Neuroscience and Biobehavioral Reviews 148 (2023) 105124

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Adult play and the evolution of tolerant and cooperative societies

Elisabetta Palagi [1]

Department of Biology - Unit of Ethology - University of Pisa, Via Alessandro Volta 6, 56126 Pisa, Italy

A R T I C L E I N F O

Keywords:
Social play
Primates
Wild carnivores
Dominance styles
Leverage
Stress release mechanism
Ice-breaker tactics
Strategies to cope with uncertainty

A B S T R A C T

Play is generally considered an immature affair. However, adult play is present in several mammal species living in complex social systems. Here, I hypothesize that adult social play is favored by natural selection in those species characterized by high level of social tolerance and/or by the need of others' cooperation to reach a goal (i.e., leverage). The integration and comparison of bio-behavioral data on non-human primates and wild social carnivores allows drawing a comprehensive picture on the importance of adult play in facing unpredictable, novel social situations and in overcoming stressful experiences. The ability to cope with potentially competitive interactions through play can favor the emergence of egalitarian societies. A further interesting and beneficial aspect of adult play is its role in synchronizing group activities and favoring collective decision making by renovating the motivation to cooperate in groupmates. As a last step, some considerations about the presence of adult play in the most egalitarian and cooperative human groups (e.g., hunter-gatherer societies) allows discussing the apparent dichotomy between cultural and biological evolution of certain behavioral traits, including social play in adulthood.

1. Introduction

Living in groups is a complex affair. The level of association and the variability of social structures derive from a delicate equilibrium between centrifugal and centripetal forces that are molded by many factors (e.g., ecological habits, reproductive systems, life span). One of the most important pillars of social group organization is dominance, which is not only an intrinsic aspect of individual phenotypes, but also the expression of social relationships connecting each dyad of groupmates (Hinde, 1976). While affirming that "the subject A is dominant over B" clarifies the type of relationship existing between the two individuals, affirming that "the subject A is dominant" does not provide any information about the real dominance status of the subject. In this perspective, if we want to determine the entity of the dominance relation between individuals we need to measure the outcome and the direction of dyadic competitive encounters such as overt agonistic events, supplantations (e.g., avoidance behaviors in *Lemur catta*, Norscia and Palagi, 2015), submissive formal gestures (e.g., bobbing in chimpanzees, *Pan troglodytes* van Lawick-Goodall, 1968) and signals (e.g., punt grunts in chimpanzees, van Lawick-Goodall, 1968; silent bared teeth in some species of macaques, Thierry, 2000; greetings in baboons and spotted hyenas, Dal Pesco and Fischer, 2020; East et al., 1993). Although during these interactions the difference in social power of the two subjects becomes obvious, formalized dominance within a dyad is only one of the possible ways in which power can be expressed. The situation can be more complex than this. The dominance within a dyad can also depend on triadic networks of which it is part. To dominate a groupmate, an individual may obtain the help from another subject, no matter if it is a subordinate. This means that subjects need to be close to the potential "helper" when provoking the potential opponent. The individual cognitive skills, the profound knowledge of competitors' capabilities, the propensity to establish bonds and form alliances with highly selected companions are all factors which may alter the dominance of an individual within a social group (Flack and de Waal, 2004). When these behavioral strategies are at work, weaker subjects can become socially dominant over physically stronger conspecifics due to their ability to recruit support. In these cases, we can speak of power asymmetries rather than a rank order (de Waal, 1986). Power asymmetries can also emerge when individuals are able to reach their goals against others' interests without engaging in any form of explicit dominant actions. This is possible due to a leverage advantage of subordinates over the dominants that, in economic terms, can lead to a debt ratio. When a subordinate individual possesses a resource that cannot be obtained by dominants through the use of force (e.g., cooperation in hunting, Gersick et al., 2015; support in disputes, Pallante et al., 2016), dominants need to negotiate with subordinates by granting and bargaining some benefits

E-mail address: elisabetta.palagi@unipi.it.
[1] ORCID: 0000–0002-2038–4596

https://doi.org/10.1016/j.neubiorev.2023.105124
Received 22 October 2022; Received in revised form 7 February 2023; Accepted 15 February 2023
Available online 16 March 2023

such as tolerance (Lewis et al., 2022). In these cases, leverage can be one of the scaffolds for cooperation to evolve also in despotic species where dominants are generally not tolerant towards subordinates (*sensu* Vehrencamp, 1983, agonistic asymmetry strongly skewed in favor of one of the subjects forming a dyad). It appears, therefore, that the concepts of dominance and power distribution have multiple shades of grey that are shaped by both proximate and ultimate factors. Such variability translates into a different expansion of social space (i.e., the dimension of individuals' social network, Sueur et al., 2011), cooperation (Anderson, 2007) and the degrees of freedom (i.e., the variability of social contacts with groupmates) that are generally higher in more tolerant than despotic species (Butovskaya, 2004).

Due to its dual nature of competitive-cooperative interaction, social play, and particularly play fighting, can be a powerful means to enter in contact with group members and acquire social/physical information on others under a relatively safe context at any stages of life (Palagi et al., 2016; Palagi and Pellis, 2022). The way in which such pieces of information are used will depend, in the long term, on the social strategies animals enact to acquire social power in their groups (Paquette, 1994), increase their survival probability (e.g., escaping from predators, gathering food resources of good quality, forming alliances against competitors) and reproductive success (e.g., building bonds with subjects of the opposite sex, obtaining help in rearing offspring). It is therefore plausible that the emergence, the consistency, and the modality of social play during the whole life span should be favored in those species characterized by an enlarged social sphere, a large degree of variability in affiliative behaviors with groupmates, and a high fluidity in social bonds as a function of affiliation efforts.

Here, I explore the possibility that adult social play is favored by natural selection in those species characterized by high level of social tolerance and/or by the need of others' cooperation to reach a goal (i.e., leverage). Primates and social carnivores are excellent models to test this hypothesis due to their complex social systems and variability in social tolerance and cooperative propensity (de Waal and Tyack, 2003). As a first step, by integrating behavioral, ecological, neurological and hormonal data, I will try to verify whether a correlation exists between relaxed dominance styles and the occurrence of adult play. Specifically, I will focus on the role of adult play in coping with immediate unpredictable, novel and potentially stressful social situations, one of the abilities that can favor the emergence of egalitarian societies. Then, I will pass to investigate the relationship between cooperation and adult play according to the fluctuation in the levels of social tolerance. To better understand such linkage, I will revise the literature possibly indicating the role of adult play in synchronizing group activities and favoring collective decision making by renovating the motivation to cooperate in groupmates. I will conclude with some considerations about the presence of adult play in the most egalitarian and cooperative human groups (e.g., hunter-gatherer societies) by discussing the false dichotomy between cultural and biological evolution of certain behavioral traits, including social play in adulthood.

2. Adult play: a social litmus test

In all the species in which it has been described, play in its multiple forms is mainly an immature affair (Burghardt, 2005). Although play is costly, immature subjects need to stretch from solitary to social playful activities to develop those cognitive, emotional and physical abilities that will be necessary in the adult phase to increase survival probabilities and reproductive opportunities (Berghänel et al., 2015; Cameron et al., 2008; Pellis et al., 2010). A clear example comes from a long-term study on wild brown bears (*Ursus arctos*) (Fagen and Fagen, 2004). The authors demonstrated that those cubs engaging in higher levels of play during their first summer of life survived better to the end of their second summer. The finding did not change even when controlling for other factors such as condition at birth, food availability, and maternal features. This study illustrates that social play in bears increases short-term survival. Another example comes from the chimpanzees of Gombe. By using a database covering 33 years of data collection, Heintz et al. (2017) found that infants who engaged in more social play acquired better motor skills and started developing social competency at earlier ages. Therefore, short- and long-term benefits seem to be the engine for juvenile play to become an evolutionary stable strategy (Pellis and Pellis, 2009). Despite evidence on the importance of immature social play accumulating, data explaining why this costly (i.e., time-consuming, risky) behavioral trait is retained into adulthood in some species, has yet to be explained in detail. One possible explanation is that adult play is difficult to study as it is infrequent, thus, requiring a lot of effort in behavioral data collection (e.g., long periods of observation, large number of individuals under different conditions). In sum, adult play is for patient and unyielding researchers. However, the few studies dedicated to such elusive behavior indicate that adult play exists in some mammal species (including ours), although its evolutionary significance is far from being completely understood.

Adult individuals have already completed their development and are supposed to know the environment in which they move, therefore the retention of play in adults should seem more a Darwinian paradox than a real beneficial evolutionary trait. Yet, the physical environment can change and there is the never-ending necessity to escape from predators or to actively search for food (i.e., hunting). In this sense, taking care of physical form is important and locomotor play, by introducing '*gravitational, kinematic, or positional shocks*' (Špinka et al., 2001, p.143), could have the important immediate function to maintain the subject in good health and ready to cope with challenging situations that strongly affect survival and fitness potentials. Such shock situations are often created by the player itself. Adult primates closing or covering their eyes by the hands or objects while jumping from a support to another are elucidating examples (Kavanagh, 1978; Palagi, 2014; Russon and Vasey, 2012).

If the benefits of adult locomotor play can be intuitive, detecting the advantages of play fighting behavior in adult mammals is much more challenging. Game theory and the agent-based modelling approaches suggest a strict linkage between the presence of social play in juveniles and their level of cooperation as adults (Dugatkin and Bekoff, 2003; Durand and Schank, 2015). A recent work also states that playing fairly may have evolved in juveniles to acquire skills for behaving fairly outside the playful sphere later in life (Schank et al., 2018). Can these concepts also apply to adult play? Can adult play be seen as an investment strategy to gain information, communicate the intention to cooperate or enact tactical deception to manage potentially dangerous situations in those fluid societies that build their relationship frames not on strict hierarchical rules but on the negotiation of resources?

We could start from the fact that in tolerant societies and in those where the dominants need cooperation from subordinates to gain benefits, adult play can involve lower costs since rank rules do not create constraints for play to emerge and the benefits deriving from knowing each other and testing others' willingness to invest in a relationship can be high (see Fig. 1 for the graphical representation of the conceptual framework). Therefore, under particular conditions, adult play seems to satisfy the sociobiological rule of the cost/benefit ratio. Although, to my knowledge, no modelling approach has ever addressed this issue, there are empirical data that concur in sustaining this hypothesis. The comparative approach is particularly fruitful in delineating the social factors underlining the retention of adult play into adulthood. The studies on taxa sharing recent common ancestors that yet differ in their social relationships and evolutionary environments are particularly helpful, because they represent the ideal models for natural experiments.

