

# Social play in captive wolves (*Canis lupus*): not only an immature affair

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## Summary

Animal social play represents an important tool for self- and social-assessment purposes during the juvenile phase. Nevertheless, this activity may continue into adulthood as well providing immediate benefits to the playmates. In this study, I investigated the dynamics of adult play in a wolf colony hosted at the Pistoia Zoo (Italy). The study wolves performed social play to a greater extent compared to solitary play. Play distribution was not affected by relationship quality (measured by body contact and agonistic support frequencies) and aggression levels. Probably, in wolves other behavioural strategies are employed for strengthening inter-individual relationships and reducing conflicts among fellows. Play was distributed throughout the entire group independently of the sex of playmates. The absence of sexual-dimorphism in play may be linked to the fact that in the wolf pack males and females share the same roles and behavioural repertoire. Rank distance between conspecifics negatively correlated with play distribution: by playing wolves with closest ranking positions tested each other for acquiring information on skills of possible competitor and gaining hierarchical advantage over it. Finally, in agreement with previous studies, my findings showed that wolves significantly reduced their playful activity during contests of high conflict of interests such as mating period and feeding time.

**Keywords:** Social-Bonding Hypothesis, cooperation, competition, rank-rules, stressful condition, *Canis lupus*.

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## Introduction

Animal sociality has been viewed as an evolutionarily advantageous state, in which members derive the benefits of cooperation (protection from predators, mate choice, collective rearing of offspring, and territory defence) balanced by the costs of competition for limiting resources (Parrish & Edelstein-Keshet, 1999; Silk, 2007). Cooperation is considered as a social phenomenon associated with many interactive components that do not occur when animals do not cooperate (Hinde, 1979; Schuster et al., 1988, 1993; Schuster, 2001, 2002). In fact, cooperating individuals may learn to fine-tune their actions in order to coordinate and anticipate each other's behaviours (see Schuster & Perelberg, 2004). A distinct category of behaviour that may contain cooperative and competitive elements at a proximate level is social play (Bauer & Smuts, 2007). Play has been thought to be more prevalent and complicated in larger-brained species because it requires socially complex skills to be performed so as to maximize its benefits and minimize its risks (Fagen, 1981; Martin & Caro, 1985; Byers, 1999; Iwaniuk et al., 2001). The real benefits of animal social play, and therefore its evolutionary significance, remain unclear (Caro, 1988; Pellis & Iwaniuk, 1999a) and many functional hypotheses have been formulated on this behaviour: providing physical training (Smith, 1982; Byers & Walker, 1995), developing cognitive skills (Loizos, 1967; Poirier et al., 1978; Fagen, 1981; Martin & Caro, 1985; Dolhinow, 1999), improving fighting abilities, achieving social assessment (Thompson, 1998; Pellis & Iwaniuk, 1999b, 2000), training for the unexpected (Špinka et al., 2001), limiting aggression, and increasing tolerance around food (Palagi et al., 2004, 2006, 2007). A widely accepted view is that the function of play is not the same in all the species; furthermore, within a given species, play can be influenced by different variables such as dominance/social relationships, context, habitat, sex, and age (Breuggeman, 1978; Poirier et al., 1978; Dolhinow, 1999). Concerning age, playful activity is most commonly reported during the juvenile phase (Fagen, 1981, 1993; Mendoza-Granados & Sommer, 1995; Dolhinow, 1999; Palagi et al., 2004). Nevertheless, play can continue into adulthood, thus suggesting that this behaviour provides benefits also at the immediate level, such as overcoming the resistance of a potential sexual partner (by promoting the familiarization), establishing and maintaining social bonds, and probing for strength/weakness in dominance relationships (Pellis & Pellis, 1991; Pellis & Iwaniuk, 2000; Palagi et al., 2004;

Palagi, 2006, 2008). The overwhelming majority of adult play involves social play, and, particularly, play fighting (Pellis & Iwaniuk, 1999b). Despite some differences (related to the lack of maturation of appropriate control systems in immature individuals), juvenile and adult play contests are similar in the organizational structure. In fact, they have more in common with each other than with serious behaviours (e.g., sexual, aggressive) (Pellis & Iwaniuk, 2000). Adult-adult play has been described in many mammals such as primates (see Pellis & Iwaniuk, 2000; Palagi, 2006, 2008), social canids (Bekoff, 1974, 1977a, 1995; Bernal & Packard, 1997; Cipponeri & Verrell, 2003; Bauer & Smuts, 2007), domestic horses (Hughes, 2002; McDonnell & Poulin, 2002), meerkats (Sharpe, 2005a,b), and rats (Pellis et al., 1993; Smith et al., 1999). For canids, most studies have focused on play behaviour of domestic dogs (*Canis lupus familiaris*), a species renowned for exhibiting high levels of intra- and inter-specific play (Russell, 1936; Lund & Vestergaard, 1998; Rooney, 1999; Bauer & Smuts, 2007; Ward et al., 2008). Playful activity in this species does not appear to be an artefact of domestication, since wolves (*Canis lupus lupus*), the ancestors of dogs, also play (Mech, 1970). Nevertheless, few standardized studies are available on adult-adult play in wolves and dogs (Zimen, 1981, 1982; Bekoff, 1995; Bernal & Packard, 1997; Cipponeri & Verrell, 2003; Bauer & Smuts, 2007). Since I had the opportunity to observe a captive pack of grey wolves, I decided to investigate adult play in *Canis lupus* to evaluate whether factors like sex, rank distance, relationship quality and context affect play dynamics and distribution. To reach this goal I tested the following predictions:

Prediction 1: Playful behaviour generally includes both solitary and social activity (Fagen, 1981; Thompson, 1998). However, compared to solitary play, social play is more frequent and more likely to continue into adulthood (Pellis & Iwaniuk, 2000). In this perspective, in the study colony I expected to find higher levels of social play compared to solitary play.

Prediction 2: Sexual dimorphism in play may be found in species in which the two sexes differ in physical skills and behavioural repertoire (Špinková et al., 2001). For example, in sea lions, rats, mountain sheep, horses and many species of primates, males that are mainly involved in competitive contests, engage in play-fighting more frequently compared to females (see Smith, 1982). A study on four litters of dogs revealed that play among males was more frequent than play among females (Lund & Vestergaard, 1998). Conversely, in a number of carnivores (spotted hyenas, domestic cats, captive

coyotes, wolves, beagles, ferrets) males and females show very similar play levels (Bekoff, 1974). In wolf society, both sexes, despite differences in body size (Paquet & Carbyn, 2003), spend similar efforts in cooperative tasks in order to maintain group cohesion (Peterson et al., 2002). The breeding pair “shares leadership in a division-of-labor-system” (Mech, 1999), especially during the early phases of pup care when the female nurses the pups and the male hunts (Packard et al., 1992; Mech et al., 1999). However, during the rest of the year, both breeders are equally involved in hunting and they cooperate in attacking large prey (Mech, 1995). Since both sexes show high levels of cooperation, a similar behavioural repertoire and similar physical skills, in the study colony I expected to find a uniform distribution of social play across the diverse sex-class combinations.

