LET'S UNITE IN PLAY! PLAY MODALITY AND GROUP MEMBERSHIP IN WILD GELADAS

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ABSTRACT

Two of the main hypotheses put forth to explain the function of immature social play are the *Social Skill Hypothesis* and the *Motor Training Hypothesis* focussing on whether play can improve social competence to develop cooperative social networks or physical abilities to outcompete others, respectively. Here, we tested these hypotheses on a monkey species, the wild gelada (*Theropithecus gelada*) from the Kundi plateau, Ethiopia. This species is organized in bands divided in One-Male Units (OMUs), united only via social play. Immatures form 'play units' in which individuals from the same and different OMUs interact. We analysed the potential differences between inter- and intra-OMU play to verify which of the two hypotheses (*Social Skill* or *Motor Training Hypothesis*) best explains the function of play in geladas. We analysed 527 video-recorded social play sessions and found mixed support for both hypotheses. In agreement with the *Social Skill Hypothesis*, we found that play in geladas shows scarce social canalization being similarly distributed across age, sex and group membership. In line with the *Motor Training Hypothesis*, we detected higher levels of competition (shorter and more unbalanced sessions) in inter-OMU compared to intra-OMU play. Hence, in geladas play can be a tool for both the development of social relationships and the improvement of the physical skills necessary to cope with either future mates or competitors. In conclusion, neither hypothesis can be discarded and both hypotheses concur in explaining why immature geladas peculiarly form 'play units' embracing both ingroup and outgroup members.

Key Words:

Motor Training Hypothesis; Play asymmetry index; Play session length; Play units; *Social Skill Hypothesis*; *Theropithecus gelada*

1. Introduction

Play is one of the most puzzling behaviours whose definition has challenged many different scholars (Burghardt, 2005; Palagi et al., 2016a). One of the most comprehensive and recent definitions describes play as a behaviour which is voluntary, autotelic and uninhibited. Moreover, play is: i) not functional in the context in which it occurs, ii) structurally or temporally modified compared to other behaviours, and iii) initiated in a relaxed context (Burghardt, 2005).

Play is present in a limited number of avian taxa (e.g., corvids) and in many mammalian taxa such as carnivores, rodents, cetaceans, and primates (Burghardt, 2005; Hill et al., 2017; Palagi et al., 2016a). From an ontogenetic viewpoint, play tends to increase at the end of infancy, reaches peak values in the middle of the juvenile period, and tends to decrease during the last months of the juvenile phase, thus showing the typical bell-shape distribution curve (Fagen, 1981, 1994; Mendoza-Granados and Sommer, 1995; Pellegrini, 2009; Pellis and Pellis, 2009). In some species, play can also be frequently performed during adulthood (Asian small-clawed otters, *Anonyx cinereal,* Allison et al., 2020, Pellis, 1991; wolves, *Canis lupus lupus*, Cordoni and Palagi, 2016; dogs, *Canis lupus familiaris*, Cordoni et al., 2016; macaques, *Macaca* sp., Ciani et al., 2012, Nahallage and Huffman, 2007, Nahallage et al., 2016; bonobos, *Pan paniscus*, Palagi, 2006; humans, *Homo sapiens*, Gray, 2009). According to the diverse phases of life in which it occurs, play can provide several important short- and long-term benefits to the subjects (Berghaenel et al., 2015; Fagen and Fagen, 2004; Graham and Burghardt, 2010).

At a short-term level, play can have a role in modulating social relationships by favouring social assessment (*Social Skill Hypothesis*, Palagi, 2007; Pellis, 2002; Pellis and Iwaniuk, 2000; Thompson, 1998), reduce individual mild anxiety under social tension conditions (Hausberger et al., 2012; Norscia and Palagi, 2010; Palagi et al., 2004, 2006), and reduce xenophobic reactions to unpredictable situations (Antonacci et al., 2011).