3. What our closer relatives tell us about the linkage between adult play and tolerance

Chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) are very

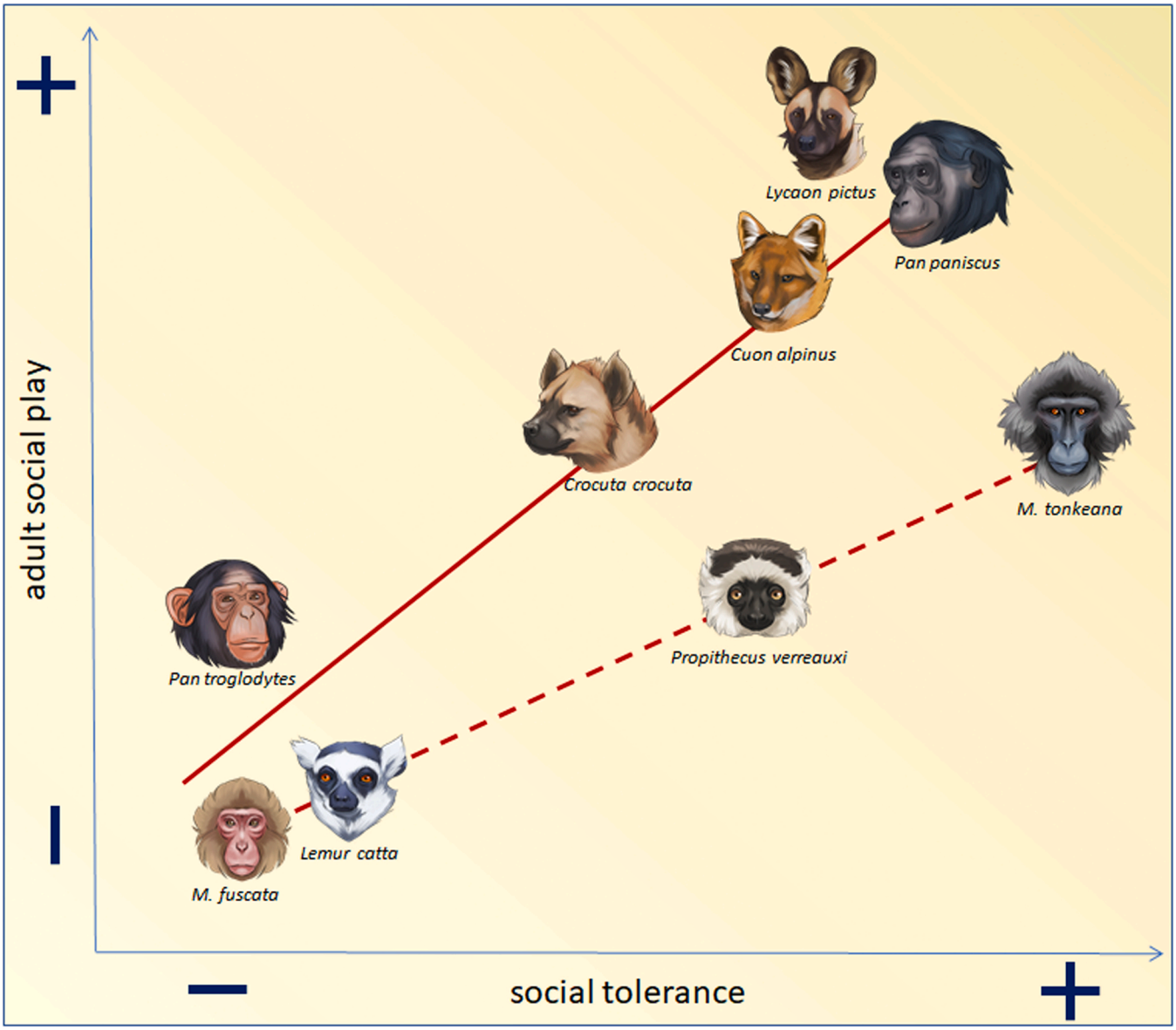

Fig. 1. The figure shows the covariation between the probability of adult social play and the level of social tolerance in a given society (non-cooperative societies – dotted line; cooperative societies – solid line). In the cooperative societies, when the dominants need the social support of subordinates (leverage power over dominants), the probability for adult play to occur increases because it becomes an important tool in social management. The species are arranged on the graph according to the data available in literature. The representation has the unique aim to illustrate the distribution from a qualitative point of view. Drawings: Fosca Mastrandrea.

good candidates to test possible ultimate (e.g., functions) and proximate mechanisms (e.g., neurobiology, development) at the basis of the evolution of adult play and its potential linkage to the tolerant and cooperative propensity of the species. The two species diverged about 1.7 million years ago when the common ancestors were separated by the Congo River. The different ecological factors which translated into a different resource distribution and feeding competition are likely at the basis of the divergent social behavior of chimpanzees and bonobos, including the presence of adult play (Doran et al., 2002).

3.1. *Ultimate mechanisms: possible functions of adult play*

Despite their genetic closeness and similarities in the fluid social structure (fission-fusion) and group dynamics (female exogamy), the two *Pan* species strongly differ in many aspects of their social behavior. Within the community, bonobos move in large mixed parties, while chimpanzees aggregate in small groups, some formed by few females with their offspring, some involving small groups of males and others including an estrus female with the dominant male (Furuichi, 2009). Chimpanzees show a strict dominance hierarchy which is led by one or a few males (often related) that can form coalitions to strategically obtain power at the expense of other males (Wrangham, 2018). In bonobos, coalitions and alliances between unrelated females lead them to occupy the top of the hierarchy which is, however, not rigidly organized or reaffirmed by formal signals (Furuichi, 2011; Gruber and Clay, 2016; Palagi, 2006). Recent data show that chimpanzees are strongly neophobic, while bonobos are strongly neophilic and, therefore, prone to socially interact with both ingroup and outgroup subjects with each group maintaining its own identity (e.g., exclusive social and spatial boundaries) (Samuni et al., 2022; Tan et al., 2017). Hence, the tolerance of bonobos leads them to have larger fluid social spheres and higher number degrees of freedom in social relationships compared to chimpanzees. This does not mean that bonobos do not compete when a conflict of interest arises, this simply means that they make less use of

agonistic encounters or formal submissive patterns probably engaging in more manipulative and cooperative strategies to manage their social relationships (Wobber et al., 2010a). Differently from the sister species, bonobos show a large repertoire of socio-sexual interactions (Anzà et al., 2021; de Waal, 1988; Palagi et al., 2020) and an exceptional propensity to engage in social play at every age, as it has been confirmed by both captive (Palagi, 2006, 2008, 2018) and wild data (Enomoto, 1994, Behncke, 2015). Play fighting in bonobos is particularly evident between adult females and it covaries more with social bonds (e.g., grooming, body contact) than with intrinsic features (e.g., body size) or dominance relationships (Palagi and Paoli, 2007). Hence, the relaxed dominance interactions of females and their need to build alliances to get power over males can be two "passports" for adult social play to evolve in this species. The larger amount of play fighting engaged by bonobo females is evident starting from adolescence with immature males and females not differing in their frequency of play fighting (Palagi, 2006; Palagi and Paoli, 2007). Similar findings have also been reported for cooperative species in which the females have large roles in social dominance and reproduction. Meerkats (*Suricata suricatta*) are a cooperative breeder species in which females compete more than males to gain reproductive advantages thus increasing their breeding success. In a long-term study on wild meerkats, Clutton-Brock et al. (2006) found that, while play fighting was well balanced between male and female pups, as animals became adult the mixed playful sessions were more unbalanced in favor of females that ended up on top of the male and "won" the session. A similar example comes from spotted hyenas (*Crocuta crocuta*). Like several primate species, spotted hyenas live in fission-fusion societies organized in a strict nepotistic but highly cooperative system (Drea and Frank, 2003; Smith et al., 2007) where the members of the clan support each other in rearing offspring (Konig, 1997), hunting, and defending territories (Holekamp et al., 2007). The females are dominant over males and reach their high ranking status by forming alliances with other females (Vullioud et al., 2019). The leverage advantage of low-ranking females over the dominants can be an important tool to manipulate power asymmetries among individuals. In this perspective, social play can have a role in increasing social knowledge between the subjects. Accordingly, adult social play is present in spotted hyenas with frequencies higher than those observed for other forms of play (Tanner et al., 2007). Play fighting provides opportunity to immature hyenas to enhance their motor/physical abilities and to adults to acquire social information on partners with whom they will have to compete in the future. While the amount of social play in immature hyenas did not differ between the sexes (Tanner et al., 2007), adult females have been observed engaging in play fighting more than males (Kruuk, 1972; Fagen, 1981; Mills, 1994). Social play between adult females of spotted hyenas can reflect their need to cooperate and form alliances for territorial defense and control over males (Vullioud et al., 2019).

All the findings on different taxa concur to suggest that the passage from juvenility to adulthood is critical in many mammal species (Graham and Burghardt, 2010) and during such transition it is possible that the functions of play can shift from satisfying developmental training necessities to manipulating social situations at least in those species where the relationships are negotiable (e.g., high levels of tolerance, leverage/cooperative behavior).

3.2. Proximate mechanisms: development and neurobiological correlates of adult play

Neoteny is a heterochronic mechanism producing an underdevelopment of certain features (or pedomorphosis) through the deceleration in the developmental rate (McKinney, 1998). As previously discussed, the two congeneric apes differ in numerous aspects of their social behavior and several authors attribute such behavioral diversity to the heterochronic processes characterizing the development of chimpanzees and bonobos (Brosnan, 2010; Hare et al., 2007; Rosati and Hare, 2012). Wobber and collegues (2010a) experimentally tested whether the changes in social tolerance between bonobos and chimpanzees were due to the slow behavioral development in the former compared to the latter. Differently from chimpanzees, bonobos were prone to share food even when it was easily monopolizable. Additionally, while chimpanzees became less tolerant as adults, bonobos did not change their propensity to share food as they aged, with juveniles being as tolerant as adults. During their experiments Wobber et al. (2010a) also recorded data on social play. In chimpanzees, they found a strong negative correlation between the age of the subjects and the number of trials during which they engaged in playful interactions; whereas in bonobos the correlation did not reach any statistical significance. In short, under the same experimental conditions, adult bonobos played more than chimpanzees.

Similar findings also come from naturalistic observations. By comparing data on social play in several colonies of immature chimpanzees and bonobos, Palagi and Cordoni (2012) explored at which stage of the developmental pathway the two species began to diverge. Overall chimpanzees engaged in less social play bouts as they aged compared to bonobos that continued to play from infancy to adulthood (Palagi, 2018). The infants of the two species did not show any difference in their playful propensity, however, differences in the engagement in play activity did emerge during the juvenile period, with chimpanzees engaging in less play. In juvenile bonobos, the playful sessions lasted longer and often included a higher number of players compared to those of chimpanzees. The lower degree of tolerance and/or the higher level of competition characterizing social play in juvenile chimpanzees led their sessions to escalate into overt aggression more frequently than in bonobos. The different ratio of competition/cooperation during play expressed by the two species seems to reflect their physiological differences. Wobber et al. (2010b) showed that, under food-related competitive contexts, the hormonal responses of the two species strongly differed, with bonobo males increasing their cortisol and chimpanzee males their testosterone levels. The authors hypothesized that chimpanzees viewed the competition as a means to reaffirm their power thus leading to an increase in testosterone. In 2014, Behringer and colleagues found that, compared to chimpanzees and humans, bonobos show prolonged circulation of the thyroid hormone (T3) levels, whose concentration negatively correlates with aggression propensity in our species (Behringer et al., 2014). In this view, the temporal extension of high T3 concentration may be one of the physiological factors responsible of the high levels of tolerance and cooperative nature of play in adult bonobos.