Prediction 3: In social animals, play may be used for establishing dominance relationships without engaging in overt fighting (Smith, 1982; Thompson, 1998; Smith et al., 1999). Palagi (2006) suggested that when relationships among group-members are not codified and structured according to rank rules play fighting may be particularly useful for social assessment because it allows playmates to compete, practice, and strategize in a safer context (Dolhinow, 1999).

In captive wolf packs, individuals may constitute a hierarchical order in which they are featured as alfa, beta until omega and in which each gender has a separate hierarchy (Zimen, 1982; van Hooff, 1987; Mech, 1999). Accordingly, the wolf colony under study showed a linear hierarchy within each sex and all males are dominant over females (Cordoni & Palagi, 2008). Nevertheless, wolves do not have a permanent hierarchical status: in both captive and wild conditions wolves change their ranking position over time (Fox, 1971; Fox & Andrews, 1973; Zimen, 1976; Wilson, 2000). In particular, wolves that are closest in ranking position may be more likely to compete for obtaining a hierarchical advantage and, thus, increasing their dominance status. According to Zimen (1982) wolves can use play to test social partners and as a prelude to contesting dominance ranking. Based on this framework, I expected to find a negative correlation between rank distance and play distribution.

Prediction 4: Many studies on diverse mammal orders (e.g., carnivores: Bekoff, 1974; Drea et al., 1996; rodents: Pellis et al., 1993; Holmes, 1995; artiodactylids: Byers, 1984; primates: Sugiyama, 1976; Lee, 1984) hypothesized that play may increase social harmony by strengthening social bonds,

cementing alliances, and reducing aggression; however, this hypothesis has not been confirmed by quantitative data, at least in canids and rodents. Based on such hypothesis, not confirmed for canids and rodents (Biben, 1983; Pellis & Iwaniuk, 1999a), I expected to find (a) a positive correlation between play frequency and both body contact levels and agonistic support, and (b) a negative correlation between play frequency and aggression levels.

Prediction 5: Play occurs in safe and familiar environments and in the presence of adequate resources (Burghardt, 2005). Indeed, when animals are under environmental (heat, cold, presence of predators), physiological (need for food, drink, sleep, or sexual activity), or social stress, the levels of play are reduced or cease altogether (Loizos, 1967; Rensch, 1973; Baldwin & Baldwin, 1976; Fagen, 1981; Martin & Caro, 1985; Sharpe et al., 2002). Play decrease under these conditions indicates that this behaviour may be 'costly' in terms of caloric expenditure and survivorship/injury risks (Martin & Caro, 1985). I had the opportunity to observe the study wolves under two highly stressful conditions, during which the conflict of interests among conspecifics for accessing resources is elevated (Aureli et al., 2002): mating period and time before food provisioning (pre-feeding). During these stressful periods, I expected to detect a decrease in playful activity throughout the entire group.

## Material and methods

### *The study group*

The study was carried out on a captive group of grey wolves (*Canis lupus*) housed in the Pistoia Zoo (Tuscany, Italy) (Table 1). The pack, composed by nine adult individuals (5 males and 4 females), was defined as a 'disrupted family', that is a family in which one or both of the original parents (the alpha female in this case) is missing (Packard, 2003). All wolves were captive-bred siblings (range of age 3–10 years) with the exception of the alpha parental male; they were housed in a part of a natural hill of about 4000 m<sup>2</sup> enriched with trees, branches, ropes, and dens. Facility enrichment features vary naturally across the seasons and small animals coming from the surrounding wood (e.g., squirrels, lizards, birds, rats) may enter wolves' enclosure. The wolves received food (meat, which was scattered on the floor) once a day in early afternoon (3.00 pm). Water was available ad libitum. No stereotypic or aberrant behaviour was observed in this group.

**Table 1.** The group of grey wolves (*Canis lupus*) housed in the Pistoia Zoo (Tuscany, Italy).

Subject	Sex	Year of birth
Wolf (alpha male)	♂	1986
Ruga	♂	1995
High-tail	♂	1999
Ookami	♂	1997
Anouk	♂	1999
Hateaia (alpha female)	♀	2002
Tala	♀	2002
Flat	♀	1995
White	♀	1999

### Data collection

Observations took place at least 2 days per week, over a 6-h period (also covering the feeding period), from March 2005 to May 2006. Before starting systematic data collection, the three observers (including the author) underwent an 80-h training period to become skilled in animal identification and behavioural pattern distinction. Training was over when the percentage agreement on animal and behaviour recognition among the observers reached 95% (Martin & Bateson, 1986).

We followed the wolves during both mating (MP, from January to March) and non-mating (NMP, from April to December) periods. Following Sands & Creel (2004), I defined mating period as the interval between the first and the last day that I witnessed mating within the pack. We were able to collect all playful and aggressive interactions by all occurrences sampling method (MP 185 h, NMP 449 h). Moreover, we recorded the frequency of affiliative body contact interactions (contact sitting, touching, social licking) by scan animal sampling (5-min intervals, 510.5 h, 6112 scans) (Altmann, 1974). The frequencies of body contact interactions were used to evaluate the degree of friendship among wolves.

A play session was deemed to begin when one partner directed any playful behaviour towards its playmate and ended when the participants stopped their activities or one of them moved away (Palagi, 2008). The instances in which one animal directed playful behaviours toward a fellow who ignored them, were not included in the analyses. For both social and solitary play sessions we recorded: (i) playmates' identity, (ii) playful patterns and their

**Table 2.** Solitary and social playful behavioural patterns recorded during the observation of the Pistoia wolves.

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Solitary play patterns	
Chase-own-tail	(locomotor play) an animal runs around itself trying to catch own tail
Play jump	(locomotor play) an animal jumps alone often on environmental objects
Play manipulation	(object play) an animal tugs, chases, pulls to piece, kicks, shakes and bites an object with mouth or paw
Play roll	(locomotor play) an animal turns its body from side to side while supine
Play run	(locomotor play) an animal runs alone in a playful manner
Squirm	(locomotor play) an animal squirms its body while supine
Social play patterns	
Hide-and-seek	an animal hides and a fellow seeks it
Play ambush	an animal waits in ambush a fellow that is coming and it usually jumps on this fellow
Play bite	an animal gives an inhibited bite to a fellow
Play bow	an animal bows in front of another. It is usually used as play invitation or as play signal. It also has a role in hunting as a good 'all-purpose' position from which the animal may easily break in any direction depending on the movements of the prey
Play fighting	an animal stands up on its hind legs and puts front legs on fellow's shoulders, usually silent and with open mouth, individuals usually bite each other
Play invitation	an animal stamps or bows on forelegs with ears up, facing other animal, or use foreleg to paw at shoulder of another animal
Play jump	an animal jumps on another wolf or leaps away
Play paw	an animal paws on another's body part
Play run	an animal chases another animal, usually with ears forward and not piloerection

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temporal sequence (see Table 2), (iii) context (circumstance in which play took place, e.g., 'pre-feeding'). Following the definition applied for primate play, within social play, we distinguished between locomotor (LP) and contact play (CP) (methods: Burghardt, 2005; Palagi, 2006).

