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Partner preferences and asymmetries in social play among domestic dog, *Canis lupus familiaris*, littermates

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We videotaped behaviour in four litters of domestic dogs to explore social play and the development of relationships within litters. We collected data when the puppies were between 3 and 40 weeks of age, but collection times varied by litter. We divided data analysis into three time periods to coincide approximately with critical periods in the early social development of dogs. Early play-partner preferences were associated with preferences in later time periods, and the tendency for puppies to prefer specific partners increased over time. Play did not conform to 50–50 symmetry of roles between partners, which some researchers claim is necessary to sustain play. In the later juvenile period (time 3), dogs who engaged in high rates of offense behaviours (e.g. chasing, forcing partners down) also initiated play at higher rates, implying that winning during play may become more important as puppies mature. Self-handicapping behaviours were positively associated with play signalling, suggesting that, like play signals, self-handicapping may function to indicate playful intent. In mixed-sex dyads, males initiated play, engaged in offense behaviours, and self-handicapped more than females. Females were more likely to initiate with females across all time periods, but males were more likely to initiate with males only in time 3. We discuss results from mixed- and same-sex interactions with reference to inter- and intrasexual competition. The types of offense and self-handicapping behaviours displayed were similar across litters, suggesting that the expression of these behaviours may follow a similar ontogeny in puppies in general.

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Social play is play directed at a conspecific (Bekoff & Byers 1981; Fagen 1981; Bekoff 1984) and in canids includes behaviours such as chasing and play-fighting games, mounting behaviour (i.e. mimicking copulatory behaviour) and inhibited biting (Bekoff 1974; Burghardt 2005). In this study, we videotaped social play within litters of domestic dogs 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 most previous studies have done. To our knowledge, this is the first study in domestic dogs to compare systematically 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 1977; Pozis-Francois et al. 2004), 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 relative to conspecifics (Thompson 1998; Smith et al. 1999; Palagi et al. 2004). Although all of these hypotheses seem reasonable, it is extremely difficult to determine the reproductive benefits of social play. In a longitudinal study of social play in

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multiple litters of wild meerkats (also social carnivores), Sharpe (2005a, b, c) concluded that several of the most frequently proposed functions of social play were not supported by the data, but she did not propose any alternative explanations for why young meerkats play. Only one study has linked play directly to survival (brown bear cubs, *Ursus arctos*, that play more in their first summer are more likely to survive until the end of the next summer), but the mechanisms involved remain unknown (Fagen & Fagen 2004).

Evidence for some species 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 (Bekoff 2001). This is called the 50–50 rule (Aldis 1975; Pellis & Pellis 1998). Individuals can 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 (Balfour 1987; 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.

Of the studies mentioned above, only Bauer & Smuts (2007) published quantitative data on adherence to the 50–50 rule, which is why additional data (like those provided here) are important. Bauer & Smuts (2007) found that adult dogs do not play in accordance with the predictions of the 50–50 rule, although the degree of divergence from egalitarian play varies among dyads (only 5.4% of the 55 dyads tested displayed 50–50 symmetry during play, whereas 21.8% displayed complete asymmetry). The 50–50 rule predicts that the dominant member of a dyad will self-handicap more (to bring the probability of winning for the subordinate closer to 50%), but they found the reverse effect. The 50–50 rule also predicts that dominance relationships outside of play will be absent (or at least very relaxed) during play, but they found that dominance relationships were still evident during play. Although it is not yet known why dog dyads display such wide variation in degrees of asymmetry during play, the study by Bauer & Smuts (2007) makes it clear that 'fair play' (Bekoff 2001) is not necessary for play to occur.

Because social play often includes motor patterns used in predatory, mating and agonistic contexts, play signals have evolved to help animals convey playful intentions (West 1974; 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 behaviours that could most easily be misinterpreted as real aggression, such as when an animal shook the head while biting another. In adult domestic dogs, the individual within a dyad who showed more self-handicapping behaviour also play-signalled more often (Bauer & Smuts 2007).

For a given species, sex differences in play should be more prominent when adult females and males differ in physical characteristics (e.g. body size), behavioural characteristics (e.g. involvement in hunting activity, intraspecific fighting, territorial defence) or social preferences (e.g. formation of strong bonds with same- versus opposite-sex individuals; Maestripieri & 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; Biben 1983; Bauer & Smuts 2007). However, among infant domestic dogs, sex differences in play have been reported (Lund & Vestergaard 1998; Pal 2008).

