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Third-party interventions in dyadic play between littermates of domestic dogs, *Canis lupus familiaris*

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Interventions occur when animals interfere in competitive interactions between two or more individuals. Interveners can alter the nature of the ongoing interaction by targeting one party (attacking, biting) and supporting the other. Three theories have been proposed to account for intervention behaviour: kin selection, reciprocity and direct benefits. The kin selection hypothesis predicts that interveners will selectively support relatives over nonrelatives; the reciprocity hypothesis predicts that when intervener 'A' supports individual 'B', later 'B' will intervene and support 'A'; and the direct benefits hypothesis predicts that target/support patterns should serve the immediate interests of the intervener. We tested the reciprocity and direct benefits hypotheses by exploring third-party interventions in play fighting among littermates of domestic dogs. Interveners in dyadic play did not preferentially target or support preferred playmates of the intervener. Interveners targeted the dog in the losing role at the time of the intervention, and they did not show reciprocity in support. Taken together, these last two findings suggest that littermates benefit directly and use interventions opportunistically to practise offence behaviours directed at littermates already behaving subordinately. Opportunities to practise targeting in a playful setting may help structure dominance relationships among littermates. Additionally, the tendency for puppies to do what the other is doing (target the dog in the losing role) may pave the way for synchronizing cooperative behaviours during group hunting and territorial defence. The types of behaviours used to intervene changed over development, but the outcome following an intervention remained stable.

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The term intervention (sometimes referred to as coalition formation) has been used to describe outsiders (third parties) becoming involved in pairwise competitive or aggressive encounters. Often interveners take sides by attacking one party (biting, pushing, jumping on, chasing away), thereby supporting the other (Grammer 1992; Silk 1992; de Waal & Harcourt 1992; Roeder et al. 2002). The ability to keep track of multiple social interactions (as in a triad) is a cognitively demanding activity most likely to occur among animals that live in social groups (Whiten & Byrne 1988). For these animals, interventions can be important in the development of social bonds and cooperative behaviours that can influence rank relationships between individuals and access to reproductive resources (de Waal & Harcourt 1992). For example, in a captive pack of wolves, *Canis lupus*, where only the dominant male and female bred each year, a subordinate male, supported by his two male

siblings, successfully challenged his father, the breeding male, since the pack's inception (Jenks 1988).

Even though interventions are expected to occur across a variety of complex social species, they have been described primarily in primates (Seyfarth 1976; de Waal 1977; Silk 1982, 1992; de Waal & Luttrell 1988; Grammer 1992; Prud'homme & Chapais 1996; Watts 1997; Roeder et al. 2002) and to a lesser extent in other mammals: bottlenose dolphins, *Tursiops* sp. (Connor et al. 1992); spotted hyaenas, *Crocuta crocuta* (Zabel et al. 1992; Engh et al. 2000); African wild dogs, *Lycaon pictus* (de Villiers et al. 2003); wolves (Zimen 1976; Jenks 1988); horses, *Equus caballus* (VanDierendonck et al. 2009); zebras, *Equus quagga boehmi* and *E. quagga antiquorum* (Schilder 1990); and goats, *Capra hircus* (Keil & Samba 1998).

Three theories have been proposed to account for interventions. One is based on kin selection. Kin selection predicts that individuals are more likely to assist relatives over nonrelatives because related individuals share genes identical by descent (Hamilton 1964a, b). Therefore, interveners in aggressive contests should often side with kin over nonkin. Such support, observed among primates (Kurland 1977; Walters 1980; Silk 1982; Silk et al. 2004), African wild dogs

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(de Villiers et al. 2003) and spotted hyaenas (Engh et al. 2000) suggests the operation of kin selection. For example, maternal interventions on behalf of offspring play a critical role in hyaena rank inheritance (Engh et al. 2000).

