly selected during a given session. We videotaped focal animals and those who interacted with them using Canon ZR50 and Canon ZR95 digital video cameras. We had limited access to litter 4 and therefore decided to maximize data by videotaping play on an *ad libitum* basis

(Altmann 1974). For identification, puppies wore colored collars or, in the case of litter 3, were marked by the breeder with nail polish in identifying locations on their bodies.

Behavioral Coding

We coded data from videotapes into a Microsoft Excel (version 2003) spreadsheet. We coded data only for play bouts that involved mutual, social play lasting for at least 2 s. Based on the log survivorship analysis (Martin & Bateson 1993), we considered a subsequent play bout between a focal and the same play partner to be independent if the interval separating successive bouts was at least 1 min.

To investigate play initiations and partner preferences, we coded play partner identities, the puppy who initiated play, how play was initiated (see Bekoff 1972), and the times that play began and ended with each partner. To investigate behaviors that involved asymmetric roles (hereafter ‘asymmetries’), we divided them into 1) offense behaviors and 2) self-handicapping behaviors (cf. Bauer & Smuts 2007). For these and other behaviors (e.g., play bows) we used a detailed ethogram (Table 2) based on prior research on domestic dogs (Bekoff 1972; Abrantes 1997; Bauer & Smuts 2007) and wolves (Schenkel 1967; van Hooff & Wensing 1987).

Data Analysis

Play-partner preferences

For focal litters, we calculated a play-partner preference (PPP) score for each animal in each litter using the following index (cf. Thompson 1996)

$$I_{ij} = \frac{B_{ij}}{B_i/(k-1)}$$

where k is the total number of puppies in a litter, B_{ij} is the number of play bouts initiated by the i^{th} puppy with the j^{th} puppy as the recipient, and B_i is the total number of play bouts initiated by the i^{th} puppy. A puppy that initiated with all other partners an equal number of times would have all I_{ij} scores equal to 1.0. Scores were greater than 1.0 in situations where individuals initiated play with some individuals more often than with others. Following Thompson (1996), we used PPP scores of ≥ 2.0 to define "strong partner preferences". We did not calculate PPP scores for litter 2, time 2 because on most occasions, only five of the six puppies were present.

We used rowwise matrix correlation tests (K_r) (MatMan software package with 10,000 permutations; Hemelrijk 1990a & 1990b; de Vries 1993) to examine several aspects of play-partner preferences. Matrices were constructed separately by litter and time period (although we calculated PPP scores for litter 3, sample size was too small [$N = 3$] to conduct matrix analyses [Hemelrijk 1990a]).

To determine if PPP scores were reciprocal (i.e., if puppy A preferred B as a play partner, did B also tend to prefer A?), we compared a data matrix of PPP scores (with actors in rows and recipients in columns) with a second matrix that was a transposition of the first. To test whether PPP scores were correlated across time periods for litter 1, we created a PPP matrix (as described above) for each time period and compared matrices. Finally, to test if mean play bout lengths were longer with preferred partners, we compared the PPP matrix with a matrix that contained mean bout play lengths for each dyad (the total amount of time each dyad played divided by the number of play bouts for that dyad [Martin & Bateson 1993]).

To test whether the number of strongly preferred partners for each puppy in litter 1 increased across the next two time periods, we conducted a McNemar test in SAS (SAS Institute 2003).

We also tested whether mean bout length varied by time period or dyadic sex composition (FF vs. FM vs. MM) with a general linear mixed model (GLMM) in SAS (SAS Institute 2003). We controlled for litter effects and repeated observations on dyads within a litter across time. By including "litter" in the model, we accounted for variables that contributed to inter-litter variation. For this and all subsequent GLMM models, all two-way interaction terms were included in the initial model, but the least significant interactions were sequentially dropped using a backward elimination procedure. Only significant interactions or those showing trend effects were included in the final models. For all GLMM procedures, we tested for normality and homogeneity of variances, as appropriate, and transformed the dependent variable when necessary to meet the assumptions.

Realized diversity

Following Thompson (1996), we used the Shannon-Weaver diversity index (Shannon & Weaver 1949) to measure the diversity in choices of play partners for each puppy in all focal litters. (As noted above, we did not calculate realized diversity scores for litter 2, time 2 because on most occasions, only five of the six puppies were present).The index (*R*) is

$$R = \frac{\sum p_i \ln(1/p_i)}{\ln(n)}$$

where p_i is the probability of a puppy initiating play with the i^{th} puppy in the litter and n is the number of available play partners. The index ranges from 0 to 1, and R is maximized when a puppy initiates play with all possible partners with equal frequency and minimized when a puppy initiates with only one partner. To test whether realized diversity scores varied by sex or time, we ran a GLMM with sex and time as fixed effects. We controlled for litter effects and repeated observations on puppies within a litter across time periods.

Asymmetries

Testing the 50–50 rule. To examine whether play conformed to the 50–50 rule, we first calculated asymmetry (or conversely, symmetry) in play as follows. For individual A in a dyad (e.g., AB dyad consisting of puppies A and B), the number of "wins" by A equaled the number of offense behaviors by puppy A directed to puppy B plus the number of self-handicapping behaviors (Table 2) by puppy B directed towards puppy A. B's wins were calculated in the same way, such that the proportion of wins for A and B combined equaled 1.0. Next, we calculated the proportion of wins for the individual with the greatest number of wins from each dyad (J) as equal to f / n, where f is the frequency of wins by the puppy with the most wins in each dyad, and n is the total number of wins for both partners in a given dyad. We normalized these proportions with an arcsine-root transformation and subtracted 0.785 (arcsine-root transformation of 0.50) from each value to obtain a measure of symmetry (or asymmetry) in play. The closer the value was to zero, the more symmetrical the play. Next, we ran a GLMM to determine if symmetry differed by time or dyadic sex composition. If neither time nor sex composition was significant, we pooled the time and sex composition data and ran a second GLMM model to determine if symmetry differed from 50% (i.e., if the arcsine-root transformation of the proportion of wins minus 0.785 differed from zero). We controlled for litter effects and repeated observations on dyads within a litter across time.

Relationship between play behaviors. We ran GLMM models to determine: 1) if offense behavior rates were associated with initiation rates (dependent variable), 2) if self-handicapping rates were associated with offense behavior rates (dependent variable), and 3) if self-handicapping and offense behavior rates (dependent variables, cf. Bauer & Smuts 2007) were associated with play bow rates. We included time as a fixed effect, and for these and all other GLMM models that follow, we controlled for litter effects and repeated observations on puppies within a litter across time. We did not test for associations between initiations and self-handicapping or initiations and play bows because scatter plots suggested no relationships.

Rates of behaviors (e.g., initiations, offenses, self-handicapping, and play bows) were calculated at the dyadic level for each puppy in each time period as the number of times each puppy in a dyad exhibited one of the behaviors divided by the total time that dyad was observed playing. For example if A and B played together for 100 s in time 1 and A displayed 20 offense behaviors and B 10, the offense rate would be 0.20 for A and 0.10 for B (recall that initiations occurred only once per play bout – at the start –, whereas offense behaviors, self-handicapping, and play bows could occur multiple times within each bout). We used mean rates of behaviors for each puppy within each time period in the following GLMM analyses.

Variation in play behavior as a function of dyadic sex composition. We tested whether initiation, offense, self-handicapping, or play bow rates (dependent variables) varied by sex or time in mixed-sex (FM) and same-sex (FF vs. MM) dyads using GLMM models as described above. We also compared rates of female behaviors when females were playing with other females (ff dyads) versus when they were playing with males (fm dyads), and similarly, we compared rates of male behaviors in male-male (mm) dyads versus male-female (mf) dyads. Note that fm and mf dyads have the same composition; we use the different abbreviations to remind the reader which sex's behavior we are measuring (the one listed first in mixed sex dyads) in the relevant analyses.

For ff and fm dyads, we obtained difference scores for each dependent variable (e.g., rates of initiations, offense behaviors, self-handicapping, and play bows) separately by subtracting the rates of female-to-female behaviors from the rates of female-to-male behaviors. Initially, we used GLMM models to determine if difference scores varied by time. If not, we pooled observations across time periods and re-ran the models to test for behavioral differences in general. We followed a similar procedure for male dyads.

All statistical tests were two-tailed, and α was set at 0.05. However, if α was between 0.05 and 0.10, we report it as a non-significant (ns) trend.

Breakdown of offense and self-handicapping behaviors. We determined the proportions of offense and self-handicapping behaviors averaged across all dyads for each litter and time period by the following method. First, we determined the rates of individual offense behaviors (Table 2) separately for each dyad and time period by dividing the frequency of individual offense behaviors by the total time played for a given dyad. We averaged the rates of individual offense behaviors by dyad across dyads to obtain a mean rate for each of the behaviors. Rates of self-handicapping were determined similarly. We calculated the proportions of offense and self-handicapping behaviors based on mean rates.

RESULTS

We analyzed 7.10 hours of dyadic play from four litters of puppies consisting of 39 dyads and 1200 total play bouts. The average number of play bouts per dyad ($\overline{X}$ ± SD) was 13.15 ± 5.13 bouts, and we coded an average of 5.22 ± 0.71 min of play per dyad across all litters and times combined.

Play-Partner Preference Scores

PPP scores were not reciprocal for puppies from litter 1 in any time period (rowwise matrix tests: $K_r = 7$, $P = 0.454$, time 1; $K_r = -14$, $P = 0200$, time 2; $K_r = -2$, $P = 0.852$, time 3) or for litter 2 puppies in time 1 (rowwise matrix test: $K_r = 0$, $P = 1.000$). PPP scores were not significantly related to mean play bout length for puppies in litters 1 and 2, time 1 (rowwise matrix tests: $K_r = -1$, $P = 0.830$, litter 1; $K_r = -8$, $P = 0.3505$, litter 2). However, PPP scores and mean bout length were positively related for litter 1 in time 2 (rowwise matrix test: $K_r = 23$, $P = 0.012$), and in time 3 ($K_r = 18$, $P = 0.079$, trend effect). For all litters combined, mean bout length varied by time period but not by dyadic sex composition (GLMM: $F_{2,76} = 4.20$, $P = 0.019$, time; $F_{2,76}=0.30$, $P = 0.744$, dyadic sex composition). Play bouts were shorter in time period 3 compared to times 1 and 2 (time 1 vs. time 2: $P = 0.172$; time 1 vs. time 3: $P = 0.065$; time 2 vs. time 3: $P=0.005$),

($\overline{X}$ estimate ± SE = 16.377 ± 3.641 s, time 1; 19.934 ± 3.966 s, time 2; 9.990 ± 4.549 s, time 3).