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 & 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 (domestic dogs: Scott & Fuller 1965; Bekoff 1972; wild red foxes: Meyer & Weber 1996). 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 analyse 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.

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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 behaviours, including play initiations, 'offense behaviours' (similar to 'attacks and pursuits' in Bauer & Smuts 2007), self-handicapping and play bows; and we determined whether play behaviours varied by sex. Last, we examined how the individual actions that comprised offense and self-handicapping behaviours 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 caesarean 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

We divided the data collection into three time periods (Table 1) to coincide approximately with critical periods associated with the development of social behaviours (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 of approximately 7.2 m^2. Litters 2 and 3 also had free access to outdoor fenced areas 99 and 72 and 99 m^2 in size, respectively. Litter 4 was kennelled 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 behaviour 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 to 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 coloured collars or, in the case of litter 3, were marked by the breeder with nail polish in identifying locations on their bodies.

Behavioural 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

Table 1. Summary of domestic dog litters

Litter	Breed	Birth date*	Sex composition†	Observation dates	Time period‡	Age range of puppies (weeks)
1	Shepherd mix	14 Feb 2004	3 ♀ 3 ♂	Feb–Nov 2004	1 2 3	3–8 11–23 27–40
2	Labrador retriever	21 Apr 2005	2 ♀ 4 ♂	May–Oct 2005	1 2	3–8 10–23
3	Doberman pincher	22 Apr 2004	1 ♀ 2 ♂	May–Jun 2004	1	3–7
4	Malamute	4 May 2005	4 ♂	May–Jun 2005	1	3–8

*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.

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Table 2. Ethogram of asymmetric behaviours in play

Behaviour	Definition
Offense behaviours	Behaviours used to maintain a dominant or superior position over a partner
Bite shake	D* bites S† and shakes head back and forth while maintaining a hold on S
Chase	D runs after S with a least two 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 hindlegs 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. 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.
†S: dog in subordinate or losing position.

times that play began and ended with each partner. To investigate behaviours that involved asymmetric roles (hereafter 'asymmetries'), we divided them into (1) offense behaviours and (2) self-handicapping behaviours (cf. Bauer & Smuts 2007). For these and other behaviours (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 ith puppy with the jth puppy as the recipient and B_i is the total number of play bouts initiated by the ith puppy. A puppy who initiated with all other partners an equal number of times would have all I_{ij} score equal to 1.0. Scores were greater than 1.0 in situations in which individuals initiated play with some individuals more often than with others. Following Thompson (1996), we used PPP scores of $\geq$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, b; de Vries 1993) to examine several aspects of play-partner preferences. Matrices were constructed separately by litter and time period for litters 1 and 2 (although we calculated PPP scores for litter 3, sample size was too small, $N = 3$, to conduct matrix analyses (Hemelrijk 1990a), and, as mentioned above, we did not collect focal data on litter 4).

To determine if PPP scores were reciprocal (i.e. if puppy A preferred puppy 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 play-bout 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 version 9.1 (SAS Institute, Cary, North Carolina, U.S.A., 2003).

We also tested whether mean bout length varied by time period or dyadic sex composition (female–female versus female–male versus male–male) 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 interlitter variation. For this and all subsequent GLMMs, all two-way interaction terms were included in the initial model, but the least significant interactions were sequentially dropped using a backwards 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. 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 ith 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. The number of 'wins' for individual A in a dyad (e.g. AB dyad consisting of puppies A and B) equalled the number of offense behaviours by A directed at B plus the number of self-handicapping behaviours (Table 2) by B directed towards A. B's wins were calculated similarly. Next, we calculated the proportion of wins for A as the number of wins for A divided by the total number of wins for both A and B. We calculated the proportion of wins for B in the same way. We subtracted the smaller proportion of wins from the larger proportion to obtain a measure of the degree of asymmetry in each dyad. We normalized this measure with an arcsine-root transformation. The closer the value was to 0, the more symmetrical the play. Next, we ran a GLMM to determine if the degree of asymmetry 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 to determine if the degree of asymmetry differed from 0. We controlled for litter effects and repeated observations on dyads within a litter across time.