Another theory to account for intervention behaviour involves reciprocity, where cooperative individuals lend each other favours that will be returned at some point in the future (Trivers 1971). Reciprocal support has been documented in chimpanzees, *Pan troglodytes*, rhesus macaques, *Macaca mulatta*, and stump-tail macaques, *Macaca arctoides*, even after controlling for potentially confounding data on kinship relationships, proximity relationships and same-sex combinations (de Waal & Luttrell 1988). In some species, support is only given to close associates (human children, *Homo sapiens*, Grammer 1992; chimpanzees, de Waal 1992), and in other species, reciprocity in support is uncommon (Barbary macaques, *Macaca sylvanus*, Widdig et al. 2000; juvenile Japanese macaques, *Macaca fuscata*, Prud'homme & Chapais 1996). Reciprocity can also exist in targeting, where individuals selectively intervene against individuals that regularly intervene against them. Such a 'revenge system' has been observed in chimpanzees (de Waal & Luttrell 1988; de Waal 1992) and male bonnet macaques, *Macaca radiata* (Silk 1992).

Finally, interventions can provide direct benefits (Prud'homme & Chapais 1996). 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, spotted hyaena cubs (Engh et al. 2000), wolves (Zimen 1975; Jenks 1988) and African wild dogs (de Villiers et al. 2003) use targeting to manoeuvre for position in the pack hierarchy. Although African wild dogs that intervene generally do so in a manner that supports the existing dominance hierarchy (an intervener will support the more dominant individual in a contest), one subordinate subadult male solicited and received support from two of his younger siblings that enabled him to rise in rank above other members in his cohort (de Villiers et al. 2003).

Very little is known about intervention behaviour outside of primates. Studies on the development of interventions in young animals of any species (including primates) are particularly sparse (Balfour 1987; Zabel et al. 1992; Prud'homme & Chapais 1996; Engh et al. 2000; de Villiers et al. 2003).

We consider an investigation of interventions in puppy play important for at least two reasons: first, they resemble triadic interventions during real fighting among adults, behaviours known to have important reproductive consequences in a number of species (above). To determine whether young animals practise intervention tactics during development, we have to study social play because it is probably the most common arena for interventions early in life. Second, triadic interventions during play might be important to the development of social relationships in general, as they often are in adults. For example, do individuals tend to support preferred playmates (see below) when they intervene in dyadic play?

Dogs, as a domestic species, can make critical contributions to developmental research. They are easy to study in their natural habitat, living with humans. In addition, dogs have undergone intensive artificial selection for specific behaviours in particular breeds; breed differences in behaviour are well documented (Duffy et al. 2008), and as a result of its medical relevance, information on the genes underlying behavioural differences is advancing with great speed (Spady & Ostrander 2008). In combination, these attributes make dogs a uniquely valuable model for the study of gene–environment interactions during social development. Before such studies can be undertaken, however, a much better understanding of basic social–developmental processes in young dogs is

required. The current study aims to contribute to this basic knowledge.

In the current study, we examined the development of intervention behaviour among littermates of domestic dogs during play fighting. In canids, play fighting includes behaviours such as chasing, rough-and-tumble wrestling, mounting behaviour (mimicking copulatory behaviour) 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 behaviour (we do not know whether the interveners expected to achieve a particular outcome). We focused on interventions during play fighting as opposed to agonistic fighting because real aggression between young littermates is exceedingly rare (Bekoff 1974; C. Ward & B. Smuts, personal observation). However, social play in canids resembles actual fighting in that it contains many of the same actions (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; Fentress et al. 1987; MacLeod 1996; MacLeod & Fentress 1997). 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 that 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 five main goals. First, we tested whether domestic dog littermates would target the dog in the losing position and thereby support the dog in the winning position at the time of the intervention, similar to juvenile Japanese macaques (Prud'homme & Chapais 1996) and infant spotted hyaenas (Zabel et al. 1992). Second, we determined whether interveners were more or less likely to target their preferred play partners. We defined preferred playmates in terms of initiations (a puppy initiated more play on average with their preferred partners than with all other littermates; see Ward & Smuts 2008). Interveners may be more likely to support (and thereby target less) a valued social partner. For example, during an aggressive attack on an individual wolf in a captive wolf pack, a 'good friend' may help defend the victim against the attacker (Zimen 1975). Conversely, interveners may target preferred playmates if they use targeting as a means to initiate play. Third, we determined whether patterns of reciprocity in support existed. Fourth, we assessed whether interventions were more consistent with patterns of reciprocity or direct benefits. Because all puppies within litters were related, we were unable to test for kin selection with our current data set. Finally, we tested for variation in the frequencies of intervention behaviours (i.e. what common behaviours do puppies use to intervene?) and intervention outcomes (i.e. what happens after an intervention occurs?) across development.