As a whole, the findings deriving from both experimental (Wobber et al., 2010a) and naturalistic approach (Palagi and Cordoni, 2012) strongly suggest that tolerance and social play covariance is sensitive to the evolutionary changes in the development of neuroendocrine system of these related species.

Undeniably, interesting hints come also from neurobiology. It has been for long hypothesized that play is more likely expressed in larger brained compared to smaller brained species (Fagen, 1981). Actually, large brained mammalian orders have been found to play more and in more complex ways (Iwaniuk et al., 2001). However, a within-order species comparison did not reveal any correlation between play and brain size. In sum, what was present at a higher taxonomic level, became inconsistent at a lower taxonomic level (Iwaniuk et al., 2001). Then, to test for a possible covariation between the different kinds of play and the brain components, scholars began to look at the different brain areas and their relative sizes (Lewis, 2000; Lewis Graham, 2011; Lewis and Barton, 2004, 2006; Pellis and Iwaniuk, 2002). Through the phylogenetic comparative approach of independent contrast, it has been found that in primate species the relative size of striatum (Lewis Graham, 2011), cerebellum (Lewis and Barton, 2004) and amygdala and hypothalamus (Lewis and Barton, 2006) is strongly correlated with the rates of social play. Cerebellum is implicated in the control of accurate cognitive and motor skills during play fighting, striatum is involved in emotional

reward and social play performance, and amygdala and hypothalamus seem to be at the basis of the appropriateness of social response processes, emotion regulation, and recognizing/mimicking others' facial expressions, all capacities that are essential for social play to successfully occur (Lewis and Barton, 2004, 2006).

Focusing on bonobos and chimpanzees and comparing their neural systems, Rilling et al. (2012) found significant differences in the neural circuitries involved in social cognition and emotional regulation between the two species. Although the average brain volume of these apes does not significantly differ, bonobos have higher local gray matter in specific areas such as the right anterior insula, right dorsal amygdala, right hypothalamus and right dorsomedial prefrontal cortex. These regions are involved in the distress perception of both oneself and others thus indicating a relevant capacity for emotional processing. Moreover, bonobos' amygdala is largely connected with the ventral anterior cingulate cortex (Rilling et al., 2012) and has about twice the density of serotonergic axons compared to chimpanzees (Stimpson et al., 2016). Such connections are involved in the inhibition of aggressive propensity. As a whole, the neural diversity of the two *Pan* species supports not only their different emotional sensitivity, but also the higher propensity of bonobos in engaging in peaceful and tolerant behaviors such as socio-sexual and playful activity to cope with social tension, avoid conflicts and restore emotional homeostasis in case of competitive interactions (Clay and de Waal, 2015; Clay et al., 2018; Palagi et al., 2004, 2006).

4. "All grown-ups were once children, but only few of them remember it": the case of macaques

Macaques are opportunistic primates living in a variety of environments (Fooden, 1982). They form multimale-multifemale groups characterized by male exogamy and female philopatry (Thierry, 2007). Despite the consistency of their social structure, the seminal work by Bernard Thierry (2004) revealed that the different macaque species can be arranged according to their distinctive social styles ranging from tolerant to despotic. Contrary to despotic ones, tolerant macaques show a lower level of unidirectional agonistic events (Duboscq et al., 2013), a low asymmetry in dominance power distribution (Balasubramaniam et al., 2012), a high propensity to reconcile their conflicts (Demaria and Thierry, 2001), and a stronger tendency to invest in allogrooming with a lower social preference for kin (Thierry, 2007; Thierry and Berman, 2010).

There is evidence that centralization within social networks affects the efficiency of networks at all levels of biological systems. The more efficient networks are those in which an optimal balance between communication and number of connections between the different entities exists (e.g., genes, proteins, cells, individuals, groups) (Oltvai and Barabási, 2002). By studying 24 primate species, Pasquaretta et al. (2014) suggested that those societies showing mild differences in centrality between subjects are characterized by high tolerance levels that can translate into a better efficiency in social exchanges and communication. Looking at macaques, comparative network analyses reveal clear differences in the distribution of power and affiliation between tolerant and despotic species. Sueur et al. (2011) found that despotic species' social networks show a higher kin-dependent modularity and that dominant individuals are more central than other groupmates in despotic compared to tolerant species.

Hence, due to their consistency in social structure and variation in their inter-individual relations, macaques (*Macaca* spp.) is another interesting taxon serving as a natural experiment to test hypotheses on the linkage between adult social play, tolerance and cooperation in non-human animals. Unfortunately, there are very few studies focused on macaque adult play thus making cross-species comparisons challenging. However, if we look at the data available, we can realize that a possible covariance between species tolerance levels and adult play distribution exists. Japanese (*Macaca fuscata*) and Tonkean macaques (*Macaca tonkeana*) occupy the two extremes of the tolerance spectrum proposed by Thierry (2000, 2007), with the former (grade 1) much more despotic than the latter (grade 4). By comparing play at all ages between the two species, Ciani et al. (2012) detected some important differences in the expression of this behavior. In general, Tonkean macaques have been found to be more playful than Japanese macaques (Caine and Mitchell, 1979a; Ciani et al., 2012) with larger playful cliques, which are punctuated by more cooperative elements (Reinhart et al., 2010). Indeed, both immatures and adults of *M. tonkeana* scored higher rates of play fighting than *M. fuscata.* The adults of the two species also differed in their partner selectivity. While adult Tonkean macaques did not show any bias towards the age of the playmates, the adult Japanese macaques preferred to engage in social play with immatures. Moreover, in Tonkean macaques, adult males and females played at comparable frequencies; whereas, in Japanese macaques adult males played more than females, which never engaged in any playful contacts with other adults for the whole duration of the data collection (Ciani et al., 2012). A similar result was also found in the despotic rhesus macaques, where adults did not substantially contribute in social playing networks compared to other age-classes (Liao et al., 2018).

As already discussed, several social factors may concur in favoring the possible retention of a playful attitude in adulthood such as a high degree of flexibility in hierarchical relations, the necessity of cooperation by subordinates to gain shared goals (i.e., leverage), and the need to engage in peaceful tactics to managing conflictual situations. Recent findings on stress (measured via cortisol concentrations in the hair) in Tonkean and in the despotic long-tailed macaques (*Macaca fascicularis*) revealed an unexpected situation, with the former showing higher levels of cortisol than the latter. Moreover, males and females of Tonkean macaques did not show any difference in their cortisol concentrations (Sadoughi et al., 2021). The authors discussed these results in the light of the different dominance styles of the two species. Due to the high level of unpredictability and fluidity characterizing their dominance hierarchy, Tonkean macaques need to continuously test and renegotiate their social relationships. The higher concentrations of cortisol found in this species may reflect the instability and lack of control around social interactions. Interestingly, the similarity in the cortisol levels found in the two sexes (Sadoughi et al., 2021) mirrors the similarity of adult play frequency recorded in males and females of Tonkean macaques (Ciani et al., 2012). Some hints also come from immature rhesus macaques. Wooddell et al. (2021) found that, in a period of high social instability, juveniles that occupied more central positions in their social play networks also exhibited smaller increases in hair cortisol concentrations, thus revealing a potential stress releasing effect of social play also in immature subjects of despotic species. In short, being tolerant is costly at least in term of emotional investment and the role of adult play can be twofold. It can help manipulate social relationships and, concurrently, limit stress arising from relaxed hierarchical relationships. Up to now, we do not have any direct information about the actual linkage between adult play and cortisol level in tolerant and despotic macaques; however, the emerging picture seems to support the emotional resilience hypothesis according to which adult play can help navigate uncertain and, sometimes, critical situations.

An interesting aspect to explore for understanding the maintenance of a playful mood in adulthood is the social environment in which infants grow up and the behavioral inputs they receive from the mothers (Berman, 1982). In short, can such striking diversity in adult play propensity between tolerant and despotic species plunge its roots in the immature period? Which is the contribution of the social environment on the development of tolerance propensity that individuals of some species exhibit as adults? To test if social environment modifies the social development in macaques, de Waal and Johanowicz (1993) performed an experiment in which juveniles of rhesus (*M. mulatta*, despotic) and stump-tailed macaques (*M. arctoides*, tolerant) were co-housed for some months. The specific goal of the study was to understand whether living together could modify the conciliatory tendency of the subjects

belonging to species with different social styles. The authors found that, compared to a control cohort, the propensity to reconcile conflicts increased three times in rhesus macaques after the period of cohabitation with stump-tailed macaques. The differences were not only limited to the post-conflict sphere. The frequency of *girneys*, a vocalization associated to affiliation and social play in juveniles, strongly increased in rhesus macaques thus indicating that prolonged contacts with a tolerant species can modify social attitude in immatures belonging to a despotic species (de Waal and Johanowicz, 1993). This study suggests that during the immature period a certain degree of social plasticity exists and that macaques can adjust their behavior according to the social inputs they receive. The infant social sphere largely varies across the different macaque species and this is also due to the control exerted by the mothers on infants' movements and social contacts (Caine and Mitchell, 1979b; Chaffin et al., 1995). Due to their intolerant propensity, some adult group members can react in an aggressive way to the infants' play invitations especially when they are frequently reiterated (Fagen, 1981; Flack et al., 2004), such events are much more frequent in despotic compared to tolerant societies (Mayhew et al., 2020). In rhesus macaques, the presence of adults inhibits social play in immature subjects. Bernstein and Draper (1964) showed that when the adults were removed from the enclosure, juveniles significantly increased their playful contacts. Moreover, the high competitive nature of play fighting in despotic species makes this social activity particularly risky for immatures (Beltrán Francés et al., 2020; Petit et al., 2008; Reinhart et al., 2010; Scopa and Palagi, 2016). For this reason, the mother often prevents infants to interact with a large number of group members thus leading to a strong selection in infants' playmates. The protectiveness of the mother depends not only on the level of the despotism of the species but also on her hierarchical status (Liu et al., 2022). In tolerant societies, mothers are more relaxed and allow their infants interacting with a variety of group members including unrelated adults (Ciani et al., 2012). The low level of mother's protectiveness contributes creating many playful opportunities for the immatures to develop those cognitive (e.g., fine modulation of communication, Scopa and Palagi, 2016) and emotional abilities (e.g., coping with stress, Sadoughi et al., 2021) necessary to react in a resilient way to uncertain situations that are typical of tolerant societies (Fig. 2).