Relationship between play behaviours. We ran GLMMs to determine: (1) if offense behaviour rates were associated with initiation rates (dependent variable), (2) if self-handicapping rates were associated with offense behaviour rates (dependent variable), and (3) if self-handicapping and offense behaviour 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 GLMMs 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.

We calculated rates of behaviours (e.g. initiations, offenses, self-handicapping and play bows) at the dyadic level for each puppy in each time period as the number of times each puppy in a dyad performed one of the behaviours 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 behaviours 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 behaviours, self-handicapping and play bows could occur multiple times within each bout). We used mean rates of behaviours for each puppy within each time period in the following GLMM analyses.

Variation in play behaviour 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 versus MM) dyads using GLMMs as described above. We also compared rates of female behaviours 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 behaviours in male–male (mm) dyads versus male–female (mf) dyads. Note that fm and mf dyads have the same composition; we use lower- versus upper-case abbreviations to remind the reader which sex's behaviour we are measuring (the one listed first in mixed-sex dyads) in the relevant analyses. For example, when measuring the rate of offense behaviours in an 'fm' dyad, we calculated only the rate for females when playing with males (see below). In contrast, when measuring the rate of offense behaviours in an FM dyad, we calculated rates for both sexes.

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

All statistical tests were two-tailed, unless otherwise specified, and α was set at 0.05. However, if α was between 0.05 and 0.10, we report it as a nonsignificant trend.

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

RESULTS

We analysed 7.10 h 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 ($\overline{X} \pm$ 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: time 1: $K_r = 7$, $P = 0.454$; time 2: $K_r = -14$, $P = 0.200$; time 3: $K_r = -2$, $P = 0.852$) 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: litter 1: $K_r = -1$, $P = 0.830$; litter 2: $K_r = -8$, $P = 0.351$). 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: time: $F_{2,76} = 4.20$, $P = 0.019$; dyadic sex composition: $F_{2,76} = 0.30$, $P = 0.744$). Play bouts were shorter in time 3 compared to times 1 and 2 (time 1 versus time 2: $P = 0.172$; time 1 versus time 3: $P = 0.065$; time 2 versus time 3: $P = 0.005$; time 1: $\overline{X}$ estimate $\pm$ SE $= 16.377 \pm 3.641$ s; time 2: 19.934 ± 3.966 s; time 3: 9.990 ± 4.549 s).

PPP scores in times 2 and 3 were positively correlated with scores in time 1 for litter 1 (rowwise matrix tests: times 1 and 2: $K_r = 16$, $P = 0.060$; times 1 and 3: $K_r = 19$, $P = 0.048$), 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 to 2.5 in time 1 and from 0 to 2.2 in time 2), but in time 3, all six puppies had one strong preference (McNemar's test: $\chi^2_1 = 5.00$, $P = 0.025$; PPP scores ranged from 0 to 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 to 1.8 for litter 2 and from 0.71 to 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: time: $F_{2,21} = 8.32$, $P = 0.002$). Scores did not differ significantly between times 1 and 2 ($P = 0.796$; Fig. 1).

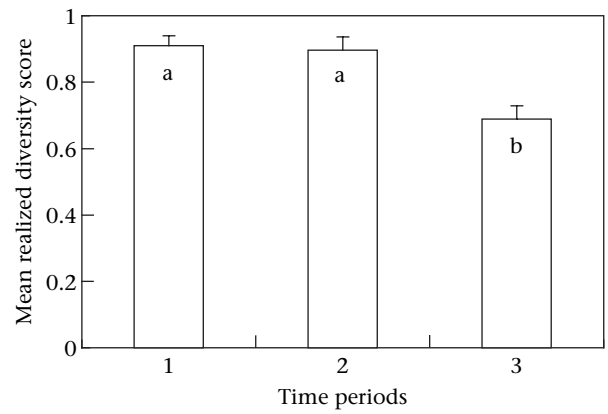

Figure 1. Realized diversity scores across three time periods. Values are mean estimates and error bars indicate SE for litters 1 (time periods 1–3), 2 (time period 1) and 3 (time period 1). Columns with a letter in common are not significantly different ($P > 0.05$). Age ranges (in weeks) of puppies: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

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: time: $F_{2,74} = 3.88$, $P = 0.025$; sex: $F_{2,74} = 0.510$, $P = 0.605$). To explore this time effect further, we ran a second GLMM 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: time 1: $t_{76} = 7.15$, $P < 0.0001$; time 2: $t_{76} = 8.52$, $P < 0.0001$; time 3: $t_{76} = 7.18$, $P < 0.0001$; all one-tailed), but symmetry was higher in time 1 relative to time 2 ($P = 0.015$) and time 3 ($P = 0.024$). For litter 1, there was no significant difference in symmetry between times 2 and 3 ($P = 0.693$). Figure 2 shows the degree of asymmetry across time periods.