In the long-term play promotes the establishment of social relationships, tolerance, and cohesion in the group. For this reason, play pervasiveness can be predictive of the level of social tolerance in a given society (Palagi et al., 2016b). At an individual level, by playing immature animals can acquire and test their own competence to manage social relationships with fellows (*Social Skill Hypothesis*, Bekoff and Pierce, 2009; Biben, 1998; Cordoni and Palagi, 2012; Loizos, 1967; Pellis and Iwaniuk, 2000, Pellis et al., 2010; Smith et al., 1999; Zahavi, 1977; Zahavi et al., 2004) and expand the necessary behavioural flexibility to cope with future unexpected situations (Špinka et al., 2001). In this case, play benefits go beyond the reinforcement of intrinsic abilities (e.g., endurance, strength, cardiovascular capacity, muscle system). Play fighting occurring between unrelated and unfamiliar conspecifics can fall into this social-oriented category (Mancini and Palagi, 2009) with being play a sort of "gate" to access social environment (Barnett, 1990; Bekoff, 1972; Heintz et al., 2017; Palagi, 2018). Moving from the social to the intrinsic individual abilities, by playing animals can also improve their own motor skills and assess those of others (*Motor Training hypothesis*, Bekoff and Byers, 1981; Bekoff and Pierce, 2009; Brownlee, 1954; Byers and Walker, 1995; Caro, 1988; Miller and Byers, 1991; Nunes et al., 2004b). The *Motor Training Hypothesis* predicts that social play can have important implications in favouring both physical and motor development which are abilities useful to animals that will have to compete in the future (Byers, 1998; Byers and Walker, 1995; Cordoni and Palagi, 2012). Play fighting, one of the most pervasive forms of play, can provide benefits to immature subjects such as developing endurance, control of body actions, and/or perceptual-motor integration (Nunes et al., 2004a). Polar bears engage in play fighting to improve their physical skills and assess the strength of conspecifics (*Thalarctos maritimus*, Latour, 1981). In human adolescents, Pellegrini (1995) found that play fighting was positively correlated with agonistic interactions and negatively correlated with social preference. The authors suggested that play fighting can be a good training to gather information on partner's skills that will be used in the future to gain advantages during real confrontations (Pellegrini, 1995).

Whether play can improve social and/or physical abilities can be predicted by the modality in which the behaviour is expressed (Smuts, 2014). Play fighting includes motor patterns that are characteristic of real fighting with the exception that the actions are modified (e.g., inhibited, mixed in their sequence) to maintain a playful mood (see Palagi et al., 2016a for an extensive review). For play fighting to occur, the subjects need to give each other the possibility to counterattack (Bekoff, 2001; Pellis and Pellis, 1998, 2009, 2017). Animals can engage in "dominant" (advantage positions/actions) and/or "subordinate" (disadvantage positions/actions) patterns to maintain an equilibrium and avoid dangerous escalation into real fighting. The active inhibition of arousal and roughness enacted by stronger individuals (self-handicapping) leads to more symmetric interactions thus increasing the probability that play sessions last longer (squirrel monkeys, *Saimiri sciureus*, Biben, 1998; hamadryas, *Papio hamadryas hamadryas*, Pereira and Preisser, 1998; rats, *Rattus norvegicus*, Pellis and Pellis, 2009). Play asymmetry and playmate selection can be influenced by several factors such as the level of tolerance of a species (Bekoff and Pierce, 2009; Ciani et al., 2012; Maglieri et al., 2020; Reinhart et al., 2010), the sex and age of the players (Bibien, 2010; Fagen, 1981; Paquette, 1994; Pellis and Pellis, 2009; Rothstein and Griswold, 1991; Smith et al., 1999; Ward et al., 2008; Watson and Croft, 1996), the social contexts (Palagi et al., 2007; Pereira and Preisser, 1998; Tacconi and Palagi, 2010) and the level of knowledge between players (Cordoni and Palagi, 2016; Panksepp, 1981; Ward et al., 2008). Hence, play fighting is the result of a sophisticated balancing between two different components: the motivation to compete to gain information on the partner physical abilities, and to cooperate to gain information on the willingness of the partner to establish a social relationship.