PPP scores in times 2 and 3 and were positively correlated with scores in time 1 for litter 1 (rowwise matrix tests: $K_r = 16$, $P = 0.060$, times 1 and 2; $K_r = 19$, $P = 0.048$, times 1 and 3), but scores in times 2 and 3 were not significantly related ($K_r = 12$, $P = 0.18$).

The number of strongly preferred partners (i.e., PPP scores ≥ 2.0) increased over time. In times 1 and 2, only one puppy from litter 1 had a strongly preferred partner (PPP scores ranged from 0–2.5 in time 1 and from 0–2.2 in time 2), but in time 3, all six puppies had one strong preference (McNemar's test: $\chi^2 = 5.00$, $df = 1$, $P = 0.025$) (PPP scores ranged from 0–3.76). In time 1 for litters 2 and 3, none of the puppies had strongly preferred play partners (PPP scores ranged from 0.32–1.8 for litter 2 and from 0.71–1.3 for litter 3), although they did appear to initiate play with particular puppies more often than with others (PPP scores > 1.0).

Realized Diversity

Variation in realized diversity scores was not attributable to sex (GLMM: $F_{1,\,21} = 0.92$, $P = 0.348$, but scores were lower in time 3 compared with scores in time 1 ($P = 0.0008$) and time 2 ($P = 0.004$) (GLMM: $F_{2,\,21} = 8.32$, $P = 0.002$, time). Scores did not differ significantly between times 1 and 2 ($P = 0.796$) (Fig. 1).

Asymmetries

Testing the 50–50 rule

The overall degree of symmetry in play did not vary by sex composition, but it decreased over time (GLMM: $F_{2, 74} = 3.94$, $P = 0.024$, time; $F_{2, 74} = 0.690$, $P = 0.504$, sex). To further explore this time effect, we ran a second GLMM model pooled across sex composition while retaining time as a fixed effect. This analysis showed that littermates as a whole did not conform to the 50–50 rule during play in any time period (GLMM: $t_{76} = 4.00$, $P = 0.0001$, time 1; $t_{76} = 5.87$, $P < 0.0001$, time 2, $t_{76} = 4.96$, $P < 0.0001$, time 3), but symmetry was higher in time 1 relative to time 2 ($P = 0.013$) and time 3 ($P = 0.024$). There was no significant difference in symmetry between times 2 and 3 ($P = 0.737$).

Relationship between play behaviors

The relationship between initiations and offense behaviors was positive in all time periods, but it was only significant in time 3 ($P < 0.0001$) (GLMM: $F_{1, 28} = 17.8$, $P = 0.0002$, offense behaviors; $F_{2, 28} = 1.92$, $P = 0.165$, time; $F_{2, 28} = 6.16$, $P = 0.006$, offense behaviors * time). Neither self-handicapping nor play bows were related to offense behaviors in any time period (GLMM: $F_{1, 30} = 0.04$, $P = 0.848$, self-handicapping; $F_{2, 30} = 0.96$, $P = 0.393$, time) (GLMM: $F_{1, 30} =1.35$, $P = 0.254$, play bows; $F_{2, 30} = 1.23$, $P = 0.305$, time). However, play bows were positively associated with self-handicapping across all time periods (GLMM: $F_{1, 30} = 9.85$, $P = 0.004$, play bows; $F_{2, 30} = 0.40$, $P = 0.677$, time).

Variation in play behavior as a function of dyadic sex combination

Rates of play initiation. In mixed-sex dyads, males initiated play more often than their female partners (Table 3). This result could reflect higher rates of play initiations by males in general, but comparisons of male and female initiation rates in same-sex dyads showed no differences except in time period 3, when MM rates of initiation were higher than FF rates (Table 3).

Females initiated play more often with other females than with males, and results did not vary with time period (Table 3) (ff vs. fm dyads). In contrast to females, male rates of initiation varied by time period. In time 3, males initiated play more often during mm play than during mf play, but in times 1 and 2, males were just as likely to initiate play with females as they were to initiate with other males (Table 3).

Offense behavior rates. In mixed-sex dyads, males displayed offense behaviors more often than females (Table 4). In same-sex dyads, males and females displayed offense behaviors at similar rates across all time periods (Table 4).

Rates of offense behaviors for both females and males were stable across time periods. Females displayed offense behaviors at similar rates whether playing with females (ff) or males (fm), but males displayed offense behaviors slightly more often when playing with females (mf) than when playing with other males (mm) (trend effect) (Table 4).

Self-handicapping rates. In mixed-sex dyads, males self-handicapped more often than females (Table 5); however, males and females self-handicapped at similar rates in same-sex dyads (Table 5).

Self-handicapping rates did not vary by sex across time periods. Females self-handicapped at similar rates whether playing with females (ff) or males (mm), and the same was true for males (Table 5).

Play bow rates. In mixed-sex dyads, males and females play bowed at similar rates (Table 6). The same was true for females compared with males in same-sex dyads (Table 6).

Play bow rates did not vary by sex across time periods. Females play bowed at similar rates whether playing with females (ff) or males (fm), and the same was true for males (Table 6).

Breakdown of offense and self-handicapping behaviors

Offense behaviors were more common than self-handicapping behaviors across all time periods and litters, accounting for between 92–97% of all behaviors (offense and self-handicapping behaviors combined; Table 2) in litters 1–4 respectively during time 1 (Fig. 2a–d), 92–93% of behaviors in litters 1 and 2 respectively during time 2 (Fig. 3a and b), and 84% of behaviors in litter 1 during time 3 (Fig. 4).

In time 1, for all four litters, forced downs and overs were the two most common offense behaviors (Fig. 2a–d). In time 2, mounts appeared for the first time in litters 1 and 2 (5% of offense and self-handicapping behaviors in both litters), and the proportion of bite shakes decreased in both litters (Fig. 3a and b). In time 3, mounts became the most common offense behavior followed by chases, and bite shakes disappeared entirely (Fig. 4). Muzzle bites and chin overs (with the exception of litter 3, Fig. 2b) were a small proportion of offense behaviors across all time periods.

In time 1, for all four litters, nearly 100% of self-handicapping behaviors involved voluntary downs (litter 1 had a small proportion of muzzle licks). In time 2, muzzle licks had grown to 43% of all self-handicapping behaviors in litter 1 and 50% in litter 2 (in addition to voluntary downs). By time 3, 75% of self-handicapping was accounted for by muzzle licks.

DISCUSSION

Partner Preferences and Diversity

In time periods 1 and 2, puppies in all focal litters initiated play with most of the other individuals in their litter. However, as they matured, puppies in litter 1 concentrated on initiating play with a smaller subset of individuals. Their preferences for specific partners increased over time as diversity in partner choice decreased, and by time 3, each puppy had one strongly preferred play partner. PPP scores were consistent between early and late time periods.

Detailed information on play partner preferences is rare, but Thompson (1996) reported distinct play partner preferences for infant sable antelope. Like the littermates in this study, sable calves played with a variety of partners early on but later (9–12 weeks) developed stable preferences with a subset of strongly preferred playmates. However, unlike young sable antelope, puppies did not show reciprocal play partner preferences, a finding we discuss later.

Asymmetries

Testing the 50–50 rule

Puppies did not adhere to the 50–50 rule in any time period; however, play was more symmetrical between very young littermates and became less so as the puppies matured. Bauer & Smuts (2007) also reported that adult dogs did not conform to the 50–50 rule in play, and they suggested that play in dogs reflects the existing dominance structure outside of play. In young rats paired together, symmetry in play also decreased over time as stable dominance relationships became established (Panksepp 1981). Like rats (Panksepp 1981; Pellis & Pellis 1991), dogs may use play to establish stable social relationships and test their place in the existing social structure of a group (Bekoff 1972). If so, then the increased asymmetry over time among littermates may simply reflect dominance relationships formed during the juvenile period, making puppy play more like that of adult dogs in this respect (cf. Bauer & Smuts 2007).

Relationships between play behaviors

In time period 3, rates of initiations were directly related to rates of offense behaviors. This finding suggests that as puppies mature, winning or being in the dominant position during play becomes more important. Similarly, young male squirrel monkeys (Biben 1998), baboons (Owens 1975), and laboratory rats (Hole 1988) preferred partners they could dominate during play. It seems likely that in dogs, as in many primates, individuals become increasingly aware of intra-group status as they mature and play becomes more competitive (Fagen 1981). Preference for partners who can be dominated could help explain why PPP scores were not reciprocal (see above).

Similar to the findings of Bauer & Smuts (2007) for adult dogs, we found no association between offense behaviors and either self-handicapping or play bows, but high rates of self-handicapping were related to high rates of play bows across all time periods. This suggests that self-handicapping and play signaling may function together to encourage play (Bauer & Smuts 2007).

Variation in play behavior as a function of dyadic sex combination

Mixed-sex partners. In mixed-sex dyads, males initiated play more often than females across all time periods (Table 3). With one possible exception (MM dyads initiated more often than FF dyads in time 3), these results were not just an artifact of males being more active in general. Similar to our findings, Lund & Vestergaard (1998) reported that males initiated social play with females more often than expected by chance in four litters of domestic dogs aged 3 to 8 weeks.

In addition to initiating at higher rates than females, males in FM dyads also displayed self-handicapping more often than females and, as indicated above, self-handicapping correlates with play signaling and appears to function to maintain play. Perhaps playing with females provides opportunities for males to learn characteristics of female behavior and gain competence in interactions with them. If so, it could translate into greater male reproductive success later in life via female mate preferences. Pal et al. (1999) found that in a population of free-ranging dogs in India, oestrous females selectively allowed some males to mate and even solicited them but avoided other males or even attacked them if they tried to mount. Beach & LeBoeuf (1967) also reported female mating preferences in captive dogs.

In FM dyads, male puppies displayed offense behaviors more often than females (Table 4). In food competition tests, male puppies also tended to dominate females by 15 weeks (Scott & Fuller 1965). Learning to dominate females may have reproductive payoffs as well. For example, in Indian free-ranging dogs, males forced copulations on unwilling, often sexually inexperienced, oestrous females who responded with a combination of aggressive, submissive, and escape postures. However, attempts to force mating were less successful than mating attempts that elicited female cooperation (Ghosh, et al. 1984; Pal et al. 1999). In summary, play with females may allow males to practice both cooperative and competitive mating strategies in a less serious context.

In contrast to our results, Bauer & Smuts (2007) found no sex differences in attack/pursuits (cf. offense behaviors this study) or self-handicapping. Possible discrepancies in the findings may be related to choice of subjects. Bauer & Smuts (2007) studied unrelated adult dogs, whereas we examined social relationships between young littermates. Ways in which age and kinship might influence intersexual play behaviors remain to be investigated.

Same-sex partners. The preference for same-sex play initiations in males and females during various time periods (Table 3) suggests that play may serve as training for intrasexual competition between same-sex littermates. Like wolves (Mech 1970; Packard 2003), both female and male domestic dogs form intrasexual dominance relationships (Pal et al. 1998), and play functions in the formation of these dominance relationships (Bekoff 1972).