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 Caesarean births) at home. The dams suckled the puppies and weaned them prior to their placement in permanent homes. Breeders supplemented nursing with solid foods starting when puppies were about 4 weeks

Table 1
Summary of domestic dog litters

Litters	Breeds	Birth dates	Sex composition*	Observation dates	Time periods†	Age ranges (in weeks) of puppies	No. of interventions
1	Shepherd mix	14 February 2004	3 ♀ 3 ♂	February–November 2004	1	3–8	58
					2	11–23	94
					3	27–40	112
2	Labrador retriever	21 April 2005	2 ♀ 4 ♂	May–October 2005	1	3–8	153
					2	10–23	125
3	Doberman pincher	22 April 2004	1 ♀ 2 ♂	May–June 2004	1	3–7	13
4	Malamute	4 May 2005	4 ♂	May–June 2005	1	3–8	19

* Only surviving puppies are listed. One puppy (female) from litter 1 died shortly after birth, and two puppies (both females) from litter 2 died shortly after birth.

† Observations were collected over three time periods.

old. Puppies from litters 2–4 remained sexually intact for the duration of the study. With the exception of one male, all puppies from litter 1 were spayed or neutered, starting at 21 weeks old.

Data Collection

Data collection was divided into three time periods (Table 1) to coincide approximately with periods associated with the development of behaviour (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 (3–12 weeks old), play and social behaviours develop, and during the juvenile period (12 weeks–sexual maturity), pups explore their surrounding environments and sexual behaviours become apparent (see Scott & Fuller 1965).

For all litters, we observed puppies in the breeders' homes when puppies were 3–8 weeks old (time period 1; Table 1). We collected data 5–7 days per week for approximately 3 h per day. During time 1, litters 1–3 were housed indoors in one-room enclosures approximately 7.2 m². Litters 2 and 3 also had free access to outdoor fenced areas (72 m² and 99 m², respectively). Litter 4 was kenneled outdoors in a 4 m² enclosure, but data were collected in the adjacent yard, a 506 m² fenced area. Although enclosure size varied by litter, living areas were large enough to allow all puppies to move and play freely.

During time period 2 (Table 1), owners of puppies from litters 1 and 2 brought the puppies back to the breeders' homes once or twice per month and placed them together for 2–3 h in outdoor enclosures (92 m² and 72 m² for litters 1 and 2, respectively; extended observations of litters 3 and 4 were not possible). This allowed us to collect longitudinal data on littermate play behaviour starting at 10–11 weeks through 23 weeks old. 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-per-month observations when puppies were 27–40 weeks old (time period 3, Table 1) under the conditions described above in time 2. All littermates attended two sessions and five attended one session.

For litters in times periods 2 and 3, all puppies lived indoors with families. Three puppies from litter 1 and four puppies from litter 2 lived with one or more dogs in their resident homes.

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

We coded data from videotapes into a Microsoft Excel spreadsheet. We coded data only for dyadic play bouts that involved

mutual social play that lasted at least 2 s. Based on a log survivorship analysis (Martin & Bateson 1993), play bouts between the same partners were considered terminated if a minimum of 1 min passed without play activity.