For each aggressive encounter we registered: (i) opponents' identity; (ii) context (circumstance in which the aggression took place, e.g., 'mating'); (iii) type of conflict, that is decided or undecided: a conflict is decided when it is possible to clearly distinguish a winner and a loser within the fighting dyad; (iv) aggressive patterns; and (v) winner's and loser's supporters (a sup-

porter was defined as an individual that provides agonistic support to one of the two combatants in an ongoing aggressive interaction).

To investigate whether the presence of food affected play distribution or not, we distinguished four different periods by preliminary observations: Pre-feeding (PRE, the last 25 min before food provisioning), Feeding (FEED, the 25 min block starting from food provisioning), Post-feeding (POST, the 25 min after Feeding), and Control (C, the time block farthest from feeding time, when individuals showed high activity levels). The parameter for delimiting the 3 periods linked to feeding activity was the usual time span necessary for complete food consumption, i.e., 25 min. We followed 1 feeding time per day (3.00 pm) and this was predictable with an imprecision of only ca.  $\pm 10$  min. In order to avoid possible confounding variables related to the high aggression levels recorded during MP, I restricted this analysis to NMP.

### *Data analysis*

Due to the small sample size ( $N = 9$ ) I employed nonparametric statistical tests (Siegel & Castellan, 1988) and I made use of exact tests according to the threshold values suggested by Mundry & Fischer (1998). To analyse data at the individual level, I used the Wilcoxon matched-pair signed-ranks test (corrected for ties) for comparing the frequency with which each wolf engaged in different kinds of play session (e.g., solitary play vs. social play or contact play vs. locomotor play). I applied the Friedman's two-way analysis of variance to test for the difference in play frequency distribution across the four conditions (PRE, FEED, POST, C). In case of significant difference across such conditions, I employed the Dunnett multiple comparison test (post-hoc test) to determine what pairs of conditions were significantly different (Zar, 1999).

To analyse data at the dyadic level, I used Matman's Row-wise matrix correlation tool with  $1 \times 10^4$  permutations (MatMan 1.0 Software, Noldus<sup>®</sup>) to check for a possible correlation of play frequency with rank distance and frequencies of body contact interaction, agonistic support and aggression.

Since David's score has been found to be a very appropriate dominance ranking index (Gammell et al., 2003), I used the absolute value of the differences of individual scores to evaluate rank distance.

All the analyses were two tailed and were performed by using Microsoft Excel and SPSS 12.0.



Comparisons with probabilities of 5% or less were regarded as significant. For the figures, conventional  $p$ -values of 0.05, 0.01 and 0.001 are shown as asterisks, single, double and triple, respectively, but in the text, the exact  $p$ -values are reported.

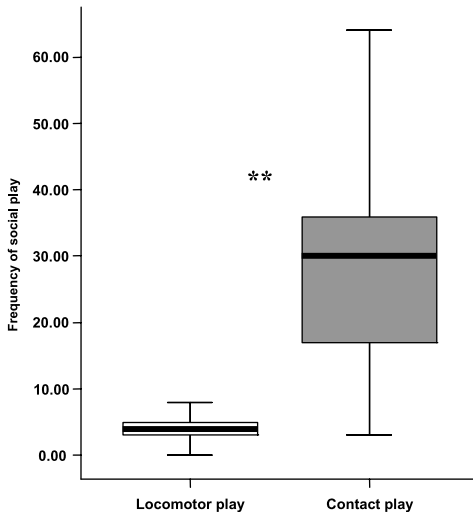
## Results

### *Prediction 1*

Play represented 0.9% of the entire activity level of wolves. Comparing the overall frequencies of social and solitary play sessions, I found that wolves performed social play to a greater extent (Wilcoxon's  $T = 0$ , ties = 0,  $N = 9$ ,  $p = 0.004$ ). In particular, contact play was more frequent than locomotor play (Wilcoxon's  $T = 0$ , ties = 0,  $N = 9$ ,  $p = 0.004$ ) (Figure 1).

### *Prediction 2*

Playmate sex-class did not affect the distribution of play, in fact, wolves performed homosexual and heterosexual play with comparable frequencies (Wilcoxon's  $T = 19.5$ , ties = 0,  $N = 9$ ,  $p = 0.762$ ).



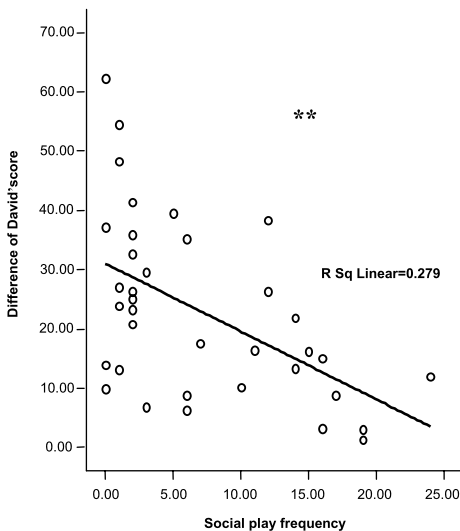
**Figure 1.** Frequency of social play between wolves distinguishing locomotor and contact play. Solid horizontal lines indicate medians; length of the boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values.

### Prediction 3

Considering hierarchical relationships, I obtained a negative correlation between dyadic play frequency and rank distance, measured by the absolute value of the differences of individual David's scores (Row-wise matrix permutation  $K_r = -105$ ,  $\tau_{rw} = -0.43$ ,  $N = 9$ ,  $p = 0.002$ ) (Figure 2). On the other hand, I found no correlation between dyadic play frequency and individual ranking positions (Row-wise matrix permutation  $K_r = -51$ ,  $\tau_{rw} = -0.21$ ,  $N = 9$ ,  $p = 0.18$ ).

### Prediction 4

The analysis revealed no significant correlation between dyadic play frequency and both body contact interaction (Row-wise matrix permutation test:  $K_r = 38$ ,  $\tau_{rw} = 0.158$ ,  $N = 9$ ,  $p = 0.21$ ) and agonistic support frequencies (the frequencies of winner and loser support were added) (Row-wise matrix permutation test:  $K_r = 23$ ,  $\tau_{rw} = 0.102$ ,  $N = 9$ ,  $p = 0.25$ ). Moreover, I found no correlation between dyadic play and aggression frequencies (Row-wise matrix permutation test  $K_r = -11$ ,  $\tau_{rw} = -0.046$ ,  $N = 9$ ,  $p = 0.68$ ). Also, no correlation was obtained between aggression



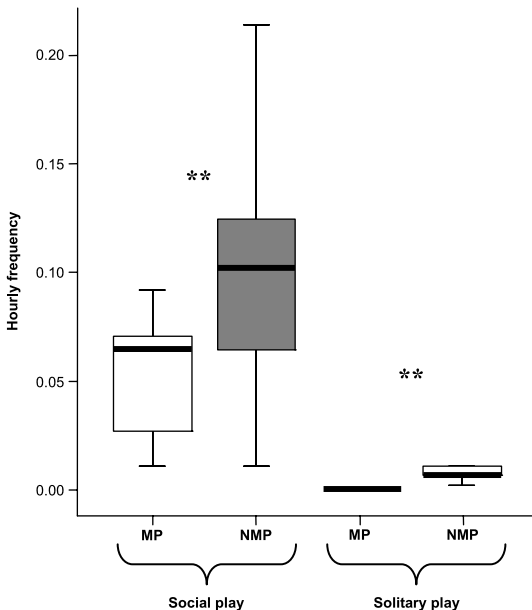
**Figure 2.** Correlation between dyadic social play frequency and difference of individual David's score values.

and body contact frequencies (Row-wise matrix permutation test  $K_r = -39$ ,  $\tau_{rw} = -0.156$ ,  $N = 9$ ,  $p = 0.043$ , Bonferroni's correction  $\alpha = 0.025$ ).