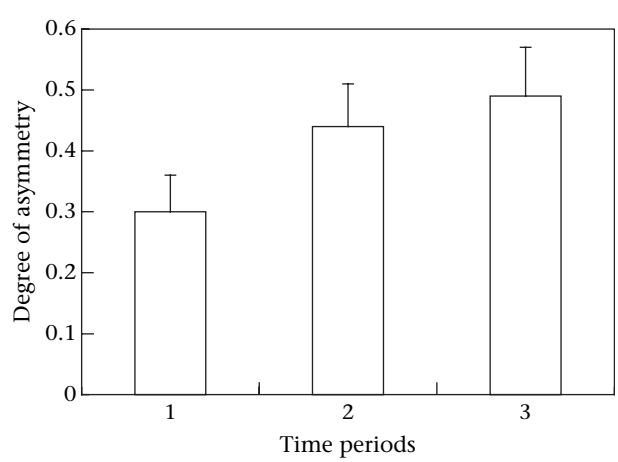

Figure 2. The degree of asymmetry across three time periods. Values are mean estimates and error bars indicate SE for litters 1 (time periods 1–3), 2 (time periods 1 and 2), 3 (time period 1) and 4 (time period 1). To obtain these values, we ran a GLMM with the degree of asymmetry (based on nontransformed data) as the dependent variable and time as an independent variable. We controlled for the random effects of litter and repeated observations on dyads within a litter across time. Age ranges (in weeks) of puppies: time 1, 3–8; time 2, 10–23; time 3, 27–40.

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Relationship between play behaviours

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

Variation in play behaviour 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 versus fm dyads). However, male initiation rates did vary by time period. In time 3, males initiated play more often with other males than with females, 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).

Table 3. Initiation rates analyses

Source of variation	*df*	*F** or *t*† value	*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 versus 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 versus fm	1	15.98	**0.039**	ff>fm
Male initiations‡: mm versus 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

FM: female–male; FF: female–female; MM: male–male; ff: female rates with females; fm: female rates with males; mm: male rates with males; mf: male rates with females. T1: time 1; T2: time 2; T3: time 3.

*Rates of initiations in mixed-sex and same-sex dyads in relation to sex of initiator and time period. GLMMs controlling for litter and repeated observations of dyad{litter} across time.

†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. GLMMs controlling for litter and repeated observations of dyad{litter} across time. GLMM was pooled across time periods for female initiations owing to nonsignificant time effects (GLMM: $F_{2,9} = 0.96$, $P = 0.418$).

‡For male initiations, results were not pooled across time because of a trend effect with time (GLMM: $F_{2,14} = 2.78$, $P = 0.096$).

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

Rates of offense behaviours for both females and males were stable across time periods. Females displayed offense behaviours at similar rates whether playing with females (ff) or males (fm), but males displayed offense behaviours 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 (fm), 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

Table 4. Offense behaviour rates analyses

Source of variation	*df*	*F** or *t*† value	*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 versus MM)				
Sex	1, 29	1.63	0.212	
Time period	2, 29	3.21	0.055	
Female offense behaviours: ff versus fm	1	0.92	0.525	
Male offense behaviours: mm versus mf	2	−3.19	0.086	

FM: female–male; FF: female–female; MM: male–male; ff: female rates with females; fm: female rates with males; mm: male rates with males; mf: male rates with females.

*Rates of offense behaviours in mixed-sex and same-sex dyads in relation to sex and time period. GLMMs controlling for litter and repeated observations of dyad{litter} across time.