The gelada (*Theropithecus gelada)*, a primate species endemic to Ethiopia (Gippoliti et al., 2019), is a good model to test specific hypotheses about potential functions of immature social play by analysing its modality according to the different level of knowledge between players. Geladas live in a multilevel system whose basic unit is the one-male unit (OMU) including one adult male, several reproductive females and their offspring (Dunbar and Dunbar, 1975). The other basic units are the so-called All-Male Units (AMU) which include sub-adult and young adult males. OMUs and AMUs can spatially associate and form bands which share the home-range (Dunbar and Dunbar, 1975; Snyder-Mackler et al., 2012). The social integrity of the OMU is not maintained by the aggressive herding of male, as it occurs in some despotic species (i.e. hamadryas baboons, Kummer, 1968), but by the strong social affiliation and tolerance among the individuals of the units (Dunbar and Dunbar, 1975).

Despite the spatial proximity, the only positive interaction occurring between different OMUs is play fighting (Dunbar and Dunbar, 1975). The immature subjects of diverse OMUs can join and play together forming so-called "play units" whose formation is fluid not always including the same subjects (Dunbar and Dunbar, 1975; Palagi and Mancini, 2009). The formation of the "play units" makes the species unique to opportunistically conduct a "naturalistic experiment" and test the *Social Skill* and the *Motor Training Hypotheses* leading to alternative predictions.

1.1. Social Skill Hypothesis

According to the *Social Skill Hypothesis*, play improves social competence by helping establish social relationships among individuals that are likely to socially interact with each other in the future (Baldwin and Baldwin, 1974; Bekoff, 1974; Fagen, 1981; Holmes, 1994, 1995; Maestripieri and Ross, 2004; Palagi, 2006). The hypothesis states that play has a role in testing one's own and others' social roles and improving communication skills that contribute to current survival (Burghardt, 2005; Dugatkin and Bekoff, 2003; Palagi and Paoli, 2007; Palagi et al., 2004; Palagi et al., 2006; Spinka et al., 2001). Since the immature geladas have to cope with social interactions both at intra- and inter-group level, their social benefits can be maximized when they engage in play fighting with other conspecifics, independently from their group membership. In this view, we expect to find no difference in the distribution of play between inter- and intra-OMUs (Prediction 1a).

Due to the cooperative nature of play predicted by the *Social Skill Hypothesis*, we expect that inter- and intra-OMU play sessions are characterized by similar asymmetry and duration (Prediction 1b).

In geladas both males and females have important social roles in maintaining tolerance, group integrity and cohesion (Palagi et al., 2018; Pallante et al., 2016; Pallante et al., 2019), for this reason they need to test their own social competence by playing with others independently from their sex. Hence, we do not expect difference in the level of asymmetry and duration of the play sessions involving players of different sexes (Prediction 1c). If play is a 'tool' to establish and maintain social relationships by engaging in a cooperative interaction, we do not expect different levels in play asymmetry and duration between either age-matched or age-mismatched dyads (e.g., same or different size) (Prediction 1d).

1.2. Motor Training Hypothesis

In agreement with the *Motor Training Hypothesis,* which predicts that play fighting is a means to physically train in order to cope with competitive situations (Byers and Walker, 1995), we expect that inter-OMU play should be more frequent than intra-OMU play (Prediction 2a). Moreover, due to the less degree of familiarity between playmates of different OMUs, we expect inter-OMU play sessions be more asymmetric and shorter than intra-OMU play (Prediction 2b).

Gender differences in play fighting tend to occur for those species that are characterized by differences between males and females in the relevance of fighting skills for adult roles (Byers, 1980; Fagen, 1993; Maestripieri and Ross, 2004; Power, 2000; Symons, 1978). The male exogamy typical of the gelada society makes it necessary for young males to become aware not only about their own fighting abilities but also about the abilities of males – future competitors - from other OMUs. In this view, we expect that, compared to play sessions involving at least one female, male-male play fighting is characterized by higher levels of competition and asymmetry thus leading to shorter playful interactions (Prediction 2c). Moreover, in agreement with the *Motor Training Hypothesis,* we expect that the dyads formed by players belonging to the same age-class (age-matched dyads), and therefore similar in size, show lower levels of inhibition leading to rougher interactions compared to mixed-age dyads (age-mismatched dyads). The higher level of competition should translate into shorter sessions thus limiting the risk of an escalation due to the competitive modules recruited by players (Prediction 2d).