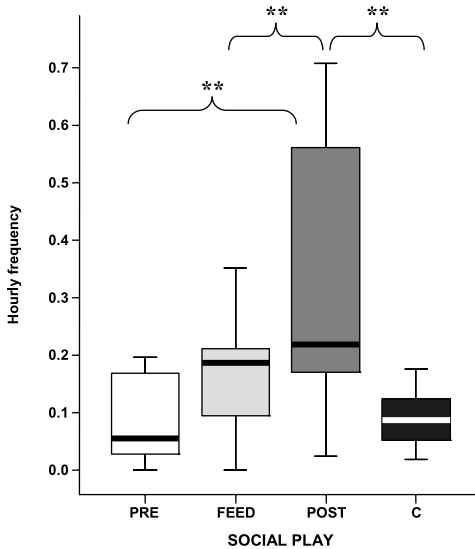
### Prediction 5

By comparing mating (MP) and non-mating period (NMP), I found that both solitary and social play sessions were most frequent during NMP (solitary play: Wilcoxon's  $T = 0$ , ties = 0,  $N = 9$ ,  $p = 0.004$ ; social play: Wilcoxon's  $T = 2$ , ties = 0,  $N = 9$ ,  $p = 0.010$ ) (Figure 3). On the other hand, the hourly frequency of aggression was higher during MP than NMP (Wilcoxon's  $T = 1$ , ties = 0,  $N = 9$ ,  $p = 0.008$ ).

Taking into account the distribution of the hourly frequency of play across four different conditions (PRE, FEED, POST, C), I found that solitary play followed a random distribution during the different periods considered (Friedman  $\chi_r^2 = 3.64$ ,  $df = 3$ ,  $N = 9$ ,  $p = 0.313$ ). Conversely, social play hourly frequency showed a significant difference in its distribution across the four conditions (Friedman  $\chi_r^2 = 18.44$ ,  $df = 3$ ,  $N = 9$ ,  $p = 0.00001$ ). Par-



**Figure 3.** Hourly frequency of both solitary and social play during mating (MP) and non-mating (NMP) period. Solid horizontal lines indicate medians; length of the boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values.



**Figure 4.** Hourly frequency (restricted to NMP) of social play between wolves across four different periods: pre-feeding (PRE), feeding (FEED), post-feeding (POST), and control (C) condition. Solid horizontal lines indicate medians; length of the boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values.

ticularly, post hoc test revealed a significant peak level of social play sessions during the post-feeding condition compared to any other possible condition (POST vs. PRE:  $q = 3.73$ ,  $N = 9$ ,  $p = 0.01$ ; POST vs. FEED:  $q = 4.50$ ,  $N = 9$ ,  $p = 0.01$ ; POST vs. C:  $q = 4.70$ ,  $N = 9$ ,  $p = 0.01$ ) (Figure 4).

## Discussion

In animal societies the development and maintenance of social stability depend upon individuals agreeing that certain rules regulate their behaviours (Bekoff, 2004). The Social-Bonding Hypothesis asserts that play behaviour may function in increasing social harmony and cohesion (Bekoff, 1977; Drea et al., 1996), reducing aggressions between fellows (Pellis et al., 1992; Soderquist & Serena, 2000), strengthening inter-individual relationships (Bekoff, 1977b), and enhancing alliance between conspecifics (Berman, 1982). According to Bekoff (1974) “animals that play together, tend to stay together”. In this perspective, social play should be associated with both an increase in affiliative interactions and a decrease in aggressive

encounters among playmates (Baldwin, 1982). Accordingly, in infant spotted hyenas (*Crocuta crocuta*), the increase of play is correlated with the reduction of aggressive interactions between siblings and with the integration of pups into the pack (Drea et al., 1996). Conversely, no correlation was found between aggression rate and social play in red-necked wallabies (Watson, 1993). Moreover, some studies on free-ranging primates did not reveal any negative influence of play reduction on social relationship strength (Baldwin & Baldwin, 1974; Lee, 1984). Accordingly, my findings on wolves revealed that neither affiliative relationship quality (evaluated by body contact and agonistic support frequencies) nor aggressive interaction level correlated with play frequency (Prediction 4 not confirmed). Similarly, previous reports on another cohesive and cooperative mammal — the meerkat (*Suricata suricatta*) — demonstrated that the frequency of play was not linked either with aggressive or with affiliative contact rates (Sharpe & Cherry, 2003; Sharpe, 2005b). This fact is in agreement with the results of inter-specific comparisons showing that play and development/maintenance of social bonds are not correlated (Biben, 1983). Probably, in wolf packs other behavioural strategies are used for strengthening inter-individual relationships and reducing conflicts among conspecifics. A recent study of Cordoni & Palagi (2008) demonstrated that, in the study colony, wolves showing more cooperative relationships (higher levels of agonistic support during aggressive encounters) exchanged more conciliatory contacts with each other. Even if it is not possible to establish a cause-effect relationship, it seems that the more the wolves cooperate during agonistic contests the more they are inclined to preserve peaceful social relationships (higher level of reconciled conflicts).

During adult social play (particularly play fighting) individuals may assess their physical and social skills and those of their partners (Pellis & Iwaniuk, 1999b; Palagi et al., 2004, 2006; Tanner et al., 2007). A study carried out on wild spotted hyenas revealed that social play continued into adulthood at hourly rates much higher than those observed for any other form of play (Tanner et al., 2007). Accordingly, in this study I found that wolves performed social play more than solitary play. In particular, contact play was more frequent than locomotor play (Prediction 1 confirmed). Contact play is one of the most complex forms of social interaction, because it involves both cooperative and competitive elements (Thompson, 1998; Bekoff, 2001; Dugatkin & Bekoff, 2003; Bauer & Smuts, 2007). A wolf pack can be considered as a division-of-labor-system in which conspecifics behave to maintain the cohesiveness of the group (Mech, 1999; Peterson et al., 2002). In

this perspective, social play may be used by wolves as a safe tool for practicing, coordinating, and fine-tuning their behaviours. Nevertheless, play also involves competitive elements and can be used for testing the weakness of possible competitive partners in order to gain social advantages over them (Pellis et al., 1993; Pellis & Iwaniuk, 2000; Palagi, 2006). A study carried out on brown hyenas showed that younger animals directed their play preferentially to older group-members, suggesting that they are testing opportunities to enter higher in the clan's dominance hierarchy (Mills, 1990). Mech (1970) hypothesized that in the wild all young wolves could be potential breeders and that they could automatically become alpha males when breeding (Mech, 1970). Also in captive packs, individuals may change their dominance status, because they do not have a permanent ranking position (Fox, 1971; Fox & Andrews, 1973; Zimen, 1976; Wilson, 2000). For example, without the stabilizing influence of parents (group defined as 'complex family', Zimen, 1975), the siblings fight to compete for the social roles of alpha and beta (Packard, 2003). In this perspective, by playing wolves may gain information about physical and cognitive abilities of fellows with whom they could compete in the near future for acquiring a higher ranking position. The results of this study support this idea. In fact, in the study colony play distribution was negatively affected by rank distances between group-members but not by the individual ranking position (Prediction 3 confirmed). Such findings suggest that wolves with closest ranking positions may need to test each other for social assessment purpose and, certainly, play may serve this function in a safer and fruitful way.