Behavioural Definitions

An 'intervention' occurred when two dogs were playing and a third dog approached (the 'intervener') the dyad and physically intervened in their play by jumping on, biting at, or mounting one of the players (Table 2). These behaviours are referred to as 'targeting' one dog (the 'target') while simultaneously 'supporting' the other dog (the 'nontarget'). (We use the term 'support' to maintain consistency with terminology used in the intervention literature, but it does not imply any specific motivation underlying the intervener's actions). We also coded the behaviour of the two playing dogs, relative to each other, at the instant the intervention occurred. If only one of the playing dogs directed 'offence behaviours' towards the other dog (biting, mounting, jumping on, standing over), we considered the dog that showed the offence behaviours to be in the 'winning role' and the other dog to be in the 'losing role'. If both dogs simultaneously directed offence behaviours to each other at the moment the intervention occurred, we assigned the winning role to the dog in the higher body position, since high postures have been identified with the 'winner' of ritualized interactions in wolves and dogs (Schenkel 1967; van Hooff & Wensing 1987; Derix et al. 1993; Bauer & 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 in the winning role.

Table 2
Ethogram of intervention behaviours

Behaviour	Definition
Bite	Intervening dog (INT) takes hold of or attempts to take hold of another dog's body with the mouth
Genital sniff	INT sniffs 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 hindlegs on the ground) to place forelegs 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 may not 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

Data Analysis

To determine whether the intervening dog was more likely to target the dog in the winning or losing 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 whether the proportion of losing targets varied by sex of the intervener or by time period. We calculated the proportion of losing targets (P_{lose}) separately for each puppy and time as: $P_{\text{lose}} = r/n$, where r is the number of times that puppy A intervenes and targets the dog in the losing role, and n 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_{lose} did not vary by sex or time, we pooled the data and ran a second GLMM model to determine whether the proportion of losing targets differed from 50% (whether the arcsine-root transformation of P_{lose} 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 used row-wise matrix correlation tests (K_r) (MatMan software package with 10 000 permutations; Hemelrijk 1990a, b; de Vries 1993) to determine whether an intervener was more likely to target/support a preferred partner and to determine whether puppies displayed reciprocity in support. 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). This test treats each matrix row independently (rather than each cell) to account for interindividual variation in behaviour (de Vries 1993). The K_r statistic tests whether the association between two matrices is greater than expected by chance. The two-tailed significance of the association is determined by comparing the percentage of all matrix permutations that yields a value as extreme or more extreme than the K_r statistic calculated from the observed data (Hemelrijk 1990a).

To determine whether the intervener was more likely to target/support a preferred partner, we compared a data matrix of play-partner preference scores (I_{ij}) with a second matrix containing the proportion of times that each puppy targeted all other puppies during an intervention (T_{ij}) (see below). We calculated I_{ij} 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), or for litter 4 (because focal samples were lacking). We calculated T_{ij} as

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

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

To determine whether puppies displayed reciprocity in support, we compared a matrix containing the proportion of times that each

intervening puppy supported each 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 support; a negative correlation implied reciprocity in targeting.

To test for differences in the frequencies of intervention behaviours (Table 2) and intervention outcomes (see the five possible outcomes listed in Fig. 2), we fit GEE (generalized estimating equation) models assuming a negative binomial distribution for the counts of each behaviour type (Diggle et al. 1994; Hardin & Hilbe 2002). Litter was included as the cluster to control for correlations on repeated observations within the same litter. 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). Post hoc tests comparing the mean counts for each behaviour type were performed using Bonferroni correction for multiple comparisons.

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

RESULTS

We analysed 7.10 h of dyadic play from four litters of puppies containing 39 total dyads, and we coded a mean \pm SD 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).

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

Puppies did not preferentially target or support their preferred partners when they intervened in dyadic play (row-wise matrix tests: litter 1: time 1: $K_r = 4$, $P = 0.772$; time 2: $K_r = 1$, $P = 0.971$; time 3: $K_r = 1$, $P = 0.950$; litter 2: time 1: $K_r = 14$, $P = 0.198$). (As noted above, we could not calculate play-partner preference scores for litter 2, time 2, or litter 4, and sample size for litter 3 ($N = 3$) was too small to conduct matrix tests).