Because dominance conflicts generally occur between same-sex dogs (Borchelt 1983; Sherman et al. 1996), same-sex partners may play to practice threat and appeasement signals that ritualize aggression. Practicing aggressive components within a safe range of intensity limits the occurrence of overt aggression later on (Lindsay 2005). In adult pet dogs, fights between females lead to more serious injuries than fights between males or fights between mixed-sex dogs (Sherman et al. 1996). The early onset and consistent preference for females to initiate play with other females may be one way females learn to moderate same-sex aggression.

In contrast to some of our findings, Lund & Vestergaard (1998) reported that male and female puppies did not prefer same- over mixed-sex play partners in a study of puppies (littermates) up to 8 weeks old. However, Lund & Vestergaard (1998) did not limit their observations to dyadic interactions, as in the current study, but also included triadic interactions, which could have influenced their findings in ways that remain to be investigated.

Additionally, the increased rates of same-sex initiations recorded in our study were not simply an artifact of play bout lengths varying by dyadic sex combination (e.g., males initiated with males more often than they initiated with females in time 3 [Table 3] because MM play bout lengths were shorter than FM bout lengths in time 3). Mean bout lengths did not vary by dyadic sex composition across any time period in the current study.

Individual offense and self-handicapping behaviors

We obtained similar patterns of offense and self-handicapping behaviors across all litters and time periods (Figs. 2–4), even with a small sample size of four litters comprised of various breeds and breed mixes. Such results suggest that littermates as whole probably exhibit similar trajectories in the development of these behaviors independent of rearing environment, litter size, or breed.

Conclusion

Our study examined the role of social play in facilitating the development of social relationships and the flexibility in those relationships among littermates. We made several determinations. We discovered that play partner preferences in puppies form very early in development and remain fairly stable at least through the juvenile period, even when littermates are not continuously housed together. To our knowledge, no other study has demonstrated the stability of play partner preferences in any litter-bearing mammal longitudinally through 40 weeks of age. Additionally, this study is the first to quantitatively test the 50–50 rule of play in littermates of domestic dogs, and we found that puppies, as a whole, behave similar to their adult counterparts (see Bauer & Smuts 2007) in regards to fair play. Finally, for all litters combined, we found similarities in the relations between specific play behaviors, in the variability of play strategies used by each sex, and in the developmental timing of specific play behaviors.

Future research addressing the formation and development of partner preferences and adherence to or deviation from the 50–50 rule in other canids would allow for cross-species comparisons.

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Table 2-1. Summary of domestic dog litters

Litters	Breeds	Birthdates[a]	Sex composition[b]	Observation dates	Time periods[c]	Age ranges (in weeks) of puppies
1	Shepherd mix	14 February 2004	3 ♀ 3 ♂	February-November 2004	1	3–8
					2	11–23
					3	27–40
2	Labrador retriever	21 April 2005	2 ♀ 4 ♂	May-October 2005	1	3–8
					2	10–23
3	Doberman pincher	22 April 2004	1 ♀ 2 ♂	May-June 2004	1	3–7
4	Malamute	4 May 2005	4 ♂	May-June 2005	1	3–8

[a]Only surviving puppy listed. [b]One puppy (female) from litter 1 died shortly after birth, and two puppies (both females) from litter 3 died shortly after birth. [c]Observations were collected over three time periods.

Table 2-2. Ethogram of asymmetric play behaviors

Behaviour	Definition
Offense behaviours	Behaviours used to maintain a dominant or superior position over a partner.
Bite shake	[a]D bites [b]S and shakes head back and forth while maintaining a hold on S.
Chase	D runs after S with a least 2 running strides while S runs or trots away from D.
Chin over	D places the underside of chin over S's back, usually right behind the neck or near S's shoulders, but sometimes over S's head.
Forced down	D uses physical force or contact to cause S to drop completely to the ground from a moving, standing, or sitting position.
Mount	D rears up (keeping hind legs on the ground) to place forelegs on S's back. D has a rounded spine with curved front legs and forepaws to grasp S's torso. Pelvic thrusting may or may not be present.
Muzzle bite	D places mouth around S's muzzle.
Over	D sits on, stands over, or lies over S with at least 25% of D's torso over S's torso.
Self-handicapping	Behaviours that place an actor in a disadvantaged or inferior position.
Muzzle lick	S licks on or around D's muzzle. Sometimes a lick may or may not be accompanied by nudging.
Voluntary down	S drops completely to the ground from a moving, standing, or sitting position without D's physical enforcement. D and S must be interacting when S goes down.
Play signal	Used to begin play or to maintain a playful mood during a play bout.
Play bow	Dog is crouched down touching or nearly touching forelimbs to the ground with rear end high in the air. Orientation is directly towards play partner.

D = dog in dominant or winning position, [b]S = dog in subordinate or losing position.

Table 2-3. Rates of initiation

Source of Variation	*df*	F^a or t^b values	*P*	Direction of effect
Mixed-sex dyads (FM)				
Initiator sex	1, 27	23.98	**<0.0001**	M>F
Time period	2, 27	0.44	0.649	
Same-sex dyads (FF vs. MM)				
Initiator sex	1, 27	1.49	0.233	
Time period	2, 27	5.50	**0.009**	T3>T1, T2
Initiator sex * time period	2, 27	4.33	**0.023**	MM>FF in T3
Female initiations				
ff vs. fm	1	15.98	**0.039**	ff>fm
Male initiations[c]				
mm vs. mf				
Time period 1	14	-1.02	0.327	
Time period 2	14	-0.62	0.543	
Time period 3	14	2.18	**0.047**	mm>mf

[a] Rates of initiations in mixed-sex and same-sex dyads in relation to sex of initiator and time period. [b]Test of the difference in female initiation rates between ff and fm dyads and the difference in male initiation rates between mm and mf dyads. [a,b]GLMM models controlling for litter and repeated observations of dyad{litter} across time. [b]GLMM model pooled across time periods for female initiations due to non-significant time effects (GLMM: $F_{2,9} = 0.96$, $P = 0.418$). [c]For male initiations, results were not pooled across time because of a trend effect with time (GLMM: $F_{2,14} = 2.78$, $P = 0.096$). FM (female-male), FF (female-female), MM (male-male), female rates with females (ff) and males (fm), male rates with males (mm) and females (mf). T1 = time 1, T2 = time 2, T3 = time 3.

Table 2-4. Rates of offense behaviors

Source of Variation	*df*	F^a or t^b values	*P*	Direction of effect
Mixed-sex dyads (FM)				
Sex	1, 27	7.79	**0.009**	M>F
Time period	2, 27	0.14	0.870	
Same-sex dyads (FF vs. MM)				
Sex	1, 29	1.63	0.212	
Time period	2, 29	3.21	0.055	
Female offense behaviours				
ff vs. fm	1	0.92	0.525	
Male offense behaviours				
mm vs. mf	2	-3.19	0.086	

[a]Rates of offense behaviors in mixed-sex and same-sex dyad in relation to sex and time period. [b]Test of the difference in rates of offense behaviors by females in ff and fm dyads and the difference in rates by males in mm and mf dyads. [a,b]GLMM models controlling for litter and repeated observations of dyad{litter} across time. [b]GLMM models pooled across time periods for female and male offense behaviors due to non-significant time effects (GLMM: $F_{2,9} = 1.39$, $P = 0.297$, females; $F_{2,14} = 1.96$, $P = 0.177$, males). FM (female-male), FF (female-female), MM (male-male), female rates with females (ff) and males (fm), male rates with males (mm) and females (mf).

Table 2-5. Rates of self-handicapping

Source of Variation	*df*	*F*[a] or *t*[b] values	*P*	Direction of effect
Mixed-sex dyads (FM)				
Self-handicapper sex	1, 27	4.87	**0.036**	M>F
Time period	2, 27	0.04	0.960	
Same-sex dyads (FF vs. MM)				
Self-handicapper sex	1, 29	0.13	0.723	
Time period	2, 29	0.92	0.442	
Female self-handicapping				
ff vs. fm	1	-1.17	0.449	
Male self-handicapping				
mm vs. mf	2	1.01	0.418	

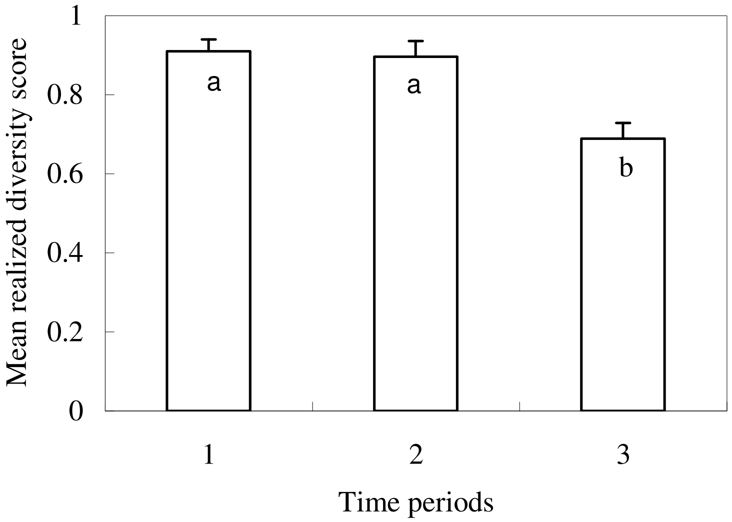
[a] Self-handicapping rates in mixed-sex and same-sex dyads in relation to sex and time period. [b]Test of the difference in female self-handicapping rates between ff and fm dyads and the difference in male self-handicapping rates between mm and mf dyads. [a,b]GLMM models controlling for litter and repeated observations of dyad{litter} across time. [b]GLMM models pooled across time periods for female and male self-handicapping behaviors due to non-significant time effects (GLMM: $F_{2,9} = 0.51$, $P = 0.615$, females; $F_{2,14} = 1.35$, $P = 0.291$, males). FM (female-male), FF (female-female), MM (male-male), female rates with females (ff) and males (fm), male rates with males (mm) and females (mf).