2. Methods

2.1. The species and the data collection

The study was carried out on a population of geladas living on the Kundi plateau (Wof-Washa area, Amhara region, Ethiopia, N9°40.402’ E39°45.060’) from January to May 2019 covering the dry (February) and early wet season (March-May). Four observers (two authors and two field assistants) collected video-data in the field (Panasonic HC-V180 Full HD optic-zoom 50x, 2csec accuracy): two observers monitored the Northern part of the plateau (about 0.1 km^2), the other two observers collected data in the Southern part of the plateau (about 0.1 km^2). If the gelada groups moved to or were found in the central area of the plateau, the four observers managed their data collection to avoid sampling the same groups. The observers’ location (Nothern versus Southern) changed on a weekly basis following a rotation schedule. At the beginning of our observation period, we spent about one month in characterizing the adult individuals and their OMU membership.

During the data collection, we counted 21 groups and characterized the adult subjects of 14 One-Male Units (OMUs) and two All-Male Units (AMUs) (27 adult males and 79 adult females). The size, sex- and age-ratio of each group size, along with particular signs of the adult male and/or other subjects were the criteria adopted to identify gelada groups. The identification of each single adult was possible thanks to long-lasting distinctive features (including sex, size, permanent scars, deformations, shapes of the red chest area). Although it was not possible to individually identify all the immature subjects, we were able to assign them to a specific age-class thanks to their body size and fur/length colour (Dunbar and Dunbar, 1975). In total, we counted 60 sub-adults, 35 juveniles and 65 infants (31 late infants, 34 early/black infants). The identification of infants was also based on their interaction with their mothers (e.g., lactation, suckling attempts, proximity).

We counted how many immature subjects belonged to each OMU (the mean number subadults per OMU was 4.21 ± 1.89SD, the mean number of juveniles was 2.43 ± 2.06SD, the mean number of late infants was 2.21 ±1.25SD, the mean number of early infants was 1.5 ± 1.02SD and the mean number of black infants was 0.93 ± 1.14SD). The criteria used to assign each immature subject to a specific OMU were i) the social interaction between immature subjects with adults (e.g., lactating, grooming, contact sitting) and ii) the spatial association during collective moving activities (e.g., following) (Dunbar and Dunbar, 1975; Johnson et al., 2014). Early in the morning when the animals climbed up from the sleeping cliffs, the observers recognized each single OMU/AMU by individually identifying the adult subjects and counting the number of immature subjects of different age classes (Snyder-Mackler et al., 2012).

Via instantaneous scan sampling (Altmann, 1974), at 10-min intervals we registered the OMU identity and the number of infants, juveniles and subadults that were present within 50 meters. We video-recorded the activities of the OMUs that were present within such range (the length of the videos ranged from 5 to 20 minutes). When the number of OMUs did not permit to determine the group membership of the players, we prolonged the time of video-registration until the OMU split into single units so that the assignment of each player to a specific OMU was possible *a posteriori*. This filming technique allowed the identification of some subjects on videos when not possible alive. In each pair, one observer managed the camera (cameramen) and the other assisted the cameramen by voice-recording the identity of adult subjects and the OMU and describing the ongoing activities (e.g., presence/absence of playful interactions, proximity of immatures with adult females, social interactions). Hence, each video also included the vocal description of the general activity of subjects, their identity (for adults), group membership/age-class (for immatures).

We collected about 120 hours of videos containing two hours of playful sessions (n=527). Of the total of 527 play sessions recorded, 152 involved males and females, 253 involved only males and 11 only females. For the remaining 109 sessions, it was not possible to determine the sex of the players.

2.2. Video analysis

The video analysis was carried out by using VLC® *media player* with extension *Jump-to-Time*. Each video required two phases of analysis. During the first phase two coders (A.G., M.C.) watched the video at normal speed to check for the presence of social play. In case social play was present, the sessions were counted and analysed frame-by-frame (two-hundredth second accuracy). It was possible that one video contained two or more concurrent playful sessions, in this case the video was analysed several times to quantify the duration and exact sequence of the patterns which the subjects engaged in.