Puppies did not display reciprocity in support or targeting in any litter or time period (row-wise matrix tests: litter 1: time 1: $K_r = -2$, $P = 0.888$; time 2: $K_r = -1$, $P = 1.000$; time 3: $K_r = -9$, $P = 0.334$; litter 2: time 1: $K_r = -8$, $P = 0.468$; time 2: $K_r = 15$, $P = 0.132$; litter 4: time 1: $K_r = 0$, $P = 1.000$).

The proportion of particular intervention behaviours changed over development for all litters combined. In time 1, interveners used biting more than any other behaviour (chi-square tests: chin overs: $\chi^2_1 = 54.43$; genital sniffs: $\chi^2_1 = 46.01$; jump ons: $\chi^2_1 = 29.86$; nose jabs: $\chi^2_1 = 22.21$; overs: $\chi^2_1 = 273.42$, $P < 0.0001$ for all) to target another puppy (Fig. 1a). In time 2, targeting by biting was more common than any other behaviour (chi-square tests: chin overs: $\chi^2_1 = 22.11$; genital sniffs: $\chi^2_1 = 248.35$; mounts: $\chi^2_1 = 91.26$; overs: $\chi^2_1 = 48.98$, $P < 0.0001$ for all) with the exception of jump ons ($\chi^2_1 = 1.57$, $P = 0.210$; Fig. 1b). By time 3, jump ons were more common than biting (chi-square test: $\chi^2_1 = 11.03$, $P = 0.0009$), chin overs ($\chi^2_1 = 13.25$, $P = 0.0003$), nose jabs ($\chi^2_1 = 12.88$, $P = 0.0003$) and overs ($\chi^2_1 = 11.91$, $P = 0.0006$), but they were not more common than genital sniffs ($\chi^2_1 = 6.15$, $P = 0.013$, Bonferroni correction set alpha at 0.003), or mounts ($\chi^2_1 = 0.14$, $P = 0.709$). Mounts were also more common than bites ($\chi^2_1 = 9.07$, $P = 0.002$), chin overs ($\chi^2_1 = 11.55$, $P = 0.0007$), nose jabs ($\chi^2_1 = 11.00$, $P = 0.0009$) and overs ($\chi^2_1 = 10.66$, $P = 0.0006$) but not genital sniffs