Table 2-6. Rates of play bows

Source of Variation	*df*	*F* [a] or *t* [b] values	*P*
Mixed-sex dyads (FM)			
Sex	1, 27	0.80	0.379
Time period	2, 27	2.24	0.126
Same-sex dyads (FF vs. MM)			
Sex	1, 29	2.29	0.141
Time period	2, 29	1.47	0.246
Female play bows			
ff vs. fm	1	0.88	0.542
Male play bows			
mm vs. mf	2	0.78	0.516

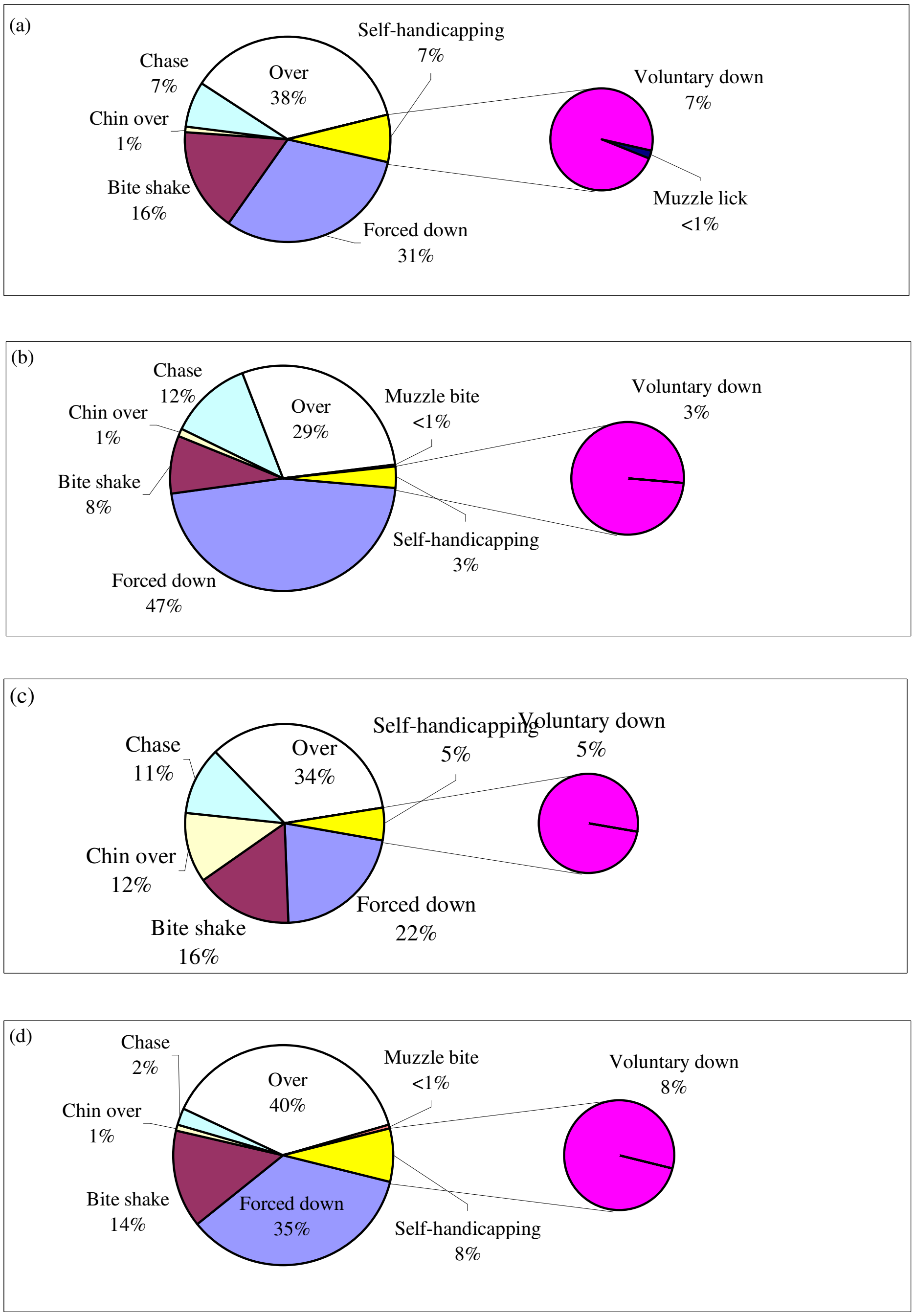
[a] Play bow rates in mixed-sex and same-sex dyads in relation to sex and time period. [b] Test of the difference in female play bow rates between ffand fm dyads and the difference in male play bow rates between mm and mf dyads. [a,b] GLMM models controlling for litter and repeated observations of dyad{litter} across time. [b] GLMM models pooled across time periods for female and male play bows due to non-significant time effects (GLMM: $F_{2,9} = 0.77$, $P = 0.490$, females; $F_{2,14} = 2.01$, $P = 0.171$, males. FM (female-male), FF (female-female), MM (male-male), female rates with females (ff) and males (fm), male rates with males (mm) and females (mf).

Figure 2-1. Realized diversity scores across three time periods



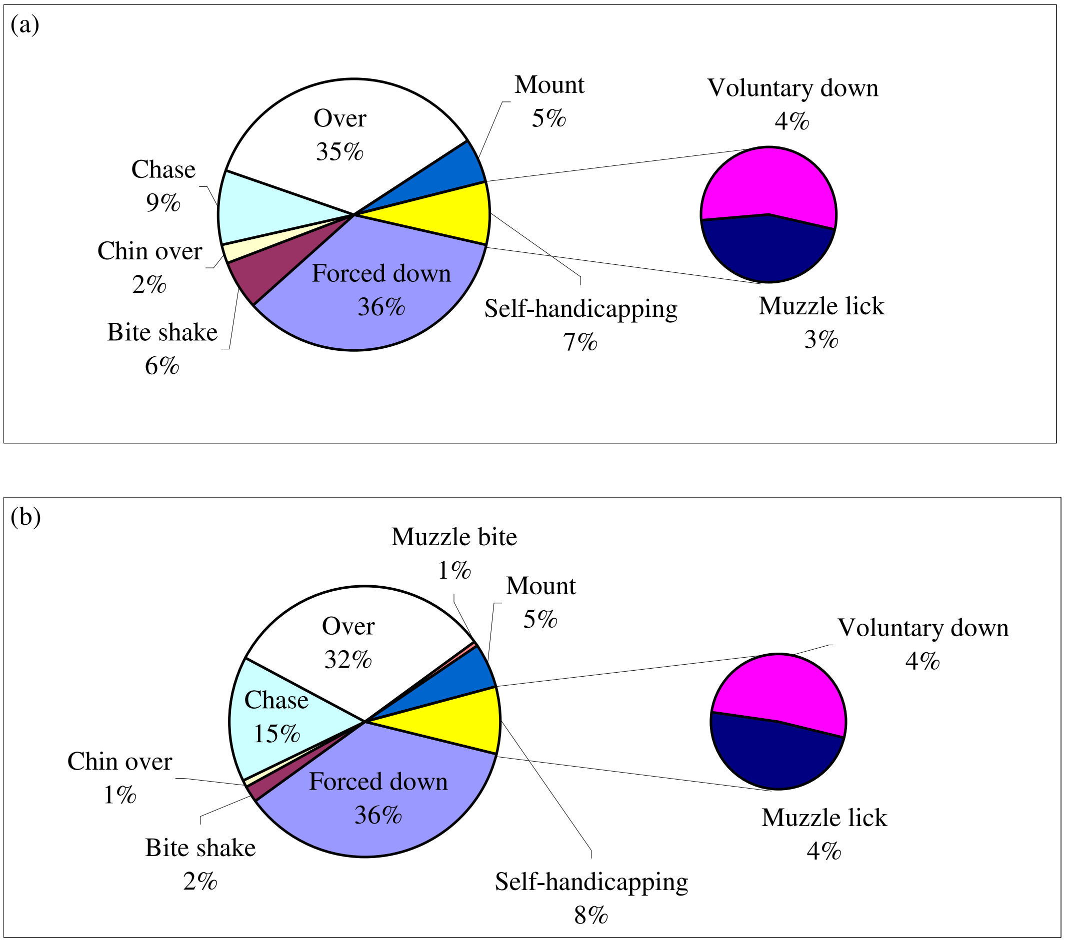
Values are mean estimates and error bars indicate SE for litters 1 (time periods 1−3), 2 (time period 1), and 3 (time period 1). Columns with a letter in common are not significantly different ($P > 0.05$). Age ranges (in weeks) of puppies: time 1 = 3–8, time 2 = 10–23, and time 3 = 27–40.

Figure 2-2. Offense and self-handicapping behaviors in time 1



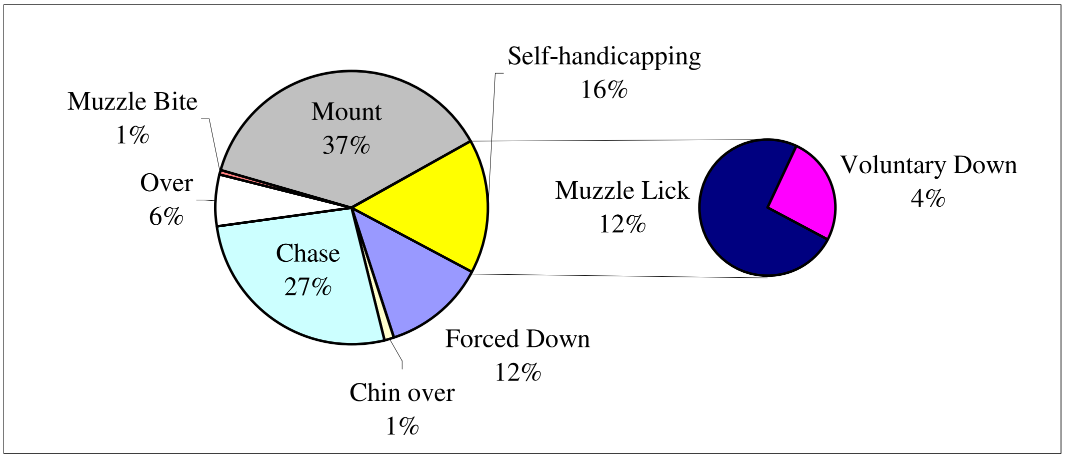
Proportion of offense and self-handicapping behaviors in time 1 for litters 1 (mixed breed) (a), 2 (Labrador retriever) (b), 3 (Doberman Pincher) (c), and 4 (malamute) (d). Large pie includes offense behaviors and small pie self-handicapping. Time 1 = puppies between 3–8 weeks of age.

Figure 2-3. Offense and self-handicapping behaviors in time 2



Proportion of all offense and self-handicapping behaviors in time 2 for litters 1 (mixed breed) (a) and 2 (Labrador retriever) (b). Large pie includes offense behaviors and small pie self-handicapping. Time 2 = puppies between 10–23 weeks of age.

Figure 2-4. Offense and self-handicapping behaviors in time 3



Proportion of all offense and self-handicapping behaviors in time 3 for litter 1 (mixed breed). Large pie includes offense behaviors and small pie self-handicapping. Time 3 = puppies between 27–40 weeks of age.