The general mammalian trend is that males perform play (particularly play fighting) more often than females (Pellis & Iwaniuk, 1999b). This sex difference in playful activity seems to be related both to the degree of sociality and to the structure of social organization (Pellis et al., 1993). Some authors have found that monogamous species such as bush dog (*Speothos venaticus*), maned-wolf (*Chrysocyon brachyurus*), crab-eating fox (*Cerdocyon thous*) grasshopper mice (*Onychomys leucogaster*) (Davies & Kemble, 1983; Pellis et al., 2000), prairie voles (*Microtus ochrogaster*) (Roberts et al., 1997; Lonstein et al., 2005), common marmosets (Stevenson & Poole, 1982), coppery titi monkeys (*Callicebus cupreus*), and cotton-top tamarins (*Saguinus oedipus*) (Cleveland & Snowdon, 1984) show neither physical sexual dimorphism nor sex differences in play behaviour (Biben, 1983). A high

proportion of wolf packs are monogamous, especially in the wild (Harrington et al., 1982), and both males and females equally contribute to group maintenance (Mech, 1999; Mech & Boitani, 2003). In the Pistoia colony I found that play behaviour was distributed throughout the entire group independently of the playmate sex-class combination (Prediction 2 confirmed). I can suggest that since both sexes play similar roles in the group, they also show similar behavioural repertoires (e.g., reconciliation, Cordoni & Palagi, 2008), including playful behaviour. In domestic dogs, sex seemed not to have broad effects on play style among the pairs that actually played (i.e., males and females performed attacks/pursuits, self-handicapping behaviours and play signalling at comparable levels), even if mounting was much more frequent in male–male dyads and given/received muzzle licks (two measures of self-handicapping) were never observed between males (Bauer & Smuts, 2007). Nevertheless, Pal (2008) reported that, in Indian free-ranging dogs, immature males played more frequently than females; in addition, Ward et al. (2008) showed that, in domestic dog puppies, when males played with females they initiated more ‘offensive’ interactions (attack and pursuit) and exhibited more self-handicapping behaviours than females did. These different findings are consistent with the concern that play can be highly variable in response to prevailing conditions (Fagen, 1981). Accordingly, Cipponeri & Verrell (2003) showed that in captive wolves, with the arrival of the breeding season, the pack experienced social disruption that may lead to unequal playful interactions among group members. Indeed, they found substantial inequalities among wolf pairs in the frequencies of both play initiation and the exhibition of positive responses by play recipients. In this study, I detected a decrease in play frequencies during the mating period, a highly competitive contest. Even if the alpha male has greater access to oestrous females, this privilege is not absolute: other group-males may compete with the leader for mating with a particular female. Therefore, subordinates may sometimes breed successfully as well (Packard, 1980; Creel & Waser, 1991; Mech, 1999; Wilson, 2000; Creel & Creel, 2002). In captivity, where more than one mature female is usually present and no dispersal is possible, multiple breeding may be very frequent (Packard, 1980). The Pistoia colony is characterized by higher frequency of aggression during MP compared to NMP, thus suggesting an elevated degree of intra-group social tension. My qualitative observations revealed the occurrence of many aggressive events between the alpha male (Wolf) and the other high ranking males (Ruga and

High-tail) for accessing oestrous females. Play mainly occurs in safe context when animals are free from environmental, physiological and social pressures (Fagen, 1981; Pellegrini et al., 1998, 2007; Burghardt, 2005). Consequently, it is not surprising that in the study colony play activity decreased during the mating days, which represent a highly risky period.

Many studies on primate and non-primate species have demonstrated that play levels are reduced during periods of nutritional stress (e.g., vervet monkeys, Lee, 1984; gelada baboons, Barrett et al., 1992; squirrel monkeys, Stone, 2008; ground squirrels, Nunes et al., 1999; meerkats, Sharpe et al., 2002), suggesting that play carries significant energetic costs (Baldwin & Baldwin, 1976; Martin & Caro, 1985). For instance, playing rats (in laboratory) consume 7% more food compared to non-playing rats (Siviy & Atrens, 1992). In highly seasonal Malagasy prosimians, such as *Propithecus verreauxi*, play was mainly or exclusively performed during the wet season when food is much available (Norscia, personal communication). On the other hand, recent studies carried out on captive chimpanzees, bonobos and lowland gorillas reveal an increase of play behaviour during the period immediately before the food distribution (the pre-feeding time) (Palagi et al., 2004, 2006, 2007) when the conflict of interests between conspecifics is more elevated (Aureli et al., 2002). Also a study carried out on spotted hyenas reveals that social play occurred more frequently during periods of low prey availability than when preys were abundant (Tanner et al., 2007). My data showed that play is significantly more frequent during the post-feeding time compared to any other possible conditions, thus suggesting that wolves restrict playful activity when their basic physiological needs are satisfied and the social context is safer. Pellis (1991) showed that in captive oriental small-clawed otters (*Anonyx cinerea*) play frequency decreases as the feeding session gets closer and increases again when animals are satiated. However, the author reported an unexpected increase of solitary object play frequency during the pre-feeding time, suggesting that such form of play may be motivationally linked to feeding. In fact, as otters became hungrier they focused their attention on pseudo-feeding behaviour, that is object play. I did not have sufficient data to rejoin this analysis in wolves, even if my finding did not reveal an increase of solitary play frequency (including solitary object play) during the pre-feeding time.

To summarize, my study on wolves shows that adult–adult play (i) is likely to be used for improving the ‘behavioural coordination’ among pack



members, independently of their sex, (ii) may represent a safe way to acquire information on potential competitors, (iii) is possibly able to provide physical training in order to compete with specific fellows for higher ranking position, and (iv) can be probably fine-tuned in relation to the prevailing conditions.

Given the importance of individual temperament (Gosling et al., 2003; Packard, 2003; Jones & Gosling, 2005) and the group history and composition in play dynamics and functions, further studies on different wolf colonies are required for comparative purposes. Obviously, captive research has inherent limitations that increase if the group structure differs greatly from that which is the norm in the wild (Erwin et al., 1979; Sadler & Ward, 1999). Nevertheless, the understanding of wolf social behaviour, and especially play, will be improved by integrating the information from both captive and wild groups, so long as we take great care to recognize the limitations of each perspective and to value the whole as the sum of the parts.