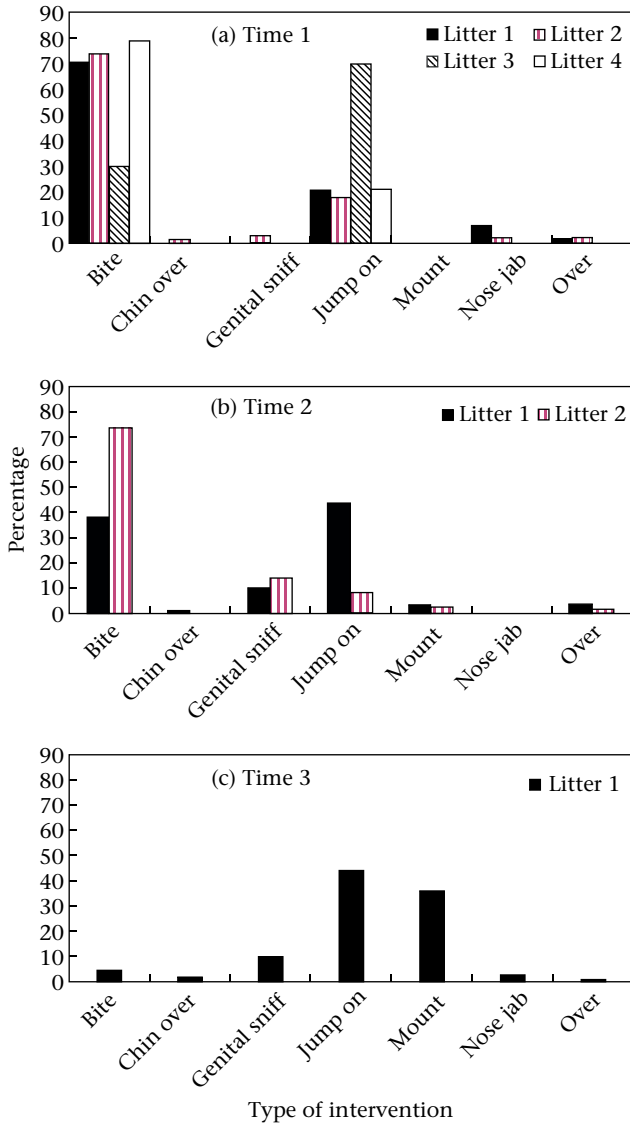


Figure 1. Percentage of times each type of intervention occurred. Results include data from (a) four litters in time 1, (b) two litters in time 2 and (c) one litter in time 3. See Table 2 for an ethogram of behaviours measured. Age ranges of puppies: time 1 = 3–8 weeks; time 2 = 10–23 weeks; time 3 =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

($\chi^2_1 = 4.53$, $P = 0.033$, Bonferroni correction set alpha at 0.003; Fig. 1c).

The outcome of interventions followed a similar pattern across litters and time periods (Fig. 2a–c). With one exception (see below), triadic play was the most common outcome following an intervention in times 1–3 (chi-square tests: time 1: triadic play versus plays with target: $\chi^2_1 = 14.03$, $P = 0.002$; plays with nontarget: $\chi^2_1 = 13.84$, $P < 0.0001$; original dyad plays: $\chi^2_1 = 9.59$, $P = 0.002$; play stops: $\chi^2_1 = 11.45$, $P = 0.0007$; Bonferroni correction set alpha at 0.005; time 2: triadic play versus plays with nontarget: $\chi^2_1 = 13.84$, $P = 0.002$; original dyad plays: $\chi^2_1 = 9.59$, $P = 0.002$; play stops: $\chi^2_1 = 6148.3$, $P < 0.0001$; Bonferroni correction set alpha at 0.005; time 3: triadic play versus plays with target: $\chi^2_1 = 15.22$, $P < 0.0001$; original dyad plays: $\chi^2_1 = 11.18$, $P = 0.0008$; play stops: $\chi^2_1 = 16.16$, $P < 0.0001$; Bonferroni correction set alpha at 0.008). In time 2, the outcomes of triadic play and plays with target were not statistically different ($\chi^2_1 = 5.94$, $P = 0.015$). In 3.6% of all interventions, the outcome could not be determined.