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CHAPTER 3

THIRD-PARTY INTERVENTIONS IN DYADIC PLAY BETWEEN LITTERMATES OF DOMESTIC DOGS (*CANIS LUPUS FAMILIARIS*)

INTRODUCTION

The term intervention (sometimes referred to as coalition formation) has been used to describe outsiders (e.g., third-parties) becoming involved in pairwise competitive or aggressive encounters. Sometimes interveners take sides by supporting one party or the other (de Waal & Harcourt 1992; Grammer 1992; Silk 1992; Roeder et al. 2002). The ability to keep track of multiple social interactions (e.g., as in a triad) is a cognitively demanding activity most likely to occur among animals who live in social groups (Whiten & Byrne 1998). Interventions have been described primarily in primates (savannah baboons *Papio cynocephalus*, Seyfarth 1976; Java monkeys *Macaca fascicularis*, de Waal 1977; bonnet macaques *Macaca radiata*, Silk 1982, 1992; chimpanzees *Pan troglodytes*, rhesus macaques *Macaca mulatta*, and stumptail macaques *Macaca arctoides*, de Waal & Luttrell 1988; Japanese macaques *Macaca fuscata*, Prud'homme & Chapais 1996; mountain gorillas *Gorilla gorilla beringei*, Watts 1997; Barbary macaques *Macaca sylvanus*, Widdig et al. 2000; brown lemurs (*Eulemur fulvus fulvus*, Roeder et al. 2002) but also in bottlenose dolphins *Tursiops* sp. (Connor, Smolker, and Richards 1992), spotted hyenas *Crocuta crocuta* (Zabel et al. 1992; Engh et al.

2000), African wild dogs *Lycaon pictus* (de Villiers et al. 2003), wolves *Canis lupus* (Zimen 1976; Jenks 1988), zebras *Equus quagga boehmi* and *Equus quagga antiquorum* (Schilder 1990), goats (Keil & Sambraus 1998), cattle (Sambraus 1969), rats (Militzer 1995), and even fish *Lamprologus ocellatus* (Walter & Trillmuch 1994).

Several theories have been proposed to explain interventions based on kin selection, reciprocity, and/or self-interest. Typically, interveners often side with kin verses non-kin in aggressive contests. Such support, observed among primates (Kurland 1977; Walters 1980; Silk 1982; Silk et al. 2004), spotted hyenas (Engh et al. 2000) and African wild dogs (de Villiers et al. 2003), suggests the operation of kin selection. In some species, support is reciprocal and given to those from whom support is received (chimpanzee, rhesus macaques, and stumptail macaques, de Waal & Lutteral 1988, de Waal 1992; savannah baboons, Wasser & Starling 1988, Smuts & Watanabe 1990), and sometimes support is biased towards close associates (human children *Homo sapiens*, Grammer 1992; chimpanzees, de Waal 1992). In other species, reciprocity in support is uncommon (Barbary macaques, Widdig et al. 2000; juvenile Japanese macaques Prud'homme & Chapais 1996). Reciprocity can also exist in targeting, where individuals selectively intervene against individuals who regularly intervene against them. Such a "revenge system" has been observed in chimpanzees (de Waal & Lutteral 1988; deWaal 1992) and male bonnet macaques (Silk 1992). Finally, interventions can be motivated by direct benefits. For example, female juvenile Japanese macaques intervene opportunistically in conflicts and target low-ranking females as a means to subordinate them (Chapais 1996; Prud'homme & Chapais 1996). Likewise, African wild dogs (de

Villiers et al. 2003), spotted hyena cubs (Engh et al. 2000), and wolves (Zimen 1975; Jenks 1988) use targeting and coalitions to maneuver for position in the pack hierarchy.

Much research has been focused on the influence of interventions in structuring matrilineal rank relations in primates (Cheney 1977; de Waal 1977; Kaplan 1977, 1978; Kurland 1977; Dunbar 1980, 1988; Walters 1980, 1981; Datta 1983, 1992; Hausfater et al. 1982; Silk 1982, 2002; Berman 1983; Bernstein & Ehardt 1985, 1986; Chapais 1985, 1992; Periera 1989; Chapais & St-Pierre 1997; Wittig et al. 2007); however, very little work has examined the development of intervention behavior in young animals (Zabel 1992; Prud'homme & Chapais 1996; Engh et al. 2000; de Villiers et al. 2003).

In the current study, we examined the development of intervention behavior among littermates of domestic dogs (*Canis lupus familiaris*) during play fighting. In canids, play fighting includes behaviors such as chasing, rough and tumble wrestling, mounting behavior (i.e., mimicking copulatory behavior), and inhibited biting (Bekoff 1974; Burghardt 2005).We use the term "intervention" solely to refer to the physical act of interfering in dyadic play without ascribing intentionality to the behavior. We focused on interventions during play fighting as opposed to agonistic fighting because real aggression between young littermates is exceedingly rare (Bekoff 1974, pers. obs.). However, social play in canids resembles actual fighting in that it contains many of the same actions (e.g., biting, assertively standing over, biting with side-to-side shaking of the head, etc.), except that in play, these actions are intermixed with a variety of other cues that help to maintain the play atmosphere (Bekoff 1995).

Some research suggests that in domestic and wild canids, play contributes to the formation of dominance relationships within litters (Scott & Fuller 1965, Bekoff 1972).

However, no one, to our knowledge, has systematically quantified the development of dominance relations among littermates in wolves or domestic dogs during naturally occurring social interactions. In our study, virtually every interaction puppies had (other than resting in body contact or sniffing) occurred in the context of play. Therefore, we did not address dominance relationships.

This study had two main goals. First, we aimed to describe the nature and outcome of third-party interventions in dyadic play among littermates of domestic dogs and how patterns of intervention change over time (from 3 weeks up until 40 weeks of age). To our knowledge, no published work has documented the occurrence or pattern of interventions in this species. Specifically, we determined whether preferred play partners of interveners were more or less likely to be targeted during an intervention. Second, we asked whether the pattern of interventions was more consistent with reciprocity or opportunism (see above).

METHODS

Subjects

We observed four litters of domestic dogs (three purebred litters and one mixed-breed litter; Table 1). All dams lived in ordinary households and all puppies whelped naturally (no Cesarean births) at home. The dams suckled the puppies and weaned them prior to placement in permanent homes. Breeders supplemented nursing with solid foods starting around 4 weeks of age. Puppies from litters 2–4 remained sexually intact for the duration of the study. With the exception of one male, all of the puppies from litter 1 were spayed or neutered, starting at 21 weeks of age.

Data Collection

Data collection was divided into three time periods (Table 1) to approximately coincide with periods associated with the development of behavior (Scott & Fuller 1965) and also to equate data collected across litters. Time 1 included the socialization period, time 2, the late socialization and early juvenile periods, and time 3, the later juvenile period. During the socialization period (from 3–12 weeks of age), play and social behaviors develop, and during the juvenile period (from 12 weeks–sexual maturity), pups explore their surrounding environments and sexual behaviors become apparent (see Scott & Fuller 1965).

For all litters, we observed puppies in the breeders' homes from 3 to 7–8 weeks of age (time period 1; Table 1). During time 1, litters 1−3 were housed indoors in one-room enclosures approximately 7.2 m^2. Litters 2 and 3 also had free access to outdoor fenced areas 99 m^2 and 72 m^2 in size, respectively. Litter 4 was kenneled outdoors in a 4 m^2 enclosure, but data were collected in the adjacent yard, a 506 m^2 fenced area. For all litters, living areas were large enough to allow puppies to move and play freely. We collected data five to seven days per week for approximately three hours per day.

During time period 2 (Table 1), owners of puppies from litters 1 and 2 brought them back to the breeders' homes once or twice a month and placed them together for a few hours in the outdoor enclosures described above (extended observations of litters 3 and 4 were not possible). This allowed us to collect longitudinal data on littermate play behavior starting at 10–11 weeks through 23 weeks of age. For litter 1, all six littermates attended four sessions. For litter 2, five puppies attended three sessions, and all six puppies came to the remaining session.

Finally, for litter 1, we continued once-a-month observations from 27–40 weeks of age (time period 3, Table 1) under the conditions described above. All littermates attended two sessions and five attended one session.

For litters 1–3 for all time periods that applied, we conducted 5-min focal samples on each puppy randomly selected during a given session. We videotaped focal animals and those who interacted with them using Canon ZR50 and Canon ZR95 digital video cameras. We had limited access to litter 4 and therefore decided to maximize data by videotaping play on an *ad libitum* basis (Altmann 1974). For identification, puppies wore colored collars or, in the case of litter 3, were marked by the breeder with nail polish in identifying locations on their bodies.

Behavioral Coding

We coded data from videotapes into a Microsoft Excel (version 2003) spreadsheet. We coded data only for dyadic play bouts that involved mutual social play lasting for at least 2 s. Based on a log survivorship analysis (Martin and Bateson 1993), play bouts between the same partners were considered terminated if a minimum of 1 min passed without play activity.

An intervention occurred when two dogs were playing and a third dog approached the dyad and physically intervened in their play by jumping on, biting at, mounting, etc. (Table 2) one of the players (the target). We recorded the identity of the dogs in the playing dyad, the intervener, the target of the intervention and the dog who was "joined" (the non-target dog), and whether the target was in the recipient or actor role (herein referred to as "R" and "AC", respectively) at the time of the intervention. We used the term "joined" rather than "support" to avoid ascribing purpose or intent to the behavior of the intervening animal. A dog in the AC role directed offense behaviors (e.g., biting, mounting, jumping on, standing over) to the dog in the R role. In contrast, the dog in the R role received offense behaviors from the dog in the AC role. If both dogs from the original dyad were directing offense behaviors to each other at the time of the intervention, we included body position to further determine AC and R roles. AC positions involve higher postures whereas R positions involve low postures that typically signal submission (Schenkel 1967; van Hooff & Wensing 1987; Derix et al. 1993; Bauer and Smuts 2007). For example, if both dogs in the dyad were biting each other and one dog was lying down and the other dog was standing over the dog on the ground, the standing dog would be coded in the AC position and the lying dog would be coded in the R position.

We also coded five possible outcomes in the 5 s following an intervention. The intervener could: (1) play with both members of the original dyad, (2) play with the target to the exclusion of the other dyad member, (3) play with the non-target to the exclusion of the target, (4) leave and the original dyad could continue to play, or (5) all play stopped.

To investigate the relationship between interventions and play partner preferences, we coded the number of times that each focal puppy initiated play with all other littermates in each time period. We used initiations to calculate a play partner preference index (see below) for each puppy in each time period.