†Test of the difference in rates of offense behaviours by females in ff and fm dyads and the difference in rates by males in mm and mf dyads. GLMMs controlling for litter and repeated observations of dyad{litter} across time. GLMMs were pooled across time periods for female and male offense behaviours owing to nonsignificant time effects (GLMM: females: $F_{2,9} = 1.39$, $P = 0.297$; males: $F_{2,14} = 1.96$, $P = 0.177$).

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Table 5. Self-handicapping rates analyses

Source of variation	*df*	*F** or *t*† value	*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 versus MM)				
Self-handicapper sex	1, 29	0.13	0.723	
Time period	2, 29	0.92	0.442	
Female self-handicapping: ff versus fm	1	−1.17	0.449	
Male self-handicapping: mm versus mf	2	1.01	0.418	

FM: female–male; FF: female–female; MM: male–male; ff: female rates with females; fm: female rates with males; mm: male rates with males; mf: male rates with females.

*Self-handicapping rates in mixed-sex and same-sex dyads in relation to sex and time period. GLMMs controlling for litter and repeated observations of dyad{litter} across time.

†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. GLMMs controlling for litter and repeated observations of dyad{litter} across time. GLMMs were pooled across time periods for female and male self-handicapping behaviours owing to nonsignificant time effects (GLMM: females: $F_{2,9} = 0.51$, $P = 0.615$; males: $F_{2,14} = 1.35$, $P = 0.291$).

females (ff) or males (fm), and the same was true for males (Table 6).

Frequency of offense and self-handicapping behaviours

Rates of individual offense and self-handicapping behaviours were similar across litters, so we pooled the data across litters and report results by time period. Offense behaviours were much more common than self-handicapping behaviours across all time periods, accounting for 94% of all behaviours (offense and self-handicapping behaviours combined; Table 2) during time 1 (Fig. 3a), 91% of behaviours during time 2 (Fig. 3b) and 84% of behaviours during time 3 (Fig. 3c).

In times 1 and 2, forced downs and overs (Table 2) were the two most common offense behaviours (Fig. 3a, b). Also in time 2, mounts appeared for the first time (5% of offense plus self-handicapping behaviours in both litters), and the proportion of bite shakes decreased (Fig. 3b) In time 3, mounts became the most common offense behaviour, followed by chases, and bite shakes disappeared entirely (Fig. 3c). Muzzle bites and chin overs (Table 2) were a small proportion of offense behaviours across all time periods.

In time 1, nearly 100% of self-handicapping behaviours involved voluntary downs (Fig. 3a; Table 2), but by time 2, muzzle licks had grown to 44% of all self-handicapping behaviours (in addition to voluntary downs; Fig. 3b). In time 3, 75% of self-handicapping was accounted for by muzzle licks (performed by one female; Fig. 3c).

Table 6. Play bow rates analyses

Source of variation	*df*	*F** or *t*† value	*P*
Mixed-sex dyads (FM)			
Sex	1, 27	0.80	0.379
Time period	2, 27	2.24	0.126
Same-sex dyads (FF versus MM)			
Sex	1, 29	2.29	0.141
Time period	2, 29	1.47	0.246
Female play bows: ff versus fm	1	0.88	0.542
Male play bows: mm versus mf	2	0.78	0.516

FM: female–male; FF: female–female; MM: male–male; ff: female rates with females; fm: female rates with males; mm: male rates with males; mf: male rates with females.

*Play bow rates in mixed-sex and same-sex dyads in relation to sex and time period. GLMMs controlling for litter and repeated observations of dyad{litter} across time.

†Test of the difference in female play bow rates between ff and fm dyads and the difference in male play bow rates between mm and mf dyads. GLMMs controlling for litter and repeated observations of dyad{litter} across time. GLMMs were pooled across time periods for female and male play bows owing to nonsignificant time effects (GLMM: females: $F_{2,9} = 0.77$, $P = 0.490$; males: $F_{2,14} = 2.01$, $P = 0.171$).

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 for litter 1.