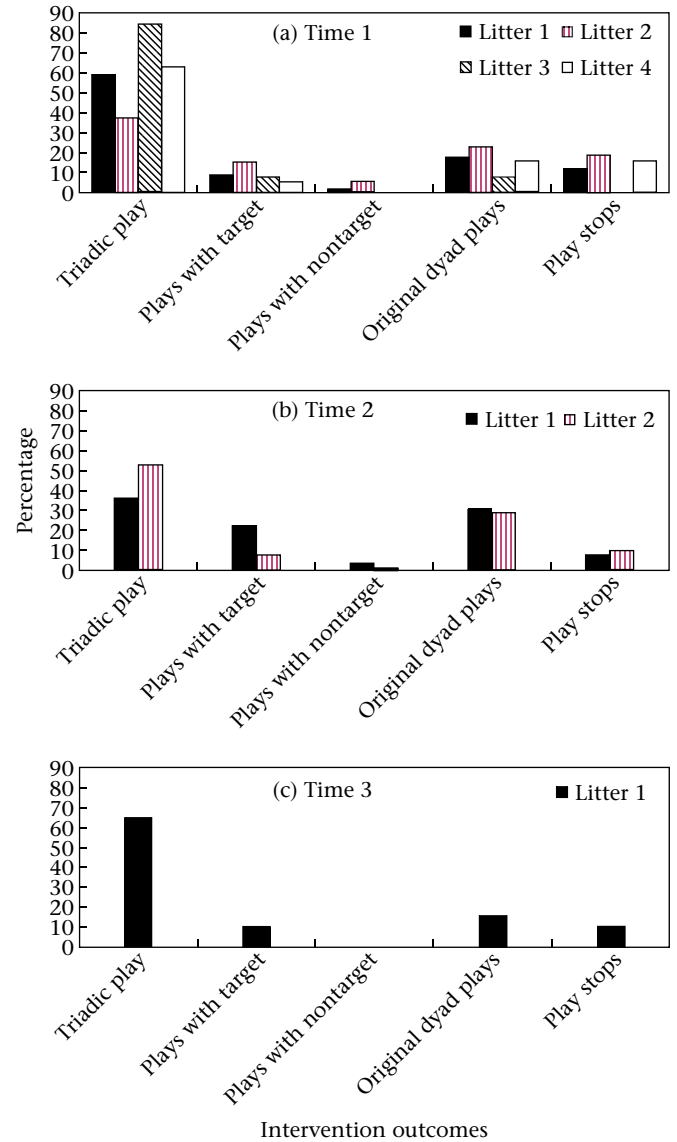


Figure 2. Percentage of times the following outcomes occurred in the 5 s following an intervention: triadic play: intervener played with both members of the original dyad; plays with target: the intervener played with the target to the exclusion of the other dyad member; plays with nontarget: the intervener played with the nontarget to the exclusion of the target; original dyad plays: the intervener left and the original dyad continued to play; play stops: play stops. Results include data from (a) four litters in time 1, (b) two litters in time 2 and (c) one litter in time 3. Age ranges of puppies: time 1 = 3–8 weeks; time 2 = 10–23 weeks; time 3 = 27–40 weeks.

DISCUSSION

We used play fighting in dogs to test two theories related to intervention behaviour: reciprocity (Trivers 1971) and direct benefits (Prud'homme & Chapais 1996). Intervention behaviour among littermates of domestic dogs appeared to be primarily opportunistic with little regard for reciprocity in support. Puppies were more likely to target the dog in the losing role at the time of the intervention, and this tendency became apparent very early in development (prior to 7 or 8 weeks old). 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 losing role is commonly seen across a variety of

species, including male bonnet macaques (Silk 1992), bonobos, *Pan paniscus* (Vervaecke et al. 2000), African wild dogs (de Villiers et al. 2003), prepubertal spotted hyaenas (Zabel et al. 1992), high-ranking children (Grammer 1992) and wolves (Zimen 1976). Typically, this strategy reinforces existing dominance relations among parties (Zabel et al. 1992). For example, in African wild dogs, interveners in conflicts generally target the dog in the losing role, but they are even more likely to do so when the intervener is dominant to the target (de Villiers et al. 2003). Used in this manner, interventions reflect social relationships, but they may also contribute to shaping those relationships (see below).

Why might puppies prefer to target individuals in the losing role most of the time? Pups may target losing dogs to improve their rank among littermates. By supporting a dog in the winning role, an intervener might rise in rank relative to the dog in the losing role if that individual becomes less likely to challenge the intervener in the future. Both the intervener and the dog in the winning role may benefit even though the intervener does not necessarily intend to provide coalitionary support. de Villiers et al. (2003) suggest that similar processes might be responsible for coalitionary attacks against subordinate African wild dogs.

Additionally, if time spent in an offence role during play among littermates correlates with dominance outside of play, as it does in unrelated, adult domestic dogs (Bauer & Smuts 2007), practising offence behaviours 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; Mech & Boitani 2003), 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 postcapture (Ballenbergh & Mech 1975).

Bekoff (1972) suggested that in domestic and wild canids, play contributes to the formation of dominance relationships within litters, as it does in rats (Panksepp 1981; Pellis & Pellis 1991). However, little is known about how dogs establish rank. In earlier studies, researchers claimed that status differences between domestic dog littermates became fairly stable by 15–16 weeks old (James 1949; Scott & Fuller 1965), but dominance among littermates was measured solely through artificial food competition tests. Food competition tests measure competitive outcomes at a single time in a specific context. More recent studies suggest that outcomes of food competition are not good predictors of stable status relationships. Instead, such relationships are most clearly reflected in role asymmetries during ritualized status displays in naturally occurring social situations (Zimen 1981; de Waal 1986; Derix et al. 1993). Our subjects did not show such displays towards littermates, and research has not systematically examined ritualized displays in domestic dogs at any age. Thus, whether patterns of puppy intervention eventually influence rank relationships is not clear.