5. As little as necessary: adult play to navigate uncertain social situations

There is the widespread idea that if a population expresses play behavior at low frequencies and only under specific circumstances it probably does not have any significant function in drawing the socio-ecology of a species. In ring-tailed lemurs (*Lemur catta*), female sexual receptivity covers about 72 h per year and during such a handful of hours all the copulations take place (Jolly, 1967). Therefore, females

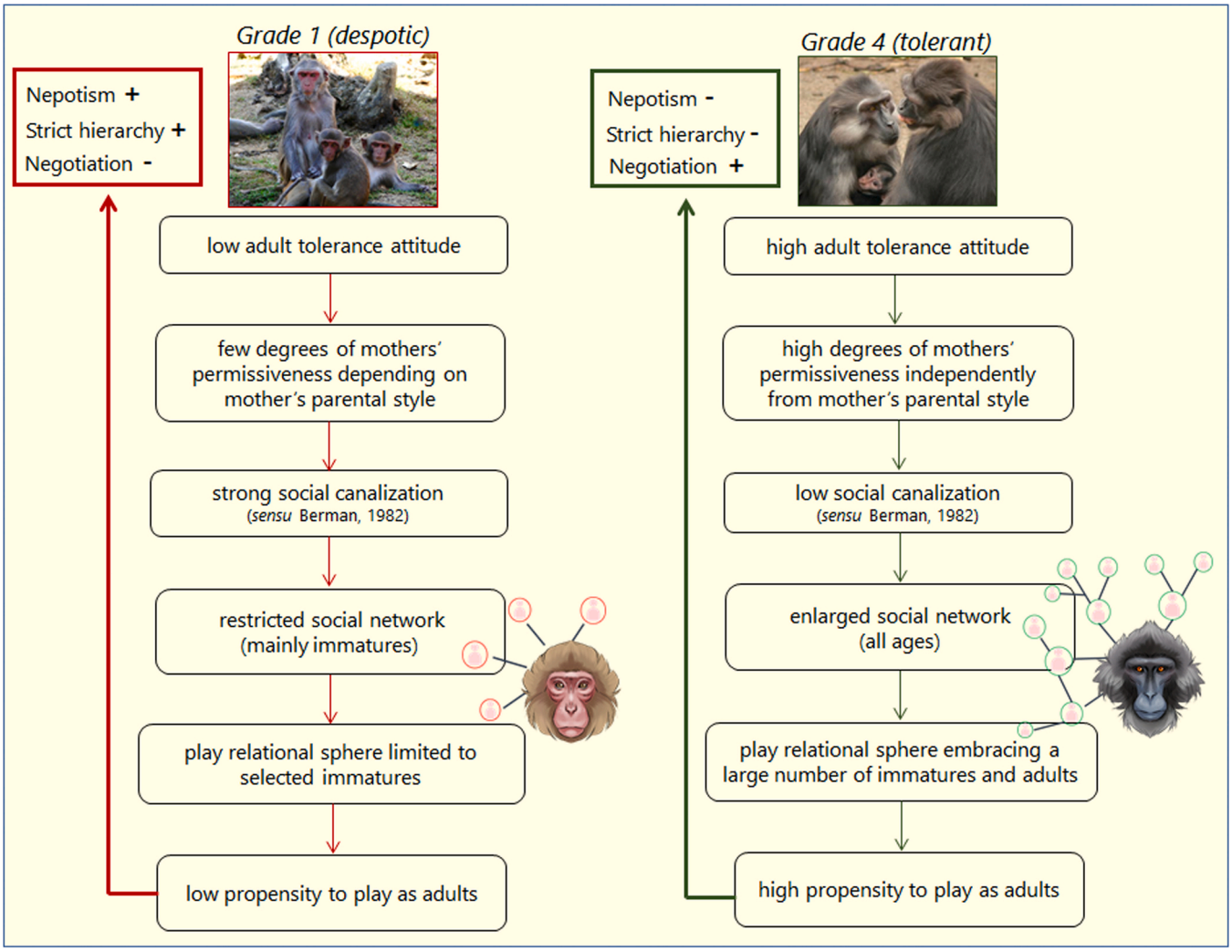

Fig. 2. Graphical abstract showing how social tolerance characterizing a given taxon can affect the social development of infants through the level of protectiveness of the mothers. The cases of the *Macaca* genus. Drawings: Fosca Mastrandrea.

spend about 0.83% of their time in mating per year and it is clearly an overestimation because copulas do not obviously cover all the period of receptivity. Despite its extremely low frequency, nobody could argue that the behavior is not crucial for the species. While the importance of copulations appears immediately clear to the eyes of an observer, the importance of play (especially in adults) is much less intuitive and leave many researchers highly skeptical about its real functions ("[…], *l'essentiel est invisible pour les yeux.*", de de de Saint Exupery, 1999, p. 76). The first of the five criteria listed by Burghardt (2005) to define play behavior reads as follow: *"[…] the performance of the behavior is not fully functional in the form or context in which it is expressed; that is, it includes elements, or is directed toward stimuli, that do not contribute to current survival*" (p. 71). The first criterion is certainly challenging and poses one of the main obstacles that often demotivates researchers to embark on a path of studying this behavior. However, there is a growing number of curious researchers who decided to explore the so called *not-obvious* functions of adult play (e.g., Asensio et al., 2022; Ciani et al., 2012; Cordoni and Palagi, 2016; Norscia and Palagi, 2011; Palagi, 2006, 2008; Paulos et al., 2010; Pellis and Iwaniuk, 1999, 2000).

Coming back to ring-tailed lemurs, some observations carried out in captive groups revealed that immediately before their restricted reproductive period, during which females increase their tolerance levels towards males, adult-adult play fighting was present in both sexes (Palagi, 2009). Males preferred other males as playmates and, at dyadic level, play fighting negatively correlated with real fighting thus supporting the hypothesis that play can be a substitute of overt aggression in a period of high male intra-sexual competition. Interestingly, during their playful interactions with females, adult males engaged in high levels of *tail-play,* a signal indicating appeasement and submission during courtship (female are always dominant over males in this species, Jolly, 1967). Interestingly, such signal was rarely displayed during play sessions involving two males. Therefore, despite the little amount of time spent playing by lemurs, their flexible use of *tail-play* indicates that male-male and male-female playful interactions have diverse functions: assessing others' competitive abilities in the former and testing females' motivation to mate in the latter.

Play fighting between adult males is also present in another lemur species, the tolerant sifaka (*Propithecus verreauxi*) (Antonacci et al., 2010). During the mating season, adult males roam from one group to another to maximize their reproductive opportunities. The first encounters between out-group and resident males are characterized by weak agonistic contacts that decrease immediately after the first inter-group play session. In a consolidated group, the presence of new incomers introduces a certain degree of uncertainty which residents need to cope with. Although limited to few days during the reproductive period, play in wild adult sifaka represents an important ice-breaker mechanism allowing subjects to assess their own and others' abilities and overcome tense situations thus limiting the risk of overt aggression. Actually, after engaging in playful interactions the out-group males appeared well integrated in the group, they spent time in proximity with other males and copulated with the females without receiving any attacks from the resident males (Antonacci et al., 2010).

Socioecological factors are fundamental to explain the presence of adult play and interpret the potential functions of such ephemeral behavior not only at a species but also at a group level. A recent study on wild mantled howler monkeys provided interesting information (Asensio et al., 2022). By studying several groups of two subspecies of *Alouatta palliata* (*A. p. mexicana* and *A. p. palliata*), Asensio et al. (2022) found that despite its low level (0.61% of the observation time), adult play can fulfil a significant function in this species. Play in general increased with group size and adult-adult play was more represented than adult-immature play. In howler monkeys, both males and females leave their natal groups at sexual maturity and this dispersal dynamic contributes to form groups mainly made up of unfamiliar subjects (Arroyo-Rodríguez et al., 2008) that continuously need to test their relationships to maintain group cohesion. Since allogrooming (hereafter, grooming) is rare in this species (Crockett and Eisenberg, 1987), this may have led to engage in other forms of interactions to build social bonds. It is therefore possible that adult-adult play can function as a substitute of grooming in this South American primate species (Asensio et al., 2022). Interestingly, the analysis also revealed that the time adults spent foraging was positively correlated with the time spent playing. The authors explained this finding in the light of socioecological factors characterizing the species. The *A. palliata* society is not organized according to strict dominance rules, with group members showing high level of tolerance and low aggression rates even when they need to face conflict of interest generated by clumped food resources (Cristobal-Azkarate et al., 2004). The correlation between the time spent playing and feeding suggests that adult play can have a role in negotiating resource distribution especially during highly competitive situations. In *A. palliata*, this is particularly true for adult females that, being more exposed to intra-group food competition compared to males (Isbell, 1991), frequently engage in play with other adults to reduce tension around food. Similar findings have been also reported for captive adult bonobos that, by intensively playing just before feeding time, are more prone to peacefully share food once it has arrived (Palagi et al., 2006). Therefore, in some cases, play serves to make animals more tolerant during situations characterized by marked conflict of interest and potentially risky.

In their interesting paper on the role of adult play in domestic and captive mammal species, Blois-Heulin et al. (2015) defined adult play as a "false friend" and stated that it cannot be considered a good indicator of welfare. Actually, play in adults seems to be effective not only in avoiding arousal escalation and overt aggression, but also in releasing anxiety and re-establishing emotional homeostasis accumulated during stressful periods or after a perturbing event (Norscia and Palagi, 2011; Palagi and Pellis, 2022; Pellis and Burghardt, 2017). Important findings coming from the same French research group (Hausberger et al., 2012) suggest that in horses (*Equus caballus*) adult play increased as the animals experienced higher level of stress measured by both behavioral (e.g., aggressive propensity against humans) and physiological indicators (e.g., plasmatic cortisol concentrations, oxidative stress). Probably play in adults, although at low frequency, can also foster emotional resilience in response to unfavorable conditions. In conclusion, if we want to use a medical metaphor, there is increasing evidence that adult play is effective to manage social situations and regulate emotional states even at low doses, depending on the modality and timing of "administration".

6. Adult play as an evolutionary convergence trait: looking at social carnivores in the wild

Primates and social carnivores show a certain level of behavioral and cognitive convergence (Holekamp and Benson-Amram, 2017). Since the two taxa are phylogenetically distant with a shared common ancestor probably living about 100 Myr ago (Springer et al., 2003), due to their playful life style, some carnivore species are a good model to explore if and how social living has favored, in an independent way, the persistence of play in adulthood and its possible linkage with cooperative propensity among group members. Despite only a handful of specific studies is available on adult play in carnivores, there are some evidence and observations suggesting the importance of this behavior in managing different aspects of social life and, again, the level of tolerance and cooperation seem to make the difference.

