



In wolves, play behaviour reflects the partners' affiliative and dominance relationship

Simona Cafazzo^{a,*}, Sarah Marshall-Pescini^a, Jennifer L. Essler^b, Zsófia Virányi^{a,b}, Kurt Kotrschal^{a,c}, Friederike Range^a

^a Wolf Science Center, Domestication Lab, Konrad Lorenz Institute of Ethology, University of Veterinary Medicine, Vienna, Austria

^b Comparative Cognition, Messerli Research Institute, University of Veterinary Medicine, Vienna, Austria

^c Department of Behavioral Biology, University of Vienna, Vienna, Austria

ARTICLE INFO

Article history:

Received 5 October 2017

Initial acceptance 14 November 2017

Final acceptance 29 March 2018

MS. number: 17-00791R

Keywords:

affiliative relationships
dominance relationships
dyadic competitive play
dyadic relaxed play
social assessment

Puppy packs (consisting of only puppies) and mixed-age packs (composed of puppies and adults) were observed to test whether social play can be used for assessing and establishing social relations in wolves, *Canis lupus*. Differently from previous studies, we looked at play behaviours in detail, allowing us to categorize play interactions as either competitive or relaxed, and predicted that different types of play would be associated with different relationships between individuals. We found that the more time dyads spent in relaxed play, the more affiliative interactions they exchanged outside of play. In the mixed-age packs, dyads that spent more time in both relaxed and competitive play showed fewer exchanges of aggressive behaviours. Conversely, in puppy packs, the more time dyads spent in competitive play, the more aggressive interactions were exchanged outside of play. Since clear dominance relationships emerged in the mixed-age packs, but not in puppy packs, we suggest that play can help to reduce the frequency of aggressive interactions only when a clear hierarchy exists between pack members. Furthermore, we found that in both puppy and mixed-age packs, dominance relationships were reflected and rarely reversed during play. Finally, dyads with a less clear dominance relationship spent more time playing in a competitive way. Overall, our results support the social assessment hypothesis suggesting that social relationships outside of play are reflected during playful interactions. Moreover, we revealed how different types of play, that is, playing in a competitive or relaxed way, may be related to different social relationships. This distinction between play types has not been acknowledged before but could help researchers better understand the functions of play in different species.

© 2018 The Authors. Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Social play is a widespread phenomenon, suggesting that it may be a critical component of ontogeny. However, little is known about its functional significance despite years of research (reviewed in Burghardt, 2005; Pellis, Burghardt, Palagi, & Mangel, 2015). Given that play most often occurs in juvenile animals, the majority of hypotheses relating to its function have focused on how playing during the immature stage of development fosters the appropriate use of behaviours essential during adulthood or learning about the potential responses of dyadic partners in 'serious' contexts (Bugnyar, Schwab, Schloegl, Kotrschal, & Heinrich, 2007). Hence, scientists have mostly concentrated on the delayed benefits of play

(Pellis, Pellis, & Bell, 2010). However, play is also common in adulthood in many species (e.g. Cohen, 2006; Cordoni, 2009; Fagen, 1981; O'Meara, Graham, Pellis, & Burghardt, 2015; Palagi, 2006; Palagi, 2011; Pellis, 2002; Pellis & Iwaniuk, 1999, 2000a, 2000b) suggesting that some benefits may be immediate (Breuggeman, 1978; Martin & Caro, 1985; Pellis, Pellis, & Bell, 2000, Pellis, Pellis, & Reinhart, 2010; Poirier, Bellisari, & Haines, 1978).

Among others, immediate benefits of play for juveniles and adults may include (1) strengthening of social bonds by increasing trust and reducing aggression between social partners (the social-bonding hypothesis, Bekoff 1977; Pellis, Pellis, & Whishaw, 1992; Soderquist & Serena, 2000) and/or (2) assessment of the competitive abilities of others to establish and maintain dominance relationships without the risks involved in overt aggression (the dominance assessment hypothesis, Dolhinow, 1999; Miller & Byers, 1998). Although both hypotheses have been widely cited as

* Correspondence: S. Cafazzo, Wolf Science Center, Dorfles 48, Ernstbrunn 2115, Austria.

E-mail address: simona.cafazzo@gmail.com (S. Cafazzo).

potential functions of social play, only a few studies have empirically tested them.

The social-bonding hypothesis has received some support from a number of studies showing either a correlation between frequency of play and affiliative behaviour (e.g. adult and immature gelada baboons, *Theropithecus gelada*, Mancini & Palagi, 2009; immature Japanese and Tonkean macaques, *Macaca fuscata* and *Macaca nigra*, Petit, Bertrand, & Thierry, 2008; Reinhart et al., 2010) or a correlation between an increase in play behaviours and a decrease in aggressive interactions (infant spotted hyaenas, *Crocuta crocuta*, Drea, Hawk, & Glickman, 1996). Conversely, other studies found no evidence supporting an association between social play and both reduced aggressiveness (Sharpe & Cherry, 2003) and increased frequency of affiliative interactions (Sharpe, 2005a).

Contrasting results have also been found for the dominance assessment hypothesis. In a number of primate species, it has been observed that the asymmetry in the exchange of behaviours during play-fighting sessions may reflect the dominance relationship between individuals outside the play context (e.g. Paquette, 1994; Pereira, 1993). In early adolescent boys, Pellegrini (1995) observed a correlation between play fighting and dominance/aggressive displays. Finally, in yellow-bellied marmots, *Marmota flaviventris*, the relative dominance rank calculated by observing the directional outcome of playful interactions in juvenile and yearling marmots correlated significantly with the subsequent dominance ranks calculated from agonistic interactions (Blumstein, Chung, & Smith, 2013). The authors suggested that relationships within play could predict the future dominance relationships outside of play at least in the short term, providing some support for the dominance assessment hypothesis (Blumstein et al., 2013). However, other studies have not found a link between dominance and play. In spotted hyaena cubs, dominance relationships are rigid and established through aggression at an early age. Interestingly, these dominance relationships are ignored, absent or temporarily reversed during play (Drea et al., 1996).