Puppies might also target littermates in the losing role as a result of social facilitation (do what the other is doing). Such behaviour could result in benefits outside the play context if it helps puppies practise the mutual reliance and cohesion necessary for synchronization of future group-related activities such as hunting and territorial defence (Zabel et al. 1992). For example, although free-ranging domestic dogs are primarily scavengers (Boitani et al. 1995; Macdonald & Carr 1995), pariah dogs in India sometimes group together to hunt deer or drive intruding dogs off foraging or hunting territories (Fox 1978). Additionally, larger groups of free-ranging dogs in the mountainous region of central Italy successfully defend food resources against smaller groups (Macdonald & Carr

1995), and these dogs also defend core territories (Boitani et al. 1995). Nesbitt (1975) reported on a pack of feral dogs preying on young deer in the United States. Dogs also prey on livestock. In 59 incidences of livestock predation, 66% of these involved two or more dogs (Coman & Robinson 1989). Social facilitation also plays a role when Norwegian elkhounds chase and attack sheep (Christiansen et al. 2001).

Puppies did not display reciprocity in support during interventions in play. Reciprocity may have failed to occur because puppies were intervening in play rather than in real aggression. During 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 losing role to support the dog in the winning role because in more than 80% of interventions, dominant and subordinate roles were apparent at the time of the intervention. Therefore, interveners did not help to induce submission, but instead they took advantage of the opportunity to practise being in an offence position over a dog already in the losing role. Similarly, juvenile Japanese macaques do not reciprocate in coalition formation (Prud'homme & Chapais 1996). Instead, juvenile females use agonistic interventions opportunistically to influence rank relationships by 'winning' contests with individuals that they may not be able to dominate regularly in one-on-one dyadic contests (Prud'homme & Chapais 1996).

Some intervention behaviours were more common early in development (bites) and became less common as puppies matured. Conversely, other behaviours were less common early in development but became more common with time (mounts and jump ons) (Fig. 1a–c). By time 3, mounts became a relatively common intervention behaviour (Fig. 1c), and 91% of all mounts were directed at the dog in the winning role. A dog in the winning role was typically on top and may have been more accessible, or there may have been something about being in the winning role that prompted a mounting intervention in dogs 6–10 months old. Future work in this area is necessary.

Both males and females engaged in mounting interventions at roughly equal frequencies (45% of mounts involved male interveners). Bauer & 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 in littermates. Twenty-three per cent of female mounts were directed to other females and 17% of male mounts were directed to other males.

In litter 1, all puppies (with the exception of one male) were neutered by time 3. This change in hormonal status could have influenced their mounting behaviour. However, mounting in dogs occurs frequently during play and is not necessarily sexual (Overall 1997). As in primates, mounting in dogs appears to have multiple functions because both sexes show the behaviour, it occurs inside and outside the breeding context, and it occurs in both juveniles and adults. These characteristics indicate that mounting is not a highly hormone-dependent behaviour (Adkins-Regan 2003).

Unlike changes in the types of intervention behaviour across time, intervention outcome was fairly consistent longitudinally (Fig. 2a–c). Interventions commonly resulted in triadic play from the time the puppies were 3 weeks old until they were 40 weeks old (for litter 1). We never observed an intervention in play fighting spill over into real fighting. Therefore, risks to the intervener were small. By joining in ongoing play, an intervener may actually be receiving multiple benefits: those associated with the opportunistic targeting of a dog in the losing role and those associated with social play (training for cognitive and motor development: Bekoff 1984; Byers 1998; development of emotional flexibility: Spinka et al. 2001).

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