In a study on the development of infant spotted hyenas, Drea and colleagues (1996) found that the propensity to aggression in cubs starts decreasing concomitantly with the emergence of social play which is intrinsically different in its modality from real aggression. Contrary to real fighting, that was highly unidirectional, play fighting was characterized by a high level of reciprocity with dominant and subordinate cubs inviting each other at similar rates. The mother frequently intervened to interrupt the true aggressive interactions, but never during play fighting (Drea et al., 1996; Nolfo et al., 2021). In hyenas, play fighting is

the gate to the social life of the pack and during this transition the cubs are not always main characters with adults playing an important role too. In the Makalali Reserve (South Africa), Nolfo et al. (2021) demonstrated that juvenile and adult hyenas spend a similar amount of time in playful activities. The play invitations between juveniles and adults were strongly reciprocated thus suggesting that the motivation to play is age-independent in this species. The playful propensity of adults was also confirmed by the presence of adult-adult spontaneous playful sessions that never escalated into real aggression, a clear sign that animals are able to synchronize their motor actions (Nolfo et al., 2021) and finely communicate their non-harmful intents (Nolfo et al., 2022). An accurate frame-by-frame video-analysis revealed that the high levels of competition characterizing hyenas' playful sessions positively correlated with their duration: the higher the arousal, the longer the duration. This led the authors to hypothesize that in a species living in despotic and nepotistic systems, play is not only a means for cubs to enter the clan, but it is also used by adults to reciprocally test their social relations and lay the foundation for future alliances and cooperation (Nolfo et al., 2021). In a long-term study on captive hyenas, Glickman et al. (1999) found that play positively correlated with greeting ceremonies, a ritualized behavior used to renovate the relationship after a period of separation (Mills, 1994). Similar data on the connection of juvenile and adult play come also from Indian Ocean bottlenose dolphins. Juveniles of this species engage in male-male sexual play, a playful trait which is maintained into adulthood. This peculiar type of play seems to translate into the formation and maintenance of life-long alliances between males (Mann, 2006). The function of play as a gate to navigate new social situations emerges also from the observations on another African carnivore: the African wild dog (*Lycaon pictus*). The species lives in packs (2–20 individuals, Maddock and Mills, 1994) which usually consist of one dominant reproductive pair and a cooperative system of pup rearing by all group members (Estes and Goddard, 1967; Malcolm and Marten, 1982). The wild dogs are also extremely cooperative in hunting and express a quasi-linear hierarchy with clear-cut dominance relations within each sex determined by ritualized displays or mild aggression at least under periods of social stability (Creel et al., 1997; de Villiers et al., 2003). To avoid inbreeding, both males and females leave their natal group (Frame and Frame, 1976; McNutt, 1996; Woodroffe et al., 2020). In this species, adult play represents a passport for entering the new pack. In a study carried out in the Serengeti National Park, Frame et al. (1979) studied the dynamics of group formation and followed some events of male and female primary migration. When the migrating females entered the new pack, they solicited resident males to play by roughly pawing and resident males responded to such invitations with defensive gestures, but never engaging in overt aggression. The behavior was similar in the case of male migration. Resident females directed play invitations to the new males that reacted with ano-genital sniffing or mounting. These observations strongly suggest that, in African wild dogs, adult play functions as a mechanism facilitating migration and transfer (ice-breaker mechanism) as it occurs also in some primate species (sifaka, Antonacci et al., 2010; howler monkeys, Asensio et al., 2022).

A further convergent trait characterizing adult play in both primates and social carnivores is its celebrating function to synchronize group activities and increase the probability to cooperate. As already stated, there are evidence that in both great apes and monkeys adult play peaks just before feeding. In captive bonobos, those dyads engaging in play sessions before food distribution are also those eating together and sharing food in a relaxed way (Palagi et al., 2006). In African wild dogs, Estes and Goddard (1967) observed that adult play is common during the daily activities of the pack and that it punctuates all the stages of a hunting event. For wild dogs, hunting is a choral event during which each member of the group, independently from its own ranking position, needs to contribute to maximize the probability of success (van Lawick and Goodall, 1970). The hunting preparatory phase starts with one or two adult individuals inviting others to play, after short time, all the dogs are involved in play fighting and chasing each other. Once the playful climax is reached, all the members of the pack start twittering thus communicating their collective agreement to start hunting. The hunting attack can often be interspersed by short time intervals, during which the dogs renovate their agreement by short playful interactions and trotting together. Play is also present at the end of hunting, when the animals are fully satiated. Due to the African wild dogs' playful attitude ("*Apart from a certain amount of play and other social activities shortly before starting to hunt and immediately after feeding, pack members were usually active only while actually hunting*", Estes and Goddard, 1967, p. 56), it is not surprising that adult play can be a regulator of the pack activity by favoring collective decision making and, thanks to its symbolic meaning, renovating cooperation among groupmates.

Another carnivore species in which adult play seems to serve as regulator of social dynamics is the dhole or the Asiatic wild dog (*Cuon alpinus*) (Fox, 1984; Johnsingh, 1982). Dholes live in fluid packs made up of a variable number of subjects ranging from 5 to 25 individuals depending on the different sites (Durbin et al., 2004). The species is characterized by a certain level of social complexity with mild hierarchical relationships between subjects although a dominant reproductive pair is present (Fox, 1984). All the pack members regularly participate in hunting activities, play together and rarely engage in severe aggression (Durbin et al., 2004). Sometimes different packs form larger aggregations and during such periods they have been observed playing but rarely hunting together (Fox, 1984). This tolerant behavior strongly resembles that expressed by wild bonobos when subjects belonging to different communities meet each other (Behncke, 2015). In dholes as well as in African wild dogs, adult-adult play is a ritualized behavior that helps synchronizing mood around hunting activities (Fox, 1984; Johnsingh, 1982). Adult-adult play, which involves same-sex and mixed-sex chasing, ambushing, and mounting, precedes and follows both successful and unsuccessful hunting events. Moreover, as for spotted hyenas, adults spend time playing with other adults and cubs at the dens (Johnsingh, 1982). Therefore, although few data on social behavior of this species are available, play seems to be an important part of the dholes' life tolerant style: "[…] *Play is a way of coming together and staying together for a time, a means of reaffirming friendships and consolidating social bonds. It is stimulating too, not only physically but in the countless variations and repetitions of sequences that can be created. It is like dancing, where two or more animals sharing the same mood take up the same cadence for a while until one sets up a new rhythm, a different pace, a new variation to the game. Animals that play together stay together; it perhaps best exemplifies the unity of a family or clan and is one of the most beautiful things to observe in the wild.*" (Fox, 1984, p. 101).

7. Conclusive remarks: intellectual humility and open minds

Humans are playful animals. Playing is a highly rewarding activity which makes us feel better, both emotionally and physically, especially when it occurs between family members and friends (Pellegrini, 2010). No doubt that free play in our species is the expression of joy and sociality that is helpful to build social relationships. In a recent study carried out via a social network approach, Lira et al. (2021) demonstrated that free social play increases group cohesiveness and mitigates ethnic group avoidance in children.

Social play can have a more or less important social roles as a function of the different human cultures we take into consideration (Boyette, 2019; Gray, 2009, 2014). It has been argued that free social play has a role in restraining aggression thus favoring cooperation also in our species (Fry, 2014). Such assumption is supported by the evidence that the persistence of free play in adulthood covaries with the levels of hierarchical relationships characterizing different human social groups, with more tolerant and cooperative societies showing higher levels of adult social play (Gray, 2014). Another evolutionary convergence, this time apparently involving culture and biology. But is this traditional dichotomy real? Hunter-gatherer societies live in small, nomadic and

"*politically acephalous groups that subsisted primarily by gathering wild plant foods and hunting wild animals*" (Boyette, 2019, p. 302). If we look at the egalitarian hunter-gatherer systems, it appears clear that adult play is a means to converge on the most important collective decisions for the group, in the same way we can find in non-human primates (Asensio et al., 2022) and social carnivores (Estes and Goddard, 1967; Johnsingh, 1982). In hunter-gatherer societies, playing together means reducing aggressive tendencies (Fry, 2014) and acting cooperatively (e.g., hunting, rearing offspring, food sharing, Gray, 2014) thus reaching shared goals with a lower energy expenditure. This lifestyle translates into an increased survival probability and a higher fitness at an individual level. In this societies, there is no space for cheaters or aggressive individuals that tend to have a marginal role in the group thus contributing less in the gene pool (Gray, 2014). That is how the boundaries of cultural and biological evolution of play vanish. For this reason, if we want to really understand the role of adult play in the evolution of tolerant and cooperative societies, we need to comparatively study the phenomenon in human and non-human animals by applying similar conceptual and methodological approaches. From an intellectually humble perspective, understanding how non-human animals can manage the complexity of their social life will redefine our place in nature.

Declarations of interest

none.

Data Availability

No data was used for the research described in the article.

Acknowledgements

This work is the result of the many ideas discussed with Sergio Pellis, Gordon Burghardt, Paul Smaldino, and Jeffrey Schank in two focus groups: "Mechanisms and Evolution of Play" at the Konrad Lorenz Institute for Evolution and Cognition Research (Klosterneuberg, Austria) and "Play, Evolution, and Sociality" at the National Institute for Mathematical and Biological Synthesis, sponsored by the National Science Foundation through NSF Award #DBI1300426, with additional support from The University of Tennessee (Knoxville, US). I wish to thank Fosca Mastrandrea for her wonderful drawings; Veronica Maglieri and Luca Pedruzzi for our lively discussions about the evolution of social play. Finally, I am grateful to Giovanni Laviola for his kind invitation and the anonymous reviewers for their useful suggestions.

References

Anderson, J.R., 2007. Animal behavior: tolerant primates cooperate best. Curr. Biol. 17 (7), R242–R244. https://doi.org/10.1016/j.cub.2007.02.005.PMID:17407752.

Antonacci, D., Norscia, I., Palagi, E., 2010. Stranger to familiar: wild strepsirhines manage xenophobia by playing. PLoS ONE 5 (10), e13218. https://doi.org/10.1371/journal.pone.0013218.

Anzà, S., Demuru, E., Palagi, E., 2021. Sex and grooming as exchange commodities in female bonobos' daily biological market. Sci. Rep. 11, 19344. https://doi.org/10.1038/s41598-021-98894-w.

Arroyo-Rodríguez, V., Asensio, N., Cristobal-Azkarate, J., 2008. Demography, life-history and migrations in a Mexican mantled howler group in a rainforest fragment. Am. J. Primatol. 70 (2), 114–118. https://doi.org/10.1002/ajp.20463.

Asensio, N., Zandonà, E., Dunn, J.C., Cristóbal-Azkarate, J., 2022. Socioecological correlates of social play in adult mantled howler monkeys. Anim. Behav. 186, 219–229. https://doi.org/10.1016/j.anbehav.2022.01.017.

Balasubramaniam, K.N., Dittmar, Berman, C.M., Butovskaya, M., Cooper, M.A., Majolo, B., Ogawa, H., Schino, G., Thierry, B., de Waal, F.B.M., 2012. Hierarchical steepness and phylogenetic models: phylogenetic signals in *Macaca*. Anim. Behav. 83 (5), 1207–1218. https://doi.org/10.1016/j.anbehav.2012.02.012.