Data Analysis

To determine if the intervening dog was more likely to target the dog in the R or AC role at the time of the intervention, we conducted a two-part analysis. In the first part, we used a general linear mixed model (GLMM) to determine if the proportion of R targets varied by sex of the intervener or time period. We calculated the proportion of R targets (P_{sub}) separately for each puppy and time period as

$$P_{sub} = \frac{s}{t}$$

where s is the number of times puppy A intervenes and targets the dog in the R role, and t is the total number of interventions by puppy A. We normalized these proportions with an arcsine-root transformation, and subtracted 0.785 (arcsine-root transformation of 0.50) from each value. If P_{sub} did not vary by sex or time, we pooled the data and ran a second GLMM model to determine if the proportion of R targets differed from 50% (i.e., if the arcsine-root transformation of P_{sub} minus 0.785 differed from zero). In all GLMM analyses, two-way interactions were included only if significant, and we controlled for litter effects and repeated observations on puppies within a litter across time periods.

We calculated play partner preference scores based on focal samples for each puppy using the following index (cf. Thompson 1996)

$$I_{ij} = \frac{B_{ij}}{B_i/(k-1)}$$

where *k* is the total number of puppies in a litter, B_{ij} is the number of play bouts initiated by the i^{th} puppy with the j^{th} puppy as the recipient, and B_i is the total number of play bouts initiated by the i^{th} puppy. Higher scores indicated greater preference. We did not calculate play partner preference scores for litter 2, time 2 (because on most occasions, only five of the six puppies were present) nor litter 4 (since focal samples were lacking).

We used rowwise matrix correlation tests (K_r) (MatMan software package with 10,000 permutations; Hemelrijk 1990a & 1990b; de Vries 1993) to examine several aspects of interventions. Matrices were constructed separately by time period and litter (sample size for litter 3 was too small [N=3] to conduct matrix analyses [Hemelrijk 1990a]).

To determine if the intervener was more likely to target/join a preferred partner, we compared a data matrix of play partner preference scores with a second matrix containing the proportion of times that each puppy targeted all other puppies during an intervention. These proportions (T_{ij}) were calculated as

$$T_{ij} = \frac{t_{ij}}{n_{ij}}$$

where n_{ij} is the number of times puppy *i* intervened when puppy *j* was in a play dyad, and t_{ij} is the number of times *i* targeted *j* in n_{ij} interventions. A significant positive correlation implied that interveners were more likely to target their preferred partners and join their preferred partners' opponents. Conversely, a significant negative correlation implied that interveners were more likely to join their preferred partners and target their preferred partners' opponents.

To determine if puppies displayed reciprocal associations in joining (e.g., if I join you when I intervene are you more likely to join me when you intervene?), we compared a matrix containing the proportion of times each intervening puppy joined each other littermate with a second matrix that was the transposition of the first (Hemelrijk 1990a). Calculations of values for the reciprocity matrix were similar to those for T_{ij} above. A significant positive correlation implied reciprocity in joining; a negative correlation implied reciprocity in targeting.

All statistical tests were two-tailed, and alpha was set at 0.05.

RESULTS

We analyzed 7.10 hours of dyadic play from four litters of puppies containing 39 total dyads, and we coded an average of 5.22 ± 0.71 min of play per dyad across all litters and times combined. We recorded 574 interventions for all litters and times combined (Table 1).

In times 1 and 2, many dogs intervened by biting at one of the members in the original dyad, although 'jump on' was also frequently used (Fig. 1a-b). In time 3, 'jump on' was the most common intervention behavior followed by mounts (Fig. 1c).

The majority of interveners targeted most of the other puppies in a litter across all time periods (on average, between 85%–90% of their littermates).

Puppies did not preferentially target or join their preferred partners when they intervened in dyadic play, and these results held across time periods (rowwise matrix tests: $K_r = 4$, $P = 0.772$, time 1; $K_r = 1$, $P = 0.971$, time 2; $K_r = 1$, $P = 0.950$, time 3; litter 1; $K_r = 14$, $P = 0.198$, time 1, litter 2). (As noted above, we could not calculate play partner preference scores for litter 2, time 2, or litter 4. However, using another measure of play partner preference that correlated with play partner preference scores–i.e., proportion of play initiations measured at the dyadic level–we obtained similar rowwise matrix results for those litters and times reported above plus litter 2, time 2 and litter 4.)

For 19.5% of the interventions, the target could not be identified as either in the R or AC role at the time of the intervention because both puppies were in the same role (e.g., both standing or both lying down). In the rest of the interventions, puppies targeted littermates in the R role more often (69% of the time) than littermates in the AC role (GLMM: $t_3 = 6.44$, $P = 0.008$). These results did not vary by sex or time (GLMM: $F_{1, 30} = 0.13$, $P = 0.721$, sex; $F_{2, 30} = 2.07$, $P = 0.144$, time).

Dogs did not display reciprocal associations in joining (or targeting) in any litter or time period (rowwise matrix tests: $K_r = -2$, $P = 0.888$, time 1, $K_r = -1$, $P = 1.000$, time 2, $K_r = -9$, $P = 0.334$, time 3, litter 1; $K_r = -8$, $P = 0.468$, time 1, $K_r = 15$, $P = 0.132$, time 2, litter 2; $K_r = 0$, $P = 1.000$, time 1, litter 4).

The outcome of interventions followed a similar pattern across litters and time periods. Triadic play was the most common outcome following an intervention, and cessation of play was the least common outcome (Fig. 2a-c). In 3.6% of all interventions, the outcome could not be determined.

DISCUSSION

Overall, intervention behavior among littermates of domestic dogs appeared to be primarily opportunistic with little regards for reciprocity in joining. Puppies were more likely to target the dog in the R role at the time of the intervention, and this tendency became apparent very early in development (prior to 7 or 8 weeks of age). Additionally, preferred play partner status had no significant effect on an intervener's targeting preference.

In real fighting, as opposed to play fighting, targeting the individual in the R role is commonly seen across a variety of species including male bonnet macaques (Silk 1992), bonobos (Vervaecke 2000), vervet monkeys (Cheney 1983), African wild dogs (de Villiers et al. 2003), prepubertal spotted hyenas (Zabel 1992), high-ranking children (Grammer 1992), and wolves (Zimen 1976). Typically this strategy reinforces existing dominance relations among parties (Zabel 1992). For example, in African wild dogs, interveners in conflicts generally target the dog in the R role but are even more likely to do so when the intervener is dominant to the target (de Villiers et al. 2003).

Why might puppies prefer to target individuals in the R role most of the time? Pups may use interventions to improve their rank among littermates. In domestic and wild canids, play is thought to contribute to the formation of dominance relationships within litters (Bekoff 1972). Although rank relations among littermates of domestic dogs became fairly stable by 15 – 16 weeks of age in some breeds (James 1949; Scott & Fuller 1965), Scott & Fuller (1965) reported that in other breeds (such as basenjis and fox terriers) dominance relations continued to develop until at least one year of age (the time when follow up was discontinued). Furthermore, status among littermates has only been measured through food competition tests; no information exists on when ritualized displays of status (Schenkel 1967) stabilize. Thus, by joining a dog in the AC role, an intervener might rise in rank relative to the dog in the R role if that individual becomes less likely to challenge the intervener in the future. Both the intervener and the dog in the

AC role may benefit even though the intention of the intervener is not necessarily to provide coalitionary support. de Villers et al. (2003) suggest that similar processes might be responsible for coalitionary attacks against subordinate African wild dogs.

Additionally, if time spent in an offense role during play among littermates correlates with dominance outside of play as it does in unrelated, adult domestic dogs (Bauer & Smuts 2007), then practicing offense behaviors whenever an easy opportunity arises may confer benefits. We know of no data on reproductive effects of dominance status among dogs, but within litters of wolves, relatively low-ranking individuals may leave the natal pack earlier than higher-ranking wolves (Zimen 1976; 1981), possibly incurring greater risks during dispersal (Bekoff & Wells 1986). Also, wolf pups compete fiercely with one another over food (Mech & Boitani 2003), and dominant pups may receive more food and gain more weight than subordinate littermates. In one population, weight in wolf pups was positively correlated with survival from age 3 months to 4 years post-capture (Ballenbergh & Mech 1975).

Puppies might also target littermates in the R role as a result of social facilitation (e.g., do what the other is doing). Such behavior does not require complex cognitive processes, but it may foster the mutual reliance and cohesiveness necessary for the synchronization of future group-related activities such as hunting and territorial defense (Zabel 1992). Although free-ranging domestic dogs are primarily scavengers, (Boitani et al. 1995; MacDonald & Carr 1995), pariah dogs in India will sometimes group together to hunt deer or drive intruding dogs off foraging or hunting territories (Fox 1978). Nesbitt (1975) reported on a pack of feral dogs preying on young deer in the United States. Social facilitation is also involved in predatory, sheep-chasing behavior and attacks by

Norwegian Elkhounds (Christiansen et. al. 2001). Additionally, larger groups of free-ranging dogs in the mountainous region of central Italy were more successful at defending food resources from smaller groups (MacDonald & Carr 1995), and these dogs also defended core territories (Boitani et al. 1995). Even though interveners may be acting opportunistically in the short-term by targeting the dog in the R role, long-term cooperative benefits could accrue to the group as a whole.

Although interveners preferentially targeted the dog in the R role, they also sometimes targeted the dog in the AC role. By time 3, mounts became a relatively common intervention behavior (Fig. 1c), and 91% of all mounts were directed at the dog in the AC role. Mounts are used in dominance testing (Abrantes 1997) but also in mating and sexual play (Scott & Fuller 1965), which might account for their increased frequency in time 3—the time at which puppies begin to reach sexual maturity (Scott & Fuller 1965). Both males and females engaged in mounting interventions at roughly equal frequencies (45% of mounts involved male interveners). Bauer and Smuts (2007) found that during play among unrelated adult domestic dogs, male-to-male mounts occurred almost 16 times more often than female-to-female mounts. We found no such difference with littermates. Twenty-three percent of female mounts were directed to other females and 17% of male mounts were directed to other males.

Puppies did not display reciprocity in joining during interventions in play. Reciprocity may fail to occur because puppies were intervening in play rather than in real aggression. With real aggression, interveners can cooperate (provide support) with either the dominant or subordinate animal engaged in a conflict (de Waal & Harcourt 1992). In this study, it is unlikely that puppies targeted the dog in the R role in order to support the dog in the AC role because in > 80% of interventions, actor and recipient roles could be identified at the time of the intervention. Therefore, interveners did not help to induce submission, but instead took advantage of the opportunity to practice being in an offense position over a dog already in the R role. Similarly, juvenile Japanese macaques do not reciprocate in coalition formation (Prud'homme & Chapais 1996). Instead, juvenile females use interventions opportunistically to influence rank relationships by "winning" contests with individuals that they may not be able to regularly dominate in one-on-one dyadic contests (Prud'homme & Chapais 1996).