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### References

- Altmann, J. (1974). Observational study of behaviour sampling methods. — *Behaviour* 49: 227-265.
- Aureli, F., Cords, M. & van Schaik, C.P. (2002). Conflict resolution following aggression in gregarious individuals: a predictive framework. — *Anim. Behav.* 63: 1-19.
- Baldwin, J.D. (1982). The nature–nurture error again. — *Behav. Brain Sci.* 5: 155-156.
- Baldwin, J.D. & Baldwin, J.I. (1974). Exploration and social play in squirrel monkeys (*Saimiri*). — *Am. Zool.* 14: 303-315.
- Baldwin, J.D. & Baldwin, J.I. (1976). Effects of food ecology on social play: a laboratory simulation. — *Z. Psychol.* 40: 1-14.
- Barrett, L., Dunbar, R.I.M. & Dunbar, P. (1992). Environmental influences on play behaviour in immature gelada baboons. — *Anim. Behav.* 44: 111-115.
- Bauer, E.B. & Smuts, B.B. (2007). Cooperation and competition during dyadic play in domestic dogs, *Canis familiaris*. — *Anim. Behav.* 73: 489-499.

- Bekoff, M. (1974). Social play and play-soliciting by infant canids. — *Am. Zool.* 14: 323-340.
- Bekoff, M. (1977a). Social communication in canids: evidence for the evolution of a stereotyped mammalian display. — *Science* 197: 1097-1099.
- Bekoff, M. (1977b). Mammalian dispersal and ontogeny of individual behavioural phenotypes. — *Am. Nat.* 111: 715-732.
- Bekoff, M. (1995). Play signals as punctuation: the structure of social play in canids. — *Behaviour* 132: 419-429.
- Bekoff, M. (2001). Social play behaviour: cooperation, fairness, trust, and the evolution of morality. — *J. Consc. Stud.* 8: 81-90.
- Bekoff, M. (2004). Wild justice and fair play: cooperation, forgiveness, and morality in animals. — *Biol. Philos.* 19: 489-520.
- Berman, C.M. (1982). Functions of play: first steps toward evolutionary explanation. — *Behav. Brain Sci.* 5: 157-158.
- Bernal, J.F. & Packard, J.M. (1997). Differences in winter activity, courtship, and social behaviour of two captive family groups of Mexican wolves (*Canis lupus baileyi*). — *Zoo Biol.* 16: 435-443.
- Biben, M. (1983). Comparative ontogeny of social behaviour in three South American canids, the maned wolf, crab-eating fox and bush dog: implications for sociality. — *Anim. Behav.* 31: 814-826.
- Breuggeman, J.A. (1978). The function of adult play in free-living *Macaca mulatta*. — In: *Social play in primates* (Smith, E.O., ed.). Academic Press, New York, NY, p. 169-192.
- Burghardt, G.M. (2005). *The genesis of animal play: testing the limits*. — MIT Press, Cambridge, MA.
- Byers, J.A. (1984). Play in ungulates. — In: *Play in animals and humans* (Smith, P.K., ed.). Blackwell Scientific, Oxford, p. 43-65.
- Byers, J.A. (1999). The distribution of play behaviour among Australian marsupials. — *J. Zool. Lond.* 247: 349-356.
- Byers, J.A. & Walker, C. (1995). Refining the motor training hypothesis for the evolution of play. — *Am. Nat.* 146: 25-40.
- Caro, T.M. (1988). Adaptive significance of play: are we getting closer? — *Trends Ecol. Evol.* 3: 50-54.
- Cipponeri, T. & Verrell, P. (2003). An uneasy alliance: unequal distribution of affiliative interactions among members of a captive wolf pack. — *Can. J. Zool.* 81: 1763-1766.
- Cleveland, J. & Snowdon, C.T. (1984). Social development during the first twenty weeks in the cotton-top tamarin (*Saguinus o. oedipus*). — *Anim. Behav.* 32: 432-444.
- Cordoni, G. & Palagi, E. (2008). Reconciliation in wolves (*Canis lupus*): new evidence for a comparative perspective. — *Ethology* 114: 298-308.
- Creel, S. & Creel, N.M. (2002). *The African wild dog: behaviour, ecology and evolution*. — Princeton University Press, Princeton, NJ.
- Creel, S. & Waser, P.M. (1991). Failures of reproductive suppression in dwarf mongooses (*Helogale parvula*): accident or adaptation? — *Behav. Ecol.* 2: 7-15.
- Davies, V.A. & Kemble, E.D. (1983). Social play behaviours and insect predation in northern grasshopper mice (*Onychomys leucogaster*). — *Behav. Proc.* 8: 197-204.
- Dolhinow, P. (1999). Play: a critical process in the developmental system. — In: *the non-human primates* (Dolhinow, P. & Fuentes, A., eds). Mayfield, Mountain Oven, CA, p. 231-236.

- Drea, C. M., Hawk, J.E. & Glickman, S.E. (1996). Aggression decreases as play emerges in infant spotted hyaenas: preparation for joining the clan. — *Anim. Behav.* 51: 1323-1336.
- Dugatkin, L.A. & Bekoff, M. (2003). Play and the evolution of fairness: a game theory model. — *Behav. Proc.* 60: 209-214.
- Erwin, J.T., Maple, L. & Mitchell, G. (1979). Captivity and behaviour: primates in breeding colonies, laboratories, and zoos. — Van Nostrand-Reinhold, New York, NY.
- Fagen, R. (1981). Animal play behaviour. — Oxford University Press, New York, NY.
- Fagen, R. (1993). Primate juvenile and primate play. — In: Juvenile primates (Pereira, M.E. & Fairbanks, L.A., eds). Oxford University Press, Oxford, p. 182-196.
- Fox, M.W. (1971). Socio-ecological implications of individual differences in wolf litters: a developmental and evolutionary perspective. — *Behaviour* 41: 298-313.
- Fox, M.W. & Andrews, R.V. (1973). Physiological and biochemical correlates of individual differences in behaviour of wolf cubs. — *Behaviour* 46: 129-140.
- Gammell, M.P., de Vries, H., Jennings, D.J., Carlin, C.M. & Hayden, T.J. (2003). David's score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index. — *Anim. Behav.* 66: 601-605.
- Gosling, S.D., Kwan, V.S.Y. & John, O.P. (2003). A dog's got personality: a cross-species comparative approach to evaluating personality judgments. — *J. Pers. Soc. Psychol.* 85: 1161-1169.
- Harrington, F.H., Paquet, P.C., Ryon, J. & Fentress, C. (1982). Monogamy in wolves: a review of the evidence. — In: Wolves of the world (Harrington, F.H. & Paquet, P.C., eds). Noyes Publisher, Park Ridge, NJ, p. 474.
- Hinde, R.A. (1979). Towards understanding relationships. — Academic Press, New York, NY.
- Holmes, W.G. (1995). The ontogeny of littermate preferences in juvenile golden-mantled ground squirrels: effects of rearing and relatedness. — *Anim. Behav.* 50: 309-322.
- van Hooff, J.A.R.A.M. & Wensing, J.A.B. (1987). Dominance and its behavioural measures in a captive wolf pack. — In: Men and wolf: advances, issues, and problems in captive wolf research (Frank, I., ed.). Junk Publishers, Boston, MA, p. 219-252.
- Hughes, C.F. (2002). Object play in the domestic horse. — PhD thesis, University of Southampton, Southampton.
- Iwaniuk, A.N., Nelson, J.E. & Pellis, S.M. (2001). Do big-brained animals play more? Comparative analyses of play and relative brain size in mammals. — *J. Comp. Psychol.* 115: 29-41.
- Jones, A.C. & Gosling, S.D. (2005). Temperament and personality in dogs (*Canis familiaris*): a review and evaluation of past research. — *Appl. Anim. Behav. Sci.* 95: 1-53.
- Lee, P.C. (1984). Ecological constraints on the social development of vervet monkeys. — *Behaviour* 91: 245-262.
- Loizos, C. (1967). Play behaviour in higher primates: a review. — In: Primate ethology (Morris, D., ed.). Anchor Books, Chicago, IL, p. 226-282.
- Lonstein, J.S., Rood, B.D. & De Vries, G.J. (2005). The unexpected effects of perinatal gonadal hormone manipulations on sexual differentiation of the extrahypothalamic arginine-vasopressin system in the prairie voles. — *Endocrinology* 146: 1559-1567.
- Lund, J.D. & Vestergaard, K.S. (1998). Development of social behaviour in four litters of dogs (*Canis familiaris*). — *Acta Vet. Scand.* 39: 183-193.

