ANIMAL BEHAVIOUR, 2008, **76**, 1187–1199
doi:10.1016/j.anbehav.2008.06.004

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

CAMILLE WARD*, ERIKA B. BAUER† & BARBARA B. SMUTS*
*Department of Psychology, University of Michigan, Ann Arbor
†Department of Animal Programs, Smithsonian National Zoological Park, Washington, D.C.

(Received 30 November 2007; initial acceptance 27 February 2008;
final acceptance 13 May 2008; published online 8 August 2008; MS. number: A07-00006)

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.

Keywords: asymmetrical play; *Canis lupus familiaris*; domestic dog; partner preferences; self-handicapping; social development

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

Correspondence: C. Ward, Department of Psychology, 530 Church Street, University of Michigan, Ann Arbor, MI 48109-1043, U.S.A. (email: rameses@umich.edu). E. B. Bauer is at the Department of Animal Programs, Smithsonian National Zoological Park, NZP-Lion/Tiger MRC: 5507, P.O. Box 37012, Washington, D.C. 20013-7012, U.S.A.

0003–3472/08/$34.00/0

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.