Conclusion

Our findings suggest that during the socialization and juvenile periods of development, littermates use interventions to practice offense behaviors directed at siblings in subordinate roles. Littermates did not use targeting to initiate play with preferred partners, and we found no evidence for reciprocity in joining, which suggests that puppies are not targeting to provide coalitionary support, at least not during the stages of development studied here. We propose that, in the short-term, puppies opportunistically intervene because winning in a contest appears to be a goal in itself and may be associated with the future acquisition of status. However, over the long-term, social facilitation (e.g., the tendency for all to target the dog in the R role) may pave the way for the development of more complex cooperative partnerships that facilitate group coordinated behaviors such as hunting and territorial defense (Chapais 1996).

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Table 3-1. Summary of domestic dog litters

Litters	Breeds	Birthdates[a]	Sex composition[b]	Observation dates	Time periods[c]	Age ranges (in weeks) of puppies
1	Shepherd mix	14 February 2004	3 ♀ 3 ♂	February-November 2004	1 2 3	3–8 11–23 27–40
2	Labrador retriever	21 April 2005	2 ♀ 4 ♂	May-October 2005	1 2	3–8 10–23
3	Doberman pincher	22 April 2004	1 ♀ 2 ♂	May-June 2004	1	3–7
4	Malamute	4 May 2005	4 ♂	May-June 2005	1	3–8

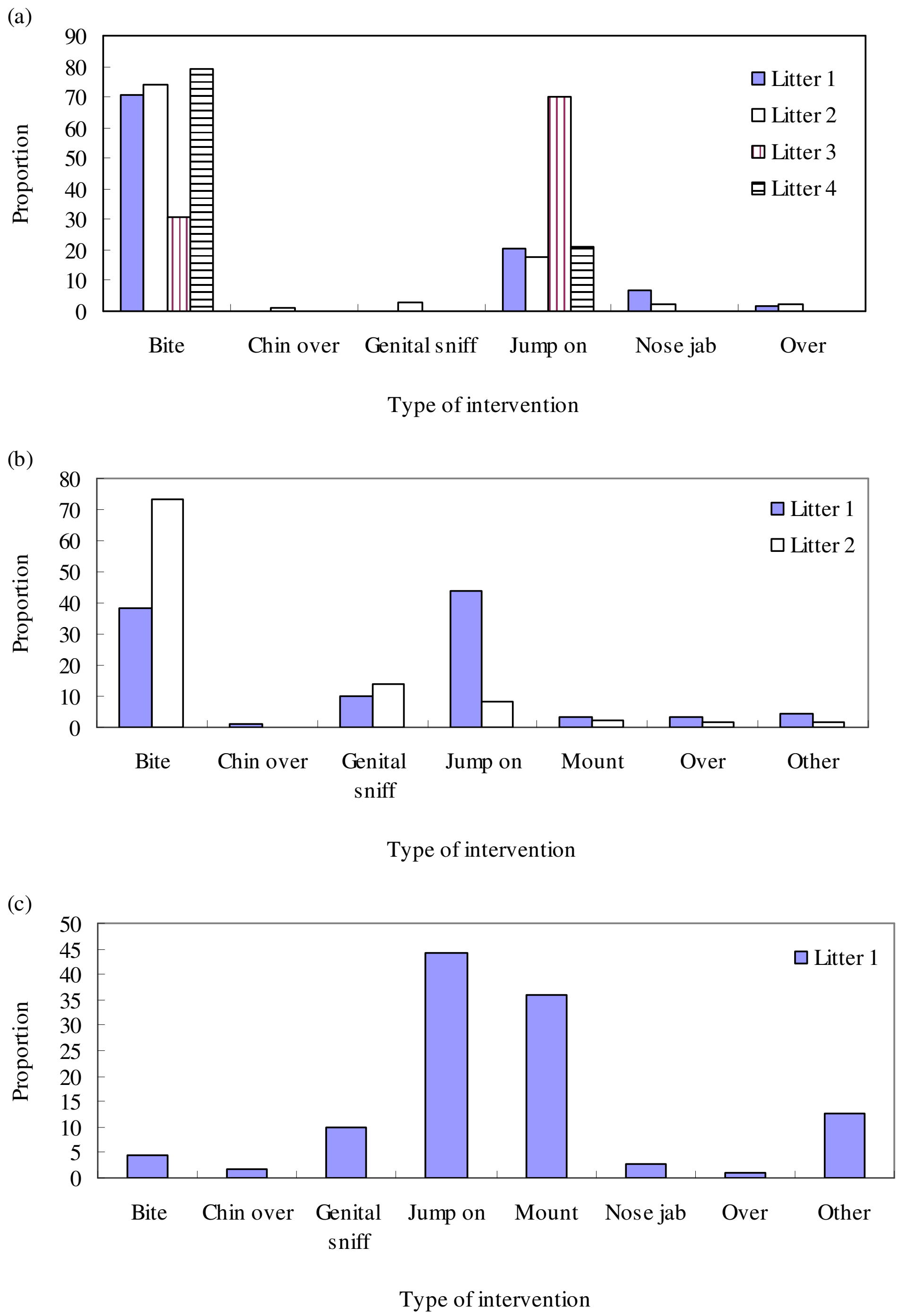
[a] Only surviving puppy listed. [b] One puppy (female) from litter 1 died shortly after birth, and two puppies (both females) from litter 3 died shortly after birth. [c] Observations were collected over three time periods.

Table 3-2. Ethogram of intervention behaviors

Behaviour	Definition
Bite	[a]INT takes hold of or attempt to take hold of another dog's body with the mouth.
Genital sniff	INT sniff the genital region of another dog while the other dog is lying belly up.
Jump on	INT jumps on, tags, pushes at or slams into another dog.
Mount/mount attempt	INT rears up (keeping hind legs on the ground) to place forelegs on on another dog's back. INT has a rounded spine with curved front legs and forepaws to grasp the other dog's torso. Pelvic thrusting may or maynot be present. With an attempt, INT attempts a mount but is unable to maintain position.
Chin over	INT places the underside of chin over the other dog's back, usually right behind the neck or near the other dog's shoulders.
Nose jab	INT rapidly pokes at another dog with the nose.
Over	INT sits on, stands over, or lies over another dog with at least 25% of INT's torso covering the other dog.

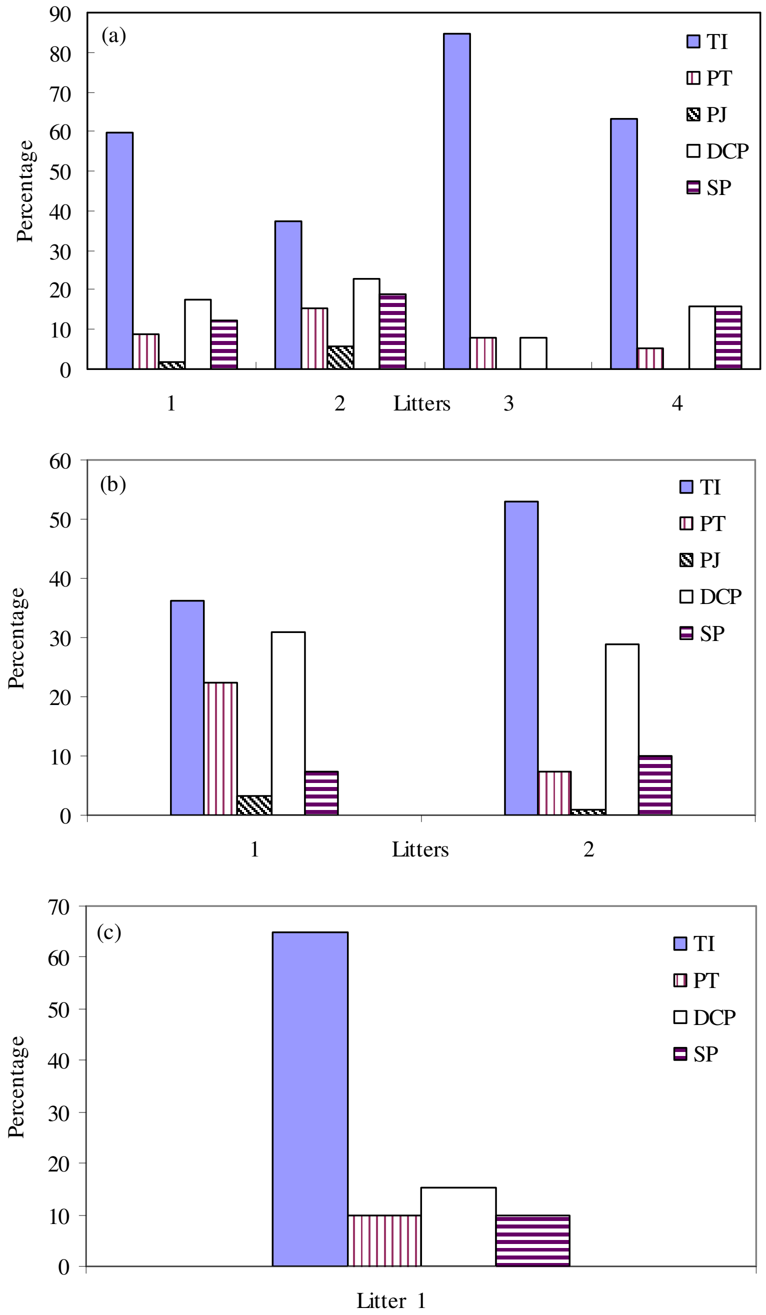
[a]INT = intervening dog.

Figure 3-1. Types of interventions



The proportion of times each type of intervention occurred. Results include data from four litters in time 1 (a), two litters in time 2 (b), and one litter in time 3 (c). See Table 2 for an ethogram of behaviors measured. Age range (in weeks) of puppies: time 1 = 3–8, time 2 = 10–23, and time 3 = 27–40.

Figure 3-2. Intervention outcomes



The number of times the following outcomes occurred in the 5 s following an intervention: TI—intervener played with both members of the original dyad, PT—the intervener played with the target to the exclusion of the other dyad member, PJ—the intervener played with the non-target to the exclusion of the target, DCP—the intervener left and the original dyad continued to play, and SP—play stops. Results include data from four litters in time 1 (a), two litters in time 2 (b), and one litter in time 3 (c). Age ranges (in weeks) of puppies: time 1 = 3–8, time 2 = 10–23, and time 3 = 27–40.

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CONCLUSION

The studies presented in this dissertation address cognition, including social cognition, in the domestic dog. Complex cognitive behaviors have been documented in taxonomic groups as diverse as primates, parrots, corvids, and dolphins. In all of these species, social relationships are at the heart of group living. Selection may have favored advanced cognitive abilities for individuals living in complex social groups. These advanced abilities may have aided individuals in dealing with the demands of group living.