- Martin, P. & Bateson, P. (1986). *Measuring behaviour-an introductory guide*. — Cambridge University Press, Cambridge.
- Martin, P. & Caro, T.M. (1985). On the functions of play and its role in behavioural development. — In: *Advances in the study of behaviour* (Rosenblatt, J., Beer, C., Bushel, M. & Slater, P., eds). Academic Press, New York, NY, p. 59-103.
- McDonnell, S.M. & Poulin, A. (2002). Equid play ethogram. — *Appl. Anim. Behav. Sci.* 78: 263-295.
- Mech, L.D. (1970). *The wolf: the ecology and behaviour of an endangered species*. — Doubleday, New York, NY.
- Mech, L.D. (1995). Summer movements and behaviour of an arctic wolf, *Canis lupus*, pack without pups. — *Can. Field-Nat.* 109: 473-475.
- Mech, L.D. (1999). Alpha status, dominance, and division of labor in wolf packs. — *Can. J. Zool.* 77: 1196-1203.
- Mech, L.D. & Boitani, L. (2003). Wolf social ecology. — In: *Behaviour, ecology, and conservation* (Mech, L.D. & Boitani, L., eds). The University of Chicago Press, Chicago, IL, p. 1-34.
- Mech, L.D., Wolf, P.C. & Packard, J.M. (1999). Regurgitative food transfer among wild wolves. — *Can. J. Zool.* 77: 1192-1195.
- Mendoza-Granados, D. & Sommer, V. (1995). Play in chimpanzees of the Arnhem zoo: self-serving compromises. — *Primates* 36: 57-68.
- Mills, M.G.L. (1990). *Kalahari hyaena. Comparative behavioural biology of two species*. — Unwin Hyman, London.
- Mundry, R. & Fischer, J. (1998). Use of statistical programs for nonparametric tests of small samples often lead to incorrect P values: examples from animal behaviour. — *Anim. Behav.* 56: 256-259.
- Nunes, S., Muecke, E., Anthony, J.A. & Batterbee, A.S. (1999). Endocrine and energetic mediation of play in free-living Belding's ground squirrels. — *Horm. Behav.* 36: 153-165.
- Packard, J.M. (1980). *Deferred reproduction in wolves (Canis lupus)*. — PhD thesis, University of Minnesota, Minneapolis.
- Packard, J.M. (2003). Wolf behaviour: reproductive, social, and intelligent. — In: *Wolves: behaviour, ecology, and conservation* (Mech, L.D. & Boitani, L., eds). University of Chicago Press, Chicago, IL, p. 35-65.
- Packard, J.M., Mech, L.D. & Ream, R.R. (1992). Weaning in an arctic wolf pack: behavioural mechanisms. — *Can. J. Zool.* 70: 1269-1275.
- Pal, S.K. (2008). Maturation and development of social behaviour during early ontogeny in free ranging dog puppies in West Bengal, India. — *App. Anim. Behav. Sci.* 111: 95-107.
- Palagi, E. (2006). Social play in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): implications for natural social systems and interindividual relationships. — *Am. J. Phys. Anthropol.* 129: 418-426.
- Palagi, E. (2008). Sharing the motivation to play: the use of signals in adult bonobos. — *Anim. Behav.* 75: 887-896.
- Palagi, E., Antonacci, D. & Cordoni, G. (2007). Fine-tuning of social play in juvenile lowland gorillas (*Gorilla gorilla gorilla*). — *Dev. Psychobiol.* 49: 433-445.
- Palagi, E., Cordoni, G. & Borgognini Tarli, S.M. (2004). Immediate and delayed benefits of play behaviour: new evidence from chimpanzees (*Pan troglodytes*). — *Ethology* 110: 949-962.

- Palagi, E., Paoli, T. & Borgognini Tarli, S.M. (2006). Short-term benefits of play behaviour: conflict prevention in captive bonobos (*Pan paniscus*). — *Int. J. Primatol.* 27: 1257-1270.
- Paquet, P.C. & Carbyn, L.N. (2003). Gray wolves. — In: *Mammals of North America* (Feldhamer, G. & Thompson, B., eds). John Hopkins University Press, Baltimore, MD, p. 482-510.
- Parrish, J. & Edelman-Keshet, L. (1999). Complexity, pattern, and evolutionary trade-offs in animal aggregation. — *Science* 284: 99-101.
- Pellegrini, A.D., Dupuis, D. & Smith, P.K. (2007). Play in evolution and development. — *Dev. Rev.* 27: 261-276.
- Pellegrini, A.D., Horvat, M. & Huberty, P.D. (1998). The relative cost of children's physical activity play. — *Anim. Behav.* 55: 1053-1106.
- Pellis, S.M. (1991). How motivationally distinct is play? A preliminary case study. — *Anim. Behav.* 42: 851-853.
- Pellis, S.M. & Iwaniuk, A.N. (1999a). The roles of phylogeny and sociality in the evolution of social play in muroid rodents. — *Anim. Behav.* 58: 361-373.
- Pellis, S.M. & Iwaniuk, A.N. (1999b). The problem of adult play: a comparative analysis of play and courtship in primates. — *Ethology* 105: 783-806.
- Pellis, S.M. & Iwaniuk, A.N. (2000). Comparative analyses of the role of postnatal development on the expression of play fighting. — *Dev. Psychobiol.* 36: 136-147.
- Pellis, S.M., Pasztor, T.J., Pellis, V.C. & Dewsbury, D.A. (2000). The organization of play fighting in the grasshopper mouse (*Onychomys leucogaster*). — *Aggress. Behav.* 26: 319-334.
- Pellis, S.M. & Pellis, V.C. (1991). Role reversal changes during the ontogeny of play fighting in male rats: attack versus defense. — *Aggress. Behav.* 17: 179-189.
- Pellis, S.M., Pellis, V.C. & McKenna, M.M. (1993). Some subordinates are more equal than others: play fighting amongst adult subordinate male rats. — *Aggress. Behav.* 19: 385-393.
- Pellis, S.M., Pellis, V.C. & Whishaw, I.Q. (1992). The role of the cortex in the play fighting by rats: developmental and evolutionary implications. — *Brain Behav. Evol.* 39: 270-284.
- Peterson, R.O., Jacobs, A.K., Drummer, T.D., Mech, L.D. & Smith, D.W. (2002). Leadership behaviour in relation to dominance and reproductive status in grey wolves, *Canis lupus*. — *Can. J. Zool.* 80: 1405-1412.
- Poirier, F.E., Bellisari, A. & Haines, L. (1978). Functions of primate play behaviour. — In: *Social play in primates* (Smith, E.O., ed.). Academic Press, New York, NY, p. 143-168.
- Rensch, B. (1973). Play and art in apes and monkeys. — *Symp. 4th Int. Congr. Primatol.* 1: 102-123.
- Roberts, R.L., Zullo, A.S. & Carter, S. (1997). Sexual differentiation in prairie voles: the effects of corticosterone and testosterone. — *Phys. Behav.* 62: 1379-1383.
- Rooney, N.J. (1999). Play behaviour of the domestic dog *Canis familiaris* and its effects on the dog-human relationship. — PhD thesis, University of Southampton, Southampton.
- Russell, E.S. (1936). Playing with a dog. — *Q. Rev. Biol.* 11: 1-15.
- Sadler, L.M. & Ward, S.J. (1999). Coalitions in male sugar gliders: are they natural? — *J. Zool. Lond.* 248: 91-96.
- Sands, J. & Creel, S. (2004). Social dominance, aggression and faecal glucocorticoid levels in a wild population of wolves, *Canis lupus*. — *Anim. Behav.* 67: 387-396.