Behncke, I., 2015. Play in the Peter *Pan* ape. Curr. Biol. 25, R24–R27. https://doi.org/10.1016/j.cub.2014.11.020.

Behringer, V., Deschner, T., Murtagh, R., Stevens, J.M.G., Hohmann, G., 2014. Age related changes in thyroid hormone levels of bonobos and chimpanzees indicate heterochrony in development. J. Hum. Evol. 66, 83–88. https://doi.org/10.1016/j.jhevol.2013.09.008.

Beltrán Francés, V., Castellano-Navarro, A., Maulany, R.I., Ngakan, P.O., MacIntosh, A.J. J., Llorente, M., Amici, F., 2020. Play behavior in immature moor macaques (*Macaca maura*) and Japanese macaques (*Macaca fuscata*). Am. J. Prima 82 (10), e23192. https://doi.org/10.1002/ajp.23192.

Berghänel, A., Schulke, O., Ostner, J., 2015. Locomotor play drives motor skill acquisition at the expense of growth: a life history trade-off. Sci. Adv. 1, e1500451 https://doi.org/10.1126/sciadv.1500451.

Berman, C.M., 1982. The ontogeny of social relationships with group companions among free-ranging infant rhesus monkeys: II. Differentiation and attractiveness. Anim. Behav. 30, 163–170. https://doi.org/10.1016/S0003-3472(82)80251-0.

Bernstein, I.S., Draper, W.A., 1964. The behavior of juvenile rhesus monkeys in groups. Anim. Behav. 12 (1), 84–91. https://doi.org/10.1016/0003-3472(64)90107-1.

Blois-Heulin, C., Rochais, C., Camus, S., Fureix, C., Lemasson, A., Lunel, C., Hausberger, M., 2015. Animal welfare: could adult play be a false friend? Anim. Behav. Cogn. 2 (2), 156–185. https://doi.org/10.12966/abc.05.04.2015.

Boyette, A.H., 2019. Play in foraging societies. In: Smith, P.K., Roopnarine, J.L. (Eds.), The Cambridge handbook of play: Developmental and disciplinary perspectives. Cambridge University Press, New York, pp. 302–321.

Brosnan, S.F., 2010. Behavioral development: timing is everything. Curr. Biol. 20 (3), R98–R100. https://doi.org/10.1016/j.cub.2009.12.009.

Burghardt, G.M., 2005. The Genesis of Animal Play: Testing the Limits. MIT Press, Cambridge.

Butovskaya, M., 2004. Social space and degrees of freedom. In: Thierry, B., Singh, M., Kaumanns, W. (Eds.), Macaque Societies: a Model for the Study of Social Organization. Cambridge University Press, Cambridge, pp. 182–185.

Caine, N., Mitchell, G., 1979a. A review of play in the genus *Macaca*; social correlates. Primates 20, 535–546.

Caine, N., Mitchell, G., 1979b. The relationship between maternal rank and companion choice in immature macaques (*Macaca mulatta* and *M. radiata*). Primates, 20, 583–590.

Cameron, E.Z., Linklater, W.L., Stafford, K.J., Minot, E.O., 2008. Maternal investment results in better foal condition through increased play behaviour in horses. Anim. Behav. 76, 1511–1518. https://doi.org/10.1016/j.anbehav.2008.07.009.

Chaffin, C.L., Friedlen, K., de Waal, F.B.M., 1995. Dominance style of Japanese macaques compared with rhesus and stumptail macaques. Am. J. Primatol. 35, 103–116.

Ciani, F., Dall'Olio, S., Stanyon, R., Palagi, E., 2012. Social tolerance and adult play in macaque societies: a comparison with different human cultures. Anim. Behav. 84, 1313–1322. https://doi.org/10.1016/j.anbehav.2012.09.002.

Clay, Z., de Waal, F.B.M., 2015. Sex and strife: post-conflict sexual contacts in bonobos. Behaviour 152 (3–4), 313–334.

Clay, Z., Palagi, E., de Waal, F.B.M., 2018. Ethological approaches to empathy in primates. In: Meyza, K.Z., Knapska, E. (Eds.), Neuronal Correlates of Empathy. San Diego (USA): Elsevier Science Publishing Co Inc, pp. 53–66. https://doi.org/10.1016/B978-0-12-805397-3.00005-X.

Cordoni, G., Palagi, E., 2016. Aggression and hierarchical steepness inhibit social play in adult wolves. Behaviour 153, 749–766. https://doi.org/10.1163/1568539X-00003326.

Creel, S., Creel, N.M., Mills, M.G.L., Monfort, S.L., 1997. Rank and reproduction in cooperatively breeding African wild dogs: behavioral and endocrine correlates. Behav. Ecol. 8 (3), 298–506. https://doi.org/10.1093/beheco/8.3.298.

Cristobal-Azkarate, J., Dias, P.A.D., Veà, J.J., 2004. Causes of intraspecific aggression in *Alouatta palliata mexicana*: Evidence from injuries, demography, and habitat. Int. J. Primatol. 25, 939–953. https://doi.org/10.1023/B:IJOP.0000029130.10312.63.

Crockett, C.M., Eisenberg, J.F., 1987. Howlers: variations in group size and demography. In: Smuts, B., Cheney, D., Seyfarth, R., Wrangham, R.W., Struhsaker, T.T. (Eds.), Primate Societies. Chicago University Press, Chicago, pp. 54–68.

Dal Pesco, F., Fischer, J., 2020. On the evolution of baboon greeting rituals, 2019042020190420 Philos. Trans. R. Soc. B 375. https://doi.org/10.1098/rstb.2019.0420.

Demaria, C., Thierry, B., 2001. A comparative study of reconciliation in rhesus and Tonkean macaques. Behaviour 138, 397–410. https://doi.org/10.1163/15685390152032514.

Doran, D.M., Jungers, W.L., Sugiyama, Y., Fleagle, J.G., Heesy, C.P., 2002. Multivariate and phylogenetic approaches to understanding chimpanzee and bonobo behavioral diversity. In: Boesch, C., Hohmann, G., Marchant, L.F. (Eds.), Behavioural Diversity in Chimpanzees and Bonobos. Cambridge (UK). Cambridge University Press, pp. 14–34.

Drea, C.M., Frank, L.G. 2003. The social complexity of spotted hyenas. In de Waal, F.B. M., Tyack, P.L. (Eds.), Animal social complexity: intelligence, culture, and individualized societies. Cambridge, M.A.: Harvard University Press. pp 121–148.

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 (6), 1323–1336. https://doi.org/10.1006/anbe.1996.0136.

Duboscq, J., Micheletta, J., Agil, M., Hodges, K., Thierry, B., Engelhardt, A., 2013. Social tolerance in wild female crested macaques (*Macaca nigra*) in Tangkoko-Batuangus nature reserve, Sulawesi, Indonesia. Am. J. Primatol. 75 (4), 361–375. https://doi.org/10.1002/ajp.22114.

Dugatkin, L.A., Bekoff, M., 2003. Play and the evolution of fairness: a game theory model. Behav. Proc. 60, 209–214.

Durand, S., Schank, J.C., 2015. The evolution of social play by learning to cooperate. Adapt. Behav. 23 (6), 340–353. https://doi.org/10.1177/1059712315608243.

Durbin, L.S., Venkataraman, A., Hedges, S., Duckworth, J.W., 2004. Dhole (*Cuon alpinus*). In: Sillero-Zubiri, C., Hoffman, M., Macdonald, D.W. (Eds.), Status Survey and Conservation Action Plan. Canids: Foxes, Wolves, Jackals and Dogs. Gland, Switzerland, and Cambridge: IUCN, pp. 210–219.