In addition to the species mentioned above, social carnivores also live in complex social groups; however, there is little empirical data on their cognitive potentials. This study has addressed the need for comparative work on cognition in social carnivores and, at the same time, has examined the cognitive abilities of a domestic carnivore, both in the social and non-social arenas. A broad-based approach, like the one taken here, provides data that can be used to draw inferences about the functional significance of observed behavioral patterns in species that may have experienced selective pressures similar to dogs (e.g., social carnivores [wolves, lions, African wild dogs] and humans). Additionally, we also compared our data on the development of social behavior among littermates with the social behavior of adult domestic dogs to examine the timing of behaviors and how specific behaviors are expressed across the lifespan.

In Chapter One, we used two experiments to examine the perceptual and cognitive abilities of domestic dogs at quantity-judgment tasks in two experiments. In experiment 1, we presented two food choices simultaneously to each dog (29 dogs tested), and these choices were visually available to the subjects at the time of choice. As a group, dogs chose the larger quantity more often than the smaller quantity across the eight different comparisons tested, but they found close comparisons more difficult (e.g., 1 vs. 4 was easier than 3 vs. 4). When we tested two dogs from experiment 1 multiple times on nine different quantity comparison in experiment 2, they too chose the larger quantity more often than the smaller quantity (conditions 1–3), even when the food was visually unavailable to the subjects at the time of choice (conditions 2 and 3). In condition 2, we presented the food choices simultaneously, and in condition 3, we presented them sequentially. In condition 1 (experiment 2), both dogs were more likely to choose the larger quantity when distance between quantities was large. However, performances in conditions 2 and 3 varied by dog. For one subject (Marty), distance affected performance in condition 2 but not in condition 3. For the other subject (Acorn), performance was independent of distance between quantities in both conditions 2 and 3.

This study demonstrated that some domestic dogs can perform on par with chimpanzees and orangutans when tested on similar quantity-judgment tasks. Because in most cases the dogs' performance was related to distance between quantities, we suggest that they are most likely using an approximate (rather than exact) mechanism of quantity representation. Chimpanzees and orangutans also represent quantity (or number) approximately, and their performances on quantity-judgment tasks are subject to distance effects similar to that found with dogs. Humans represent small numbers, like those tested in this study, exactly rather than approximately. This suggests that dogs perform more like chimpanzees and orangutans and less like humans when judging the differences between small quantities. Additionally, the fact that both dogs were still able to choose the larger quantity when we presented the food sequentially (condition 3) rather than simultaneously (condition 2), and the food was visually unavailable at the time of choice, suggests that dogs, like apes tested on similar tasks, can form internal representations and make mental comparisons of quantity.

In Chapter's 2 and 3, we focused on social cognition and the development of social relationships among littermates of domestic dogs. We videotaped behavior in four litters of dogs when the puppies were between 3 and 40 weeks of age (collection times varied by litter). We divided data collection and analysis into three time periods to approximately coincide with critical periods in the social development of dogs. Time period 1 reflected the early socialization period; time period 2, the late socialization and early juvenile period; and time period 3, the later juvenile period.

In Chapter 2, we focused on play partner preferences and asymmetries in social play. We found that early in development, puppies tended to initiate play with most other littermates, but later on, they focused their efforts on a smaller subset of partners. Early play partner preferences formed prior to 8 weeks of age (time 1) tended to be fairly stable across time and were associated with later partner preferences measured when the puppies were between 27 and 40 weeks of age (time 3). Although data on the development of play partner preferences are scarce, Thompson (1996) demonstrated similar findings in infant sable antelope. They, too, tended to sample a variety of partners early in development but then later concentrated on initiating play with their most preferred playmates. Stability in choice of playmates was also consistent over the developmental time period measured (up through 12 weeks of age).

We also found that in no time period did play conform to the 50–50 rule, although play was more symmetrical in time period 1 compared to time periods 2 and 3. Our results in testing the 50–50 rule are consistent with research on play in adult domestic dogs. Adult dogs do not conform to the 50–50 rule during play; instead dogs dominant to their current play partner outside the play context are more likely to adopt the dominant role during play (Bauer & Smuts 2007). Because virtually all social behaviors in our study occurred in the context of play, we did not attempt to measure dominance relationships of puppies outside of play.

We examined the associations between offense behaviors (e.g., chasing, forcing partners down), initiations, self-handicapping, and play bows and found significance in a number of areas. Dogs who engaged in high rates of offense behaviors also initiated play at significantly higher rates, but only in time 3. This implies that winning during play may become more important as puppies mature. However play is about more than just practicing dominance or offense behaviors. Play also involves elements of cooperation. For example, self-handicapping behaviors were positively associated with play bows, suggesting that self-handicapping, like play signals, may function to indicate playful intent. Similarly, adult dogs use self-handicapping and play signaling in conjunction with one another to facilitate play (Bauer & Smuts 2007).

In mixed-sex dyads, males initiated play, self-handicapped, and engaged in offense behaviors more than females. These first two findings suggest that males may be using play to gain skills useful in attracting mates. Data on feral dogs suggest that female-mate choice influences male reproductive success (Pal et al. 1999); therefore, males may initiate and self-handicap more often than females in mixed-sex dyads in order to learn about female behavior and establish social bonds with them. However, males also engaged in offense behaviors more often than females, suggesting that males may also be practicing an alternative strategy—one related to sexual coercion. In feral dog groups, males will sometimes force copulations on young and sexually inexperienced oestrus females, although these forced copulations are not as successful as copulations in which the females cooperate (Ghosh, et al. 1984; Pal et al. 1999). Thus, we hypothesize that males may use play to practice both cooperative and competitive strategies to gain future mating opportunities. To test this hypothesis, longitudinal studies on feral dogs would need to examine whether patterns of male play with females early in development later translate into increased male reproductive success.

Females initiated play with females more often than they initiated with males across all time periods. This finding suggests that same-sex play in females may serve as training for intrasexual competition. In contrast to many mammals, intrasexual aggression in both wolves and domestic dogs tends to be more serious among females than among males (Derix et al. 1993; Sherman et al. 1996). In a wolf pack, usually (but not always) only the alpha female mates, and other subordinate females cooperate in rearing pups. The alpha female works to suppress expansionary tendencies by other female pack members year round (whereas male-to-male aggression is concentrated around the breeding season), although female-female tensions are especially high during the mating seasons (Derix et al. 1993). The high incidence of female-to-female aggression in domestic dogs may be a reflection of their wolf ancestry. If one function of female-

female play is to serve as practice for serious, intrasexual fighting, we would expect females to engage in higher rates of offense behaviors with other females than with males, given that fights between females and males are uncommon. Instead we found that females displayed offense behaviors at similar rates whether playing with males or females. This suggests that females are probably not playing with one another primarily to practice fighting skills. Instead females might prefer to initiate play with other females in order to develop social bonds and practice behaviors that might ultimately serve to ritualize aggression.

Males initiated play with males more often than they initiated with females, but only in time period 3. As with female-female play, males may play with other male littermates to establish social relationships with one another that ultimately may help to keep overt aggression in check. The less serious nature of fights between adult male dogs compared to fights between adult female dogs (Sherman et al. 1996) may account for the finding that males preferred to initiate play with other males only in the latest time period, whereas females preferred to initiate with females across all time periods.

Lastly, the types of offense and self-handicapping behaviors displayed were similar across litters, suggesting that the expression of these behaviors may follow a similar ontogeny in puppies in general.

In Chapter 3, we examined the development of third-party interventions in play among littermates. We found that when dogs intervened in dyadic play, they preferentially targeted the receiver (i.e., the dog receiving offense behaviors) rather than the actor (i.e., the dog directing offense behaviors) most of the time. This finding is consistent with the intervention literature that emphasizes “winner support”. Interveners did not preferentially target or join (i.e., not target) their preferred playmates, and they did not show reciprocity in joining.

Our findings suggest that littermates use interventions opportunistically to practice offense behaviors directed at littermates already behaving subordinately. In such instances, an intervener does not need to force an animal into a subordinate role but rather simply takes advantage of a target animal who is already in a subordinate position and receiving offense behaviors. If play in dogs aids in the formation of dominant-subordinant relationships, as some researchers suggest (Scott & Fuller 1965, Bekoff 1972), it makes sense for individuals to practice offense behaviors whenever an "easy opportunity" arises, especially if by continually practicing such behaviors, an individual actually gains in status.

Additionally, third-party interventions might be one way that animals can gain competence when performing group-coordinated behaviors used in territorial defense and cooperative hunting. Wolves hunt big game such as elk, deer, and even bison, and their success in bringing down large prey depends heavily on the coordination of group behavior. Even among feral dogs, who tend to be scavengers, there are reports of packs bringing down deer (Nesbitt 1975).

The studies described in this dissertation provide new kinds of information on cognition in domestic dogs, and further research is clearly important. Below, I describe future areas of research relevant to numerical abilities and the development of social behavior.

Further work on numerical cognition should incorporate a larger sample of dogs than used here (Chapter One) to examine quantity-judgment skills when quantities are not visually available at the time of choice (experiment 2, conditions 2 and 3). The two dogs used in our sample could discriminate the larger from the smaller quantity in conditions 2 and 3, but a larger sample would provide for greater generalizability of our results to the general dog population. As an extra challenge, dogs could be asked to distinguish between three or more quantities in situations where the food is both visually available and unavailable at the time of choice. In the conditions where food was visually unavailable at the time of choice (conditions 2 and 3), we waited 3 s after covering the plates before allowing the dogs to choose either the larger or smaller quantity. This 3 s limit could gradually be extended to determine the upper limit of time in which dogs could keep track of quantities mentally and chose optimally.

We are unsure as to why distance effects were not correlated with performance when food was presented sequentially and visually unavailable at the time of choice (experiment 2, condition 3), even though both dogs still chose optimally overall. A similar breakdown of the distance effect also occurred for chimpanzees when they were required to keep track of quantities mentally (Beran 2004). Research on the mechanisms that account for this breakdown effect would be especially interesting for comparative work.

Future work on social cognition among littermates would benefit by addressing variability both within and across litters. In our study (Chapter’s Two and Three), we focused on overall patterns across a variety of breeds and breed mixes, but research that looks at breed effects would be especially interesting. For example, is the development of social relationships among littermates different for dogs that have been generally bred to live and work in packs (e.g., huskies and many of the hounds) compared to dogs that have been bred primarily for human companionship (e.g., many of the toy breeds)? Does social development vary depending on whether dogs are free-ranging or "pampered pets"? Additionally, what does the development of social relationships among littermates of wolves look like? Do ancient breeds of dogs that are more genetically similar to the gray wolf (e.g., Akita, Alaskan malamute, chow chow, etc.—see Parker et al. 2004) develop more like wolf pups than breeds that are less genetically similar to the wolf? Answers to such questions will expand the scope of comparative work among different breeds and between dogs and other social carnivores as well as between dogs and humans. Addressing such questions will also contribute greatly to understanding how social variations early in life between individuals, between breeds, and between dogs and wolves compare with variations in adult social behavior.

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