These results indicate that puppies begin to form differentiated relationships very early in life. Detailed information on play partner preferences in other animals is rare, but preferences for specific play partners occur in infant sable antelope, *Hippotragus niger* (Thompson 1996) and juvenile Belding's ground squirrels, *Spermophilus beldingi* (Nunes et al. 2004). 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. Red fox littermates of approximately 4–8 weeks of age (three litters consisting of two trios and one pair) also showed considerable asymmetry during social play (the proportion of 'wins' by the fox who won most often within each dyad varied from 62 to 82%; values derived

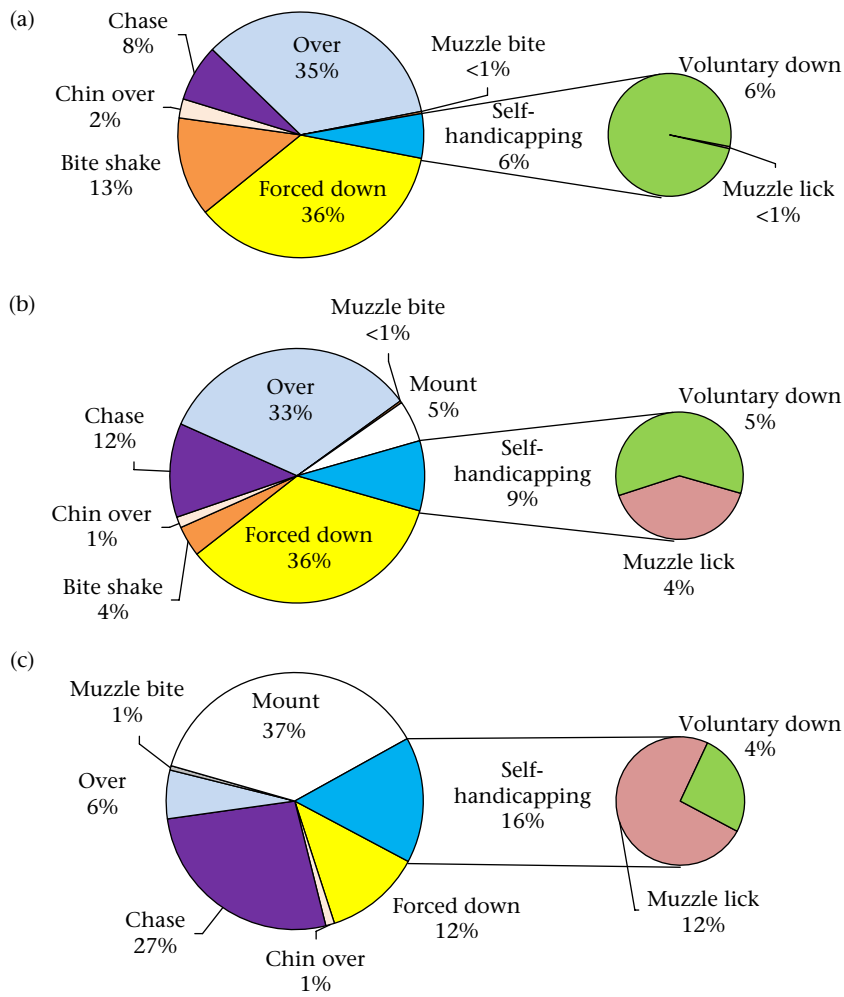

Figure 3. Proportions of all offense and self-handicapping behaviours for (a) time 1 (litters 1–4), (b) time 2 (litters 1 and 2) and (c) time 3 (litter 1). Large pie includes offense behaviours and self-handicapping; small pie shows proportions of specific self-handicapping behaviours. Age ranges (in weeks) of puppies: time 1, 3–8; time 2, 10–23; time 3, 27–40.

from Table 2; Meyer & Weber 1996). Bauer & Smuts (2007) reported that adult dogs did not conform to the 50–50 rule during dyadic play, and they found that play in adult dogs reflects the existing dominance structure outside of play. The same is true for adult meerkats (Sharpe 2005a).

The studies mentioned above, however, did not provide data on changes in the degree of asymmetry over time. In young rats paired together, symmetry in play decreased over time as stable dominance relationships developed (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). Domestic dogs, like wild meerkats (Sharpe 2005a), do not use aggression (distinct from play fighting) to establish stable dominance relationships in the first few weeks of life, in contrast to some other social carnivores (captive coyotes: Bekoff 1974; spotted hyaenas, *Crocuta crocuta*: Wahaj & Holekamp 2006). As far as we know, researchers have not addressed the functional significance of interspecific variation in the presence or absence of early fighting to establish stable dominance relationships within litters.