East, M.L., Hofer, H., Wickler, W., 1993. The erect 'penis' is a flag of submission in a female-dominated society: greetings in Serengeti spotted hyenas. Behav. Ecol. Sociobiol. 33, 355–370. https://doi.org/10.1007/BF00170251.
Estes, R.D., Goddard, J., 1967. Prey selection and hunting behavior of the African wild dog. J. Wildl. Manag. 31 (1), 52–57.
Fagen, R., 1981. Animal play behavior. Oxford University Press, New York.
Fagen, R., Fagen, J., 2004. Juvenile survival and benefits of play behavior in brown bears, *Ursus arctos*. Evol. Ecol. Res. 6, 89–102.
Flack, J.C., de Waal, F.B.M., 2004. Dominance style, social power, and conflict management. In: Thierry, B., Singh, M., Kaumanns, W. (Eds.), Macaque societies: a Model for the Study of Social Organization. Cambridge University Press, Cambridge, pp. 157–181.
Flack, J.C., Jeanotte, L.A., de Waal, F.B.M., 2004. Play signalling and the perception of social rules by juvenile chimpanzees (*Pan troglodytes*.). J. Comp. Psychol. 118, 149–159.
Fooden, J., 1982. Ecogeographic segregation of macaque species. Primates 23, 574–579. https://doi.org/10.1007/BF02373969.
Fox, M.W., 1984. The Whistling Hunters: Field Studies of the Asiatic Wild Dog (*Cuon alpinus*). State University of New York Press, Albany.
Frame, L.H., Frame, G.W., 1976. Female African wild dogs emigrate. Nature 263, 227–229.
Frame, L.H., Malcolm, J.R., Frame, G.W., Van, Lawick, H., 1979. Social organization of African wild dogs (*Lycaon pictus*) on the Serengeti Plains. Tanzan. 1967-1978. Z. Tierpsychol. 50, 225–249.
Fry, D.P., 2014. Environment of evolutionary Adapteness, rough-and-tumble play, and the selection of restraint in human aggression. In: Narvaez, D., Valentino, K., Fuentes, A., McKenna, J.J., Gray, P. (Eds.), Ancestral landscapes in human evolution: Culture, childrearing and social wellbeing. Oxford University Press, New York, pp. 169–188. https://doi.org/10.1093/acprof:oso/9780199964253.003.0012.
Furuichi, T., 2009. Factors underlying party size differences between chimpanzees and bonobos: a review and hypotheses for future study. Primates 50 (3), 197–209. https://doi.org/10.1007/s10329-009-0141-6.
Furuichi, T., 2011. Female contributions to the peaceful nature of bonobo society. Evol. Anthr. 20 (4), 131–142, 10.1002/evan.20308.PMID: 22038769.
Gersick, A.S., Cheney, D.L., Schneider, J.M., Seyfarth, R.M., Holekamp, K.E., 2015. Long-distance communication facilitates cooperation among wild spotted hyaenas, *Crocuta crocuta*. Anim. Behav. 103, 107–116. https://doi.org/10.1016/j.anbehav.2015.02.003.
Glickman, S.E., Zabel, C.J., Yoerg, S.I., Weldele, M.L., Drea, C.M., Frank, L.G., 1999. Social facilitation, affiliation, and dominance in the social life of spotted hyenas. In: Carter, C.S., Lederhendler, I.I., Kirkpatrick, B. (Eds.), The Integrative Neurobiology of Affiliation. The MIT Press, Cambridge, Massachusetts, pp. 131–140.
Graham, K.L., Burghardt, G.M., 2010. Current perspectives on the biological study of play: signs of progress. Q. Rev. Biol. 85, 393–418. https://doi.org/10.1086/656903.
Gray, P., 2009. Play as a foundation for hunter-gatherer social existence. Am. J. Play 1, 476–522.
Gray, P., 2014. Play theory of hunter-gatherer egalitarianism. In: Narvaez, D., Valentino, K., Fuentes, A., McKenna, J.J., Gray, P. (Eds.), Ancestral landscapes in human evolution: Culture, childrearing and social wellbeing. Oxford University Press, New York, pp. 192–215. https://doi.org/10.1093/acprof:oso/9780199964253.003.0014.
Gruber, T., Clay, Z., 2016. A comparison between bonobos and chimpanzees: A review and update. Evol. Anthropol. 25 (5), 239–252. https://doi.org/10.1002/evan.21501.
Hare, B., Melis, A.P., Woods, V., Hastings, S., Wrangham, R., 2007. Tolerance allows bonobos to outperform chimpanzees on a cooperative task. Curr. Biol. 17, 619–623.
Hausberger, M., Fureix, C., Bourjade, M., Wessel-Robert, S., Richard-Yris, M.A., 2012. On the significance of adult play: What does social play tell us about adult horse welfare? Naturwissenschaften 99, 291–302.
Heintz, M.R., Murray, C.M., Markham, A.C., Pusey, A.E., Lonsdorf, E.V., 2017. The relationship between social play and developmental milestones in wild chimpanzees (*Pan troglodytes schweinfurthii*), 10.1002/ajp.22716 Am. J. Prima 79 (12). https://doi.org/10.1002/ajp.22716.
Hinde, R.A., 1976. Interactions, relationships, and social structure. Man 11, 1–17. https://doi.org/10.2307/2800384.
Holekamp, K.E., Benson-Amram, S., 2017. The evolution of intelligence in mammalian carnivores. Interface Focus 7 (3), 20160108. https://doi.org/10.1098/rsfs.2016.0108.
Holekamp, K.E., Sakai, S.T., Lundrigan, B.L., 2007. Social intelligence in the spotted hyena (*Crocuta crocuta*). Philos. Trans. R. Soc. Lond. B 362 (1480), 523–538. https://doi.org/10.1098/rstb.2006.1993.
Isbell, L.A., 1991. Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. Behav. Ecol. 2, 143–155. https://doi.org/10.1093/beheco/2.2.143.
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. https://doi.org/10.1037/0735-7036.115.1.29.
Johnsingh, A.J.T., 1982. Reproductive and social behaviour of the dhole, *Cuon alpinus*. Canidae, J. Zool. 198, 443–463.
Jolly, A., 1967. Breeding synchrony in wild *Lemur catta*. In: Altmann, S.A. (Ed.), Social communication among primates. University of Chicago Press, Chicago, pp. 3–13.
Kavanagh, M., 1978. The social behavior of doucs (*Pygathrix nemaeus nemaeus*) at San Diego Zoo. Primates 19 (1), 101–114.
Konig, B., 1997. Cooperative care of young in mammals. Naturwissenschaften 84, 95–104. https://doi.org/10.1007/s001140050356.
Lewis, K.P., Barton, R.A., 2004. Playing for keeps: Evolutionary relationships between social play and the cerebellum in nonhuman primates. Hum. Nat. 15 (1), 5–21. https://doi.org/10.1007/s12110-004-1001-0.
Lewis, K.P., Barton, R.A., 2006. Amygdala size and hypothalamus size predict social play frequency in nonhuman primates: a comparative analysis using independent contrasts. J. Comp. Psychol. 120 (1), 31–37. https://doi.org/10.1037/0735-7036.120.1.31.
Lewis, M., 2000. The emergence of human emotions. In: Lewis, M., Haviland-Jones, J.M. (Eds.), Handbook of Emotions, Second ed. Guilford, New York, pp. 623–636.
Lewis, R.J., Bueno, G.L., Di Fiore, A., 2022. Variation in female leverage: the influence of kinship and market effects on the extent of female power over males in Verreaux's sifaka. Front. Ecol. Evol. https://doi.org/10.3389/fevo.2022.851880.
Lewis Graham, K., 2011. Coevolutionary relationships between striatum size and social play in nonhuman primates. Am. J. Primatol. 73, 314–322. https://doi.org/10.1002/ajp.20898.
Liao, Z., Sosa, S., Wu, C., Zhang, P., 2018. The influence of age on wild rhesus macaques' affiliative social interactions. Am. J. Prima 80 (2). https://doi.org/10.1002/ajp.22733.
Lira, P., Moretti, C., Guimarães, D., Resende, B., 2021. Group cohesiveness in children free-play activity: a social network analysis. Int. J. Psychol. 56 (6), 941–950. https://doi.org/10.1002/ijop.12777.
Liu, C.C., Chen, S.W., Wei, Q.B., Sun, B.H., Wang, X., Xia, D.P., 2022. Effects of mother's dominance hierarchy on the development of social relationships among immature Tibetan macaques. Animals 12, 904. https://doi.org/10.3390/ani12070904.
Maddock, A.H., Mills, M.G.L., 1994. Population characteristics of African wild dogs *Lycaon pictus* in the eastern Transvaal lowveld, South Africa, as revealed through photographic records. Biol. Conserv. 67, 57–62.
Malcolm, J.R., Marten, K., 1982. Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). Behav. Ecol. Sociobiol. 10, 1–13. https://doi.org/10.1007/BF00296390.
Mann, J., 2006. Establishing trust: Socio-sexual behaviour and the development of male-male bonds among Indian Ocean bottlenose dolphins. In: Sommer, V., Vasey, P.L. (Eds.), Homo-sexual behaviour in animals: An evolutionary perspective. XX. Cambridge University Press, pp. 107–130.
Mayhew, J.A., Funkhouser, J.A., Wright, K.R., 2020. Considering social play in primates: a case study in juvenile Tibetan macaques (Macaca thibetana). In: Li, JH., Sun, L., Kappeler, P. (eds), The Behavioral Ecology of the Tibetan Macaque. Fascinating Life Sciences Series. Cham (Switzerland): Springer. https://doi.org/10.1007/978-3-030–27920-2_6.
McKinney, M.L., 1998. The juvenilized ape myth — our 'overdeveloped' brain. BioScience 48, 109–116.
McNutt, J.W., 1996. Sex-biased dispersal in African wild dogs, *Lycaon pictus*. Anim. Behav. 52, 1067–1077. https://doi.org/10.1006/anbe.1996.0254.
Mills, M.G.L., 1994. Kalahari Hyenas. Comparative Behavioral Ecology of Two Species. London (UK): Chapman & Hall.
Nolfo, A.P., Casetta, G., Palagi, E., 2021. Play fighting in wild spotted hyenas: like a bridge over the troubled water of a hierarchical society. Anim. Behav. 180, 363–373. https://doi.org/10.1016/j.anbehav.2021.07.012.
Nolfo, A.P., Casetta, G., Palagi, E., 2022. Visual communication in social play of a hierarchical carnivore species: the case of wild spotted hyenas. Curr. Zool. 68(4), 411–422. zoab076. https://doi.org/10.1093/cz/zoab076.
Norscia, I., Palagi, E., 2011. When play is a family business: adult play, hierarchy, and possible stress reduction in common marmosets. Primates 52, 101–104. https://doi.org/10.1007/s10329-010-0228-0.
Norscia, I., Palagi, E., 2015. The socio-matrix reloaded: from hierarchy to dominance profile in wild lemurs. PeerJ 3, e729. https://doi.org/10.7717/peerj.729.
Oltvai, Z.N., Barabási, A.L., 2002. Life's complexity pyramid. Science 298, 763–764. https://doi.org/10.1126/science.1078563.
Palagi, E., 2006. Social play in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): Implications for natural social systems and inter-individual relationships. Am. J. Phys. Anthropol. 129, 418–426. https://doi.org/10.1002/ajpa.20289.
Palagi, E., 2008. Sharing the motivation to play: the use of signals in adult bonobos. Anim. Behav. 75, 887–896. https://doi.org/10.1016/j.anbehav.2007.07.016.
Palagi, E., 2009. Adult play fighting and potential role of tail signals in ringtailed lemurs (*Lemur catta*.). J. Comp. Psychol. 123, 1–9. https://doi.org/10.1037/0735-7036.123.1.1.
Palagi, E., 2014. A view from biology – playing alone and with others: a lesson from animals. In: Coplan, R.J., Bowker, J.C. (Eds.), The Handbook of Solitude – Psychological Perspectives on Social Isolation, Social Withdrawal, and being Alone. Wiley Blackwell, Malden, pp. 463–482.
Palagi, E., 2018. *Not just for fun*! Social play as a springboard for adult social competence in human and non-human primates. Behav. Ecol. Sociobiol. 72, 90. https://doi.org/10.1007/s00265-018-2506-6.
Palagi, E., Cordoni, G., 2012. The right time to happen: play developmental divergence in the two *Pan* species. PLoS ONE 7 (12), e52767. https://doi.org/10.1371/journal.pone.0052767.
Palagi, E., Paoli, T., 2007. Play in adult bonobos (*Pan paniscus*): modality and potential meaning. Am. J. Phys. Anthropol. 134 (2), 219–225. https://doi.org/10.1002/ajpa.20657.
Palagi, E., Pellis S.M., 2022. Play behavior: a comparative perspective. In: Ridley, A.R., d'Ettorre, P., Freeberg, T.M. (Eds.), Routledge Handbook of Comparative Psychology. New York (US): Routledge Francis and Taylor Group. pp. 202–212.
Palagi, E., Paoli, T., Borgognini Tarli, S.M., 2004. Reconciliation and consolation in captive bonobos (*Pan paniscus*). Am. J. Prima 62, 15–30. https://doi.org/10.1002/ajp.20000.

Palagi, E., Paoli, T., Borgognini Tarli, S., 2006. Short-term benefits of play behavior and conflict prevention in *Pan paniscus*. Int. J. Prima 27, 1257–1270. https://doi.org/10.1007/s10764-006-9071-y.

Palagi, E., Burghardt, G.M., Smuts, B., Cordoni, G., Dall'Olio, S., Fouts, H.N., Řeháková-Petrů, M., Siviy, S.M., Pellis, S.M., 2016. Rough-and-tumble play as a window on animal communication. Biol. Rev. 91, 311–327. https://doi.org/10.1111/brv.12172.

Palagi, E., Bertini, M., Annicchiarico, G., Cordoni, G., 2020. Mirror replication of sexual facial expressions increases the probability of successful sexual contacts in bonobos. Sci. Rep. 10, 18979. https://doi.org/10.1038/s41598-020-75790-3.

Pallante, V., Stanyon, R., Palagi, E., 2016. Agonistic support towards victims buffers aggression in geladas (*Theropithecus gelada*). Behaviour 153, 1217–1243.