- Schuster, R. (2001). An animal model of cooperating dyads: methodological and theoretical issues. — *Mexican J. Behav. Anal.* 27: 165-200.
- Schuster, R. (2002). Cooperative coordination as a social behaviour: experiments with an animal model. — *Hum. Nat.* 13: 47-83.
- Schuster, R., Berger, B.D. & Swanson, H.H. (1988). Cooperative social coordination and aggression: sex and strain differences in the effects of housing on gonadectomized rats with hormone replacement. — *Aggress. Behav.* 14: 275-290.
- Schuster, R., Berger, B.D. & Swanson, H.H. (1993). Cooperative social coordination and aggression. II. Effects of sex and housing among three strains of intact laboratory rats differing in aggressiveness. — *Q. J. Exp. Psychol.* 46B: 367-390.
- Schuster, R. & Perelberg, A. (2004). Why cooperate? An economic perspective is not enough. — *Behav. Proc.* 66: 261-277.
- Sharpe, L.L. (2005a). Frequency of social play does not affect dispersal partnerships in wild meerkats. — *Anim. Behav.* 70: 559-569.
- Sharpe, L.L. (2005b). Play does not enhance social cohesion in a cooperative mammal. — *Anim. Behav.* 70: 551-558.
- Sharpe, L.L. & Cherry, M.I. (2003). Social play does not reduce aggression in wild meerkats. — *Anim. Behav.* 66: 989-997.
- Sharpe, L.L., Clutton-Brock, T.H., Brotherton, P.N.M., Cameron, E.Z. & Cherry, M.I. (2002). Experimental provisioning increases play in free-ranging meerkats. — *Anim. Behav.* 64: 113-121.
- Siegel, S. & Castellan, N.J.J. (1988). *Non-parametric statistics for the behavioural sciences.* — McGraw Hill, New York, NY.
- Silk, J.B. (2007). The adaptive value of sociality in mammalian groups. — *Phil. Trans. R. Soc. B* 362: 539-559.
- Siviy, S.M. & Atrens, D.M. (1992). The energetic costs of rough-and-tumble play in the juvenile rat. — *Dev. Psychobiol.* 25: 137-148.
- Smith, P.K. (1982). Does play matter? Functional and evolutionary aspects of animal and human play. — *Behav. Brain Sci.* 5: 139-184.
- Smith, L.K., Fantella, S.L. & Pellis, S.M. (1999). Playful defensive responses in adult male rats depend upon the status of the unfamiliar partner. — *Aggress. Behav.* 25: 141-152.
- Soderquist, T.R. & Serena, M. (2000). Juvenile behaviour and dispersal of chuditch (*Dasyurus geoffroii*) (Marsupialia: Dasyuridae). — *Aust. J. Zool.* 48: 551-560.
- Špinka, M., Newberry, R.C. & Bekoff, M. (2001). Mammalian play: training for the unexpected. — *Q. Rev. Biol.* 76: 141-167.
- Stevenson, M.F. & Poole, T.B. (1982). Playful interactions in family groups of the common marmoset (*Callithrix jacchus jacchus*). — *Anim. Behav.* 30: 886-900.
- Stone, A.I. (2008). Seasonal effects on play behaviour in immature *Saimiri sciureus* in Eastern Amazonia. — *Int. J. Primatol.* 29: 195-205.
- Sugiyama, Y. (1976). Life history of male Japanese monkeys. — In: *Advances in the study of behaviour*, Vol. 7 (Rosenblatt, J.S., Hinde, R.A., Shaw, E. & Beer, C., eds). Academic Press, New York, NY, p. 255-284.
- Tanner, J.B., Smale, L. & Holekamp, K.E. (2007). Ontogenetic variation in the play behaviour of spotted hyenas. — *J. Dev. Proc.* 2: 5-30.
- Thompson, K.V. (1998). Self assessment in juvenile play. — In: *Animal play – evolutionary, comparative and ecological perspectives* (Bekoff, M. & Byers, J.A., eds). Cambridge University Press, Cambridge, p. 183-204.

- Ward, C., Bauer, E.B. & Smuts, B.B. (2008). Partner preferences and asymmetries in social play among domestic dog, *Canis lupus familiaris*, littermates. — *Anim. Behav.* 76: 1187-1199.
- Watson, D.M. (1993). The play associations of red-necked wallabies (*Macropus rufogriseus banksianus*) and relation to other social contexts. — *Ethology* 94: 1-20.
- Wilson, E.O. (2000). *Sociobiology — the new Synthesis*. — The Belknap Press of Harvard University Press, Cambridge, MA.
- Zar, J.H. (1999). *Biostatistical analysis*, 4th edn. — Prentice Hall, Englewood Cliffs, NJ.
- Zimen, E. (1975). Social dynamics of the wolf pack. — In: *The wild canids: their systematics, behavioural ecology and evolution* (Fox, M.W., ed.). Van Nostrand Reinhold, New York, NY, p. 336-368.
- Zimen, E. (1976). On the regulation of pack size in wolves. — *Z. Tierpsychol.* 40: 300-341.
- Zimen, E. (1981). *The Wolf*. — Souvenir Press, London.
- Zimen, E. (1982). A wolf pack sociogram. — In: *Wolves of the world* (Harrington, F.H. & Paquet, P.C., eds). Noyes Publishers, Park Ridge, NJ, p. 282-322.
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