Relationships between play behaviours

In time period 3, rates of initiations were directly related to rates of offense behaviours. 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 rats, male bison *Bison bison*, and many primates, individuals become increasingly aware of intragroup status as they mature, and play becomes more competitive (Fagen 1981; Rothstein & Griswold 1991; Smith et al. 1999). 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 behaviours 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 signalling may function together to encourage play (Bauer & Smuts 2007).

Variation in play behaviour 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 artefact 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 ages 3 to 8 weeks. Male free-ranging dog puppies studied in India engaged in social play more frequently than female puppies; however, it is not clear whether these male puppies were playing with other males, other females or both (Pal 2008).

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 signalling and appears to function to maintain play. Perhaps playing with females provides opportunities for males to learn characteristics of female behaviour 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 behaviours 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 attacks/pursuits (cf. offense behaviours this study) or self-handicapping. Possible discrepancies in the findings may be related to the 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 behaviours 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 may function 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 could limit 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 (littermates up to 8 weeks of age) did not prefer same- over mixed-sex play partners. 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 artefact 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 because MM play-bout lengths were shorter than FM bout lengths in time 3; Table 3). Mean bout lengths did not vary by dyadic sex composition across any time period in the current study.

Preferences for play with same-sex partners have been reported in other species, including juvenile male bison (Rothstein & Griswold 1991), rats of both sexes (Laviola & Terranova 1998) and juvenile male Belding's ground squirrels (Nunes et al. 2004).

Individual offense and self-handicapping behaviours

Some behaviours were more common early in development (e.g. forced downs and overs) and became less common as puppies matured. Conversely, other behaviours were less common early in development but became more common with time (e.g. mounts). These findings suggest that the style and possibly the function of play, even between the same play partners, may change over time. This is clearly the case for male (but not female) rats, who, at puberty, shift the type of defensive strategy used with other males as they begin to establish dominance relationships (Smith et al. 1996). It is not clear, however, whether puppies show sharp discontinuities in frequencies of different play behaviours, as is the case for rats

(Smith et al. 1996) and domestic cats (Barrett & Bateson 1978; Caro 1981), but future work could address this area.

Even with a small sample of four litters comprising various breeds, litter sizes, and sex ratios, we found consistent patterns of partner preferences, role asymmetries, and sex differences (for example, in rates of offense behaviours). These results suggest that domestic dog littermates, in general, show important similarities in social development. It would be interesting to determine whether these general patterns evolved during domestication or were inherited from wolf ancestors, but comparable data are not available for wolves.

Despite the similarities we found across litters, studies of other species suggest that important interlitter variations in play behaviour are likely to occur. Play behaviour varies among litters as a function of litter size, litter sex ratio, and nutritional state or weight (Caro 1981; Laviola & Alleva 1995; D'Eath & Lawrence 2004; Nunes et al. 2004). Such interlitter variability is also correlated with major differences in adult behaviours, including aggressiveness, sexual behaviour, maternal behaviour and behavioural, hormonal and neurochemical responses to stress and novelty (Sharpe et al. 1973; Namikas & Wehmer 1978; Laviola & Terranova 1998; D'Eath & Lawrence 2004). Experimental studies in rodents manipulating these variables show that in at least some cases, interlitter variation in size, sex ratios and play-fighting behaviours are not only correlated with, but actually *cause*, differences in adult behaviours (Laviola & Terranova 1998; Pellis & Pellis 2007).

It is no surprise that social interactions early in life affect adult behaviour. However, we know very little about *why* particular early experiences affect adult behaviour in the ways they do. Most of the data relating developmental variation to adult behaviour come from laboratory rodents or domestic piglets reared in environments different from those of their wild counterparts, which limits our ability to analyse these relationships from an adaptive perspective. We think that domestic dogs afford an exceptional opportunity to pursue such questions because different breeds have undergone systematic selection for adult differences in behaviour (including social behaviour, e.g. hounds and sled dogs must be able to work peacefully with conspecifics in groups and terriers, as rodent hunters, tend to work as individuals). Future research on domestic dog littermates can help to: (1) reveal how specific selection pressures alter early social experiences and (2) explain why some aspects of social development remain similar across litters and across breeds. Such studies are likely to advance our theoretical understanding of relationships between evolutionary and ontogenetic processes.

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