Paquette, D., 1994. Fighting and playfighting in captive adolescent chimpanzees. Aggr. Behav. 20, 49–65. https://doi.org/10.1002/1098-2337.

Pasquaretta, C., Levé, M., Claidière, N., van de Waal, E., Whiten, A., et al., 2014. Social networks in primates: smart and tolerant species have more efficient networks. Sci. Rep. 4, 7600. https://doi.org/10.1038/srep07600.

Paulos, R.D., Trone, M., Kuczaj, S.A., 2010. Play in wild and captive cetaceans. Int. J. Comp. Psychol. 23, 701–722.

Pellegrini, A.D. (Ed.), 2010. The Role of Play in Human Development. Oxford University Press, New York. https://doi.org/10.1093/acprof:oso/9780195367324.003.0007.

Pellis, S.M., Burghardt, G.M., 2017. Play and exploration. In: Call, J. (Ed.), APA Handbook of Comparative Psychology: Vol 1. Concepts, History, and Methods, edited by. Washington, DC: American Psychological Association, pp. 699- 722.

Pellis, S.M., Iwaniuk, A.N., 1999. The problem of adult play-fighting: a comparative analysis of play and courtship in primates. Ethology 105, 783–806. https://doi.org/10.1046/j.1439-0310.1999.00457.x.

Pellis, S.M., Iwaniuk, A.N., 2000. Adult-adult play in primates: comparative analyses of its origin, distribution and evolution. Ethology 106, 1083–1104. https://doi.org/10.1046/j.1439-0310.2000.00627.x.

Pellis, S.M., Iwaniuk, A.N., 2002. Brain system size and adult-adult play in primates: a comparative analysis of the roles of the non-visual neocortex and the amygdala. Behav. Brain Res. 134 (1–2), 31–39. https://doi.org/10.1016/s0166-4328(01)00455-7.

Pellis, S.M., Pellis, V.C., 2009. The playful brain: venturing to the limits of neuroscience. Oneworld, Oxford.

Pellis, S.M., Pellis, V.C., Reinhart, C.J., 2010. The evolution of social play. In: Worthman, C.M., Plotsky, P.M., Schechter, D.S., Cummings, C.A. (Eds.) Formative experiences: The interaction of caregiving, culture, and developmental psychobiology. Cambridge: Cambridge University Press, pp. 404–431. https://doi.org/10.1017/CBO9780511711879.037.

Petit, O., Bertrand, F., Thierry, B., 2008. Social play in crested and Japanese macaques: testing the covariation hypothesis. Dev. Psychobiol. 50, 399–407. https://doi.org/10.1002/dev.20305.

Reinhart, C., Pellis, V.C., Thierry, B., Gauthier, C., VanderLaan, D.P., Vasey, P.L., Pellis, S.M., 2010. Targets and tactics of play fighting: competitive versus cooperative styles of play in Japanese and Tonkean macaques. Int. J. Comp. Psychol. 23, 166–200.

Rilling, J.K., Scholz, J., Preuss, T.M., Glasser, M.F., Errangi, B.K., Behrens, T.E., 2012. Differences between chimpanzees and bonobos in neural systems supporting social cognition. Soc. Cogn. Affect. Neurosci. 7 (4), 369–379. https://doi.org/10.1093/scan/nsr017.

Rosati, A.G., Hare, B., 2012. Chimpanzees and bonobos exhibit divergent spatial memory development. Dev. Sci. 15 (6), 840–853, 10.1111/j.1467-7687.2012.01182.x.PMID: 23106738.

Russon, A.E., Vasey, P.L., 2012. Eye-covering play in Japanese macaques and orang-utans. In: Leca, J.B., Huffman, M.A., Vasey, P.L. (Eds.), The Monkeys of Stormy Mountain: 60 Years of Primatological Research on the Japanese Macaques of Arashiyama. University of Cambridge Press, Cambridge, pp. 293–302.

Sadoughi, B., Lacroix, L., Berbesque, C., Meunier, H., Lehmann, J., 2021. Effects of social tolerance on stress: hair cortisol concentrations in the tolerant Tonkean macaques (*Macaca tonkeana*) and the despotic long-tailed macaques (*Macaca fascicularis*). Stress 24 (6), 1033–1041. https://doi.org/10.1080/10253890.2021.1998443.

de Saint Exupery, A., 1999. Le Petit Prince. Éditions Gallimard, Paris.

Samuni, L., Langergraber, K.E., Surbeck, M.H., 2022. Characterization of *Pan* social systems reveals in-group/out-group distinction and out-group tolerance in bonobos. e2201122119 Proc. Natl. Acad. Sci. Usa. 119 (26). https://doi.org/10.1073/pnas.2201122119.

Schank, J.C., Burghardt, G.M., Pellis, S.M., 2018. Toward a theory of the evolution of fair play. Front. Psychol. 9, 1167. https://doi.org/10.3389/fpsyg.2018.01167.

Scopa, C., Palagi, E., 2016. Mimic me while playing! Social tolerance and rapid facial mimicry in macaques (*Macaca tonkeana* and *Macaca fuscata*.). J. Comp. Psychol. 130 (2), 153–161. https://doi.org/10.1037/com0000028.

Smith, J.E., Memenis, S.K., Holekamp, K.E., 2007. Rank-related partner choice in the fissionefusion society of the spotted hyena (*Crocuta crocuta*). Behav. Ecol. Sociobiol. 61, 753–765. https://doi.org/10.1007/s00265-006-0305-y.

Špinka, M., Newberry, R.C., Bekoff, M., 2001. Mammalian play: training for the unexpected. Q. Rev. Biol. 76, 141–168. https://doi.org/10.1086/393866.

Springer, M.S., Murphy, W.J., Eizirik, E., O'Brien, S., 2003. Placental mammal diversification and the Cretaceous-Tertiary boundary. Proc. Natl. Acad. Sci. USA 100, 1056–1061. https://doi.org/10.1073/pnas.0334222100.

Stimpson, C.D., Barger, N., Taglialatela, J.P., Gendron-Fitzpatrick, A., Hof, P.R., Hopkins, W.D., Sherwood, C.C., 2016. Differential serotonergic innervation of the amygdala in bonobos and chimpanzees. Soc. Cogn. Affect. Neurosci. 11 (3), 413–422. https://doi.org/10.1093/scan/nsv128.

Sueur, C., Petit, O., De Marco, A., Jacobs, A.T., Watanabe, K., Thierry, B., 2011. A comparative network analysis of social style in macaques. Anim. Behav. 82 (4), 845–852. https://doi.org/10.1016/j.anbehav.2011.07.020.

Tan, J., Ariely, D., Hare, B., 2017. Bonobos respond prosocially toward members of other groups. Sci. Rep. 7 (1), 14733. https://doi.org/10.1038/s41598-017-15320-w.

Tanner, J.B., Smale, L., Holekamp, K.E., 2007. Ontogenetic variation in the play behavior of spotted hyenas (*Crocuta crocuta*). J. Dev. Proc. 2, 5–30.

Thierry, B., 2000. Covariation of conflict management patterns across macaque species. In: Aureli, F., de Waal, F.B.M. (Eds.), Natural Conflict Resolution. University of California Press, Berkeley, pp. 106–128.

Thierry, B., 2004. Social epigenesis. In: Thierry, B., Singh, M., Kaumanns, W. (Eds.), Macaque Societies. Cambridge University Press, Cambridge, pp. 267–290.

Thierry, B., 2007. Unity in diversity: lessons from macaque societies. Evol. Anthropol. 16, 224–238. https://doi.org/10.1002/evan.20147.

Thierry, B., Berman, C., 2010. Variation in kin bias: species differences and time constraints in macaques. Behaviour 147, 1863–1887. https://doi.org/10.1163/000579510X539691.

van Lawick, H., Goodall, J., 1970. Innocent killers. Houghton Mifflin Harcourt, New York.

van Lawick-Goodall, J., 1968. The behaviour of free-living chimpanzees in the Gombe Stream Reserve. Anim. Behav. Monogr. 1, 161–311. https://doi.org/10.1016/S0066-1856(68)80003-2.

Vehrencamp, S.L., 1983. A model for the evolution of despotic versus egalitarian societies. Anim. Behav. 31 (3), 667–682. https://doi.org/10.1016/S0003-3472(83)80222-X.

de Villiers, M.S., Richardson, P.R.K., van Jaarsveld, A.S., 2003. Patterns of coalition formation and spatial association in a social carnivore, the African wild dog (*Lycaon pictus*.). J. Zool. Lond. 260, 377–389. https://doi.org/10.1017/S0952836903003832.

Vullioud, C., Davidian, E., Wachter, B., Rousset, F., Courtiol, A., Honer, O.P., 2019. Social support drives female dominance in the spotted hyaena. Nat. Ecol. Evol. 3, 71–76. https://doi.org/10.1038/s41559-018-0718-9.

de Waal, F.B.M., 1986. The integration of dominance and social bonding in primates. Q. Rev. Biol. 61 (4), 459–479.

de Waal, F.B.M., 1988. The communicative repertoire of captive bonobos (*Pan paniscus*), compared to that of chimpanzees. Behaviour 106, 183–251.

de Waal, F.B.M., Johanowicz, D.L., 1993. Modification of reconciliation behavior through social experience: an experiment with two macaque species. Child Dev. 64 (3), 897–908.

Animal Social Complexity. Intelligence. In: de Waal, F.B.M., Tyack, P.L. (Eds.), 2003. Culture, and Individualized Societies. Cambridge, M.A. Harvard University Press, p. 640.

Wobber, V., Wrangham, R., Hare, B., 2010a. Bonobos exhibit delayed development of social behavior and cognition relative to chimpanzees. Curr. Biol. 20 (3), 226–230. https://doi.org/10.1016/j.cub.2009.11.070.

Wobber, V., Hare, B., Maboto, J., Lipson, S., Wrangham, R., Ellison, P.T., 2010b. Differential changes in steroid hormones before competition in bonobos and chimpanzees. Proc. Natl. Acad. Sci. U. S. A 107, 12457–12462. https://doi.org/10.1073/pnas.1007411107.

Wooddell, L.J., Kaburu, S.S.K., Dettmer, A.M., 2021. Behavioral and hormonal changes following social instability in young rhesus macaques (*Macaca mulatta*). J. Comp. Psychol. 135 (4), 568–580. https://doi.org/10.1037/com0000297.

Woodroffe, R., Rabaiotti, D., Ngatia, D.K., Smallwood, T.R.C., Strebel, S., O'Neill, H.M.K., 2020. Dispersal behaviour of African wild dogs in Kenya. Afr. J. Ecol. 58 (1), 46–57. https://doi.org/10.1111/aje.12689.

Wrangham, R.W., 2018. Two types of aggression in human evolution. Proc. Natl. Acad. Sci. USA 115, 245–253. https://doi.org/10.1073/pnas.1713611115.