The wolf, *Canis lupus*, is an interesting species in which to investigate the pattern and potential function of social play: wolf packs are characterized by cooperation, high social cohesion and dominance relationships between pack members (Cassidy & McIntyre, 2016; Cassidy, MacNulty, Stahler, Smith, & Mech, 2015; van Hooff & Wensing, 1987; MacNulty, Smith, Mech, Vucetich, & Packer, 2011; Mech & Boitani, 2003; Packard, 2003, 2012). Social play may therefore represent an important means of allowing the establishment of dominance relationships in a safe context, potentially reducing aggression and strengthening social bonds to promote cooperation and pack cohesiveness, and of assessing relationships. In this species, social play is common during the juvenile phase (Mech, 1970) and continues into adulthood (Cordoni, 2009). Few studies have been carried out on wolf play behaviour, however, with most focusing on adult individuals (Bekoff, 1995; Bernal & Packard, 1997; Cipponeri & Verrell, 2003; Zimen, 1981, 1982). Only one study has investigated the potential validity of the social-bonding and dominance assessment hypotheses in this species (Cordoni, 2009). In a captive group of adult grey wolves, no significant correlations emerged between dyadic play frequencies and affiliative behaviours outside the play context (i.e. body contact and agonistic support frequencies), nor was there a negative correlation between play and aggressive interactions. Nevertheless, play interactions were observed more frequently between partners closest in rank, suggesting that adult wolves may use play to test social partners and as a prelude to contesting rank (Cordoni, 2009). These results would hence provide some support for the dominance assessment hypothesis, but not for the social-bonding hypothesis. Further suggestive evidence for the dominance assessment hypothesis is provided by a recent study investigating

play behaviour in wolf pups. Essler et al. (2016) found that pups did not adhere to the 50:50 rule, that is, dyads did not alternate in their winning and losing roles during play, but rather an individual was likely to maintain a constant dominant or submissive role during play with a specific partner. The maintenance of postural asymmetry during play may support the hypothesis that play contributes to the formation of dominance relationships within wolf litters, as has been suggested for other canids (domestic dogs, *C. lupus familiaris*: Scott & Fuller, 1965; Bekoff, 1972; wild red foxes, *Vulpes vulpes*: Meyer & Weber, 1996).

To sum up, previous results on both canids and other species have revealed some correlative support for both the social-bonding and dominance assessment hypotheses. Although we acknowledge that correlative evidence cannot conclusively identify the cause–effect direction between play and social behaviour (Blumstein et al., 2013; Ghiselin, 1982; Sharpe, 2005b), we deem it important to further investigate whether and how behaviours displayed during social play may reflect the partners' affiliative and dominance relationships. Since wolves rely on cooperation between pack members and show relationships moderated according to dominance hierarchies, the social-bonding and dominance assessment hypotheses are not mutually exclusive. Therefore, here we propose a more embracing version of the two hypotheses and suggest that a major function of play in wolves may be social assessment in general; thus, social play may help individuals assess both affiliative and dominance relationships, thereby potentially reducing aggression between pack members ('social assessment hypothesis'), but also strengthen cooperation. However, we also suggest that different types of play may help individuals assess different types of relationships, as also proposed in previous studies (Bateson 1981; Biben, 1986; Gomendio, 1988; Martin & Caro, 1985). Sequences of attack, defence and counterattack may characterize a competitive type of play (or play fighting), but sometimes a different form of physical contact between playmates is observed, which includes gentle and friendly behaviours such as pawing and rubbing, resulting in a seemingly relaxed form of contact play. While individuals need to coordinate and modulate their reciprocal behaviours during both types of social play (Bauer & Smuts, 2007; Bekoff, 2001; Biben, 1986; Dugatkin & Bekoff, 2003; Thompson, 1998), it is reasonable to assume that competitive play is better suited to testing the weakness/strength of potential competitive partners and therefore clarifying the reciprocal dominance rank in a potentially safe context (as stated by the dominance assessment hypothesis) and/or decrease the occurrences of aggressive encounters (as stated by the social-bonding hypothesis; Pellis, Pellis, & McKenna, 1993; Pellis & Iwaniuk, 2000b; Palagi, 2006). In contrast, relaxed play should occur mainly between playmates sharing strong affiliative bonds, thus when there is no risk of escalation into aggression. In line with this reasoning, we distinguished between these two types of play to better evaluate their potentially different roles in the social assessment hypothesis.

To test our hypothesis, in the current study we used data on wolf social interactions collected on puppy–puppy and puppy–adult dyads in two consecutive periods: when wolf puppies lived in packs consisting of only puppies (puppy packs) and after their introduction into previously established packs of adult wolves (mixed-age packs).

Based on all the considerations for variation in the form and function of social play given above, some specific predictions were tested.

In particular, according to the social-assessment hypothesis, social play may be associated with both a low frequency of aggressive encounters and a high frequency of affiliative interactions. Therefore, based on our previous assumption about competitive and relaxed play, we predicted that dyads spending

Download English Version:

<https://daneshyari.com/en/article/8488492>

Download Persian Version:

<https://daneshyari.com/article/8488492>

[Daneshyari.com](https://daneshyari.com)