Training was performed by E.P. and ended when the Cohen's values were higher than 0.75 for each behavioural pattern considered in the study (number of play sessions per observer = 10 for a total of about 10 minutes). Since the video analysis was performed by two coders, the observation reliability was checked at a bi-weekly frequency. The observers measured their agreement in the categorization of each behavioural pattern included in the ethogram (Table S1). Each check included at least 10% of the total amount of minutes analysed within 15 days by each observer. For each behavioural pattern defined in Table S1 we obtained Cohen's values never below 0.75.

2.3. Operational definitions

A dyadic playful session began when one subject approached another subject and directed a playful pattern towards him/her and ended when the subject moved away. If after 10 seconds the subject engaged again in another playful session, this session was considered as a new one.

The analyses have been performed on the dyadic playful interactions which included at least three motor patterns. The number of sessions that fulfilled this criterion was 268 out of the 527 play sessions recorded. For each behavioural pattern occurring during a social play session, we recorded the group membership of each player (intra-OMU vs inter-OMU) and its age- and sex-class (when possible), the duration (in seconds) and the exact sequence of the patterns displayed. Those playful sessions (n=56) for which it was not possible to determine the sex of either player, the sex-class was assigned randomly (as per Dunbar and Dunbar, 1975).

To calculate the *Play Asymmetry Index* (PAI), we classified the playful patterns as advantageous and disadvantageous (Bauer and Smuts, 2007; Cordoni et al., 2016; Llamazares-Martín et al., 2017; Palagi et al., 2019; Ward et al., 2008) (Table S1). We calculated the PAI for each session as follows: in a dyad A's "advantage" equalled the number of advantageous play patterns by A directed at B plus the number of disadvantageous play patterns by B directed towards A. B's "advantage" was calculated in the same way. Next, we subtracted B's "advantage" value from A's "advantage" value. The value obtained from this calculation was divided per the total number of patterns forming the sessions (A's advantage + B's advantage + neutral patterns).

The neutral patterns (defined and listed in Table S1) are not directional, therefore, they cannot be attributed to either A or B's advantages. The application of the following formula gives the measure of the degree of asymmetry (Cordoni et al., 2016; Palagi et al., 2014; Ward et al., 2008). The PAI ranges from -1 to 1 and was calculated of each dyadic playful session.

$$\frac{(\text{ADV play patterns A} + \text{DISADV play patterns B}) - (\text{ADV play patterns B} + \text{DISADV play patterns A})}{(\text{ADV play patterns A} + \text{DISADV play patterns B}) + (\text{ADV play patterns B} + \text{DISADV play patterns A}) + \text{NEUTRAL patterns}}$$

2.4. Statistics

To test whether the inter- and intra-OMU play frequency was affected by the number of OMUs present in the range of 50 meters, we defined three different clusters (2-4 OMUs; 5-7 OMUs; > 7 OMUs). For each cluster, we counted how many inter- and intra-OMU sessions occurred. Then, we applied a randomization paired sample t-test to compare the number of inter- and intra-OMU sessions within each cluster. For this comparison we used randomization procedures to take under consideration the pseudo-replication due to the possible non-independence of the data (same individuals involved in more than one session). The randomized paired sample t-test was employed with a number of 10,000 permutations by using the software Resampling Procedures 1.3 (David C. Howell, freeware).

To determine which variables affected the Play Asymmetry Index (PAI) and the Play Duration (PD), we ran multi-model comparisons of Linear Mixed Models (LMM). In both models the random variable was the same (player1*player2) (see Table S2 for the definitions of each variable).

PAI model. In the PAI model, the dependent variable was normally distributed ($p>0.05$, Anderson-Darling, EasyFit 5.5 Professional). The fixed variables included season, sex combination, OMU membership, age combination, LOGduration of the session (for the definition of each variable see Table S2).

PD model. In the PD model, the dependent variable was the logarithmic values of the play duration (seconds) (Normal distribution, Anderson-Darling, ns, EasyFit 5.5 Professional). The fixed factors included season, sex combination, OMU membership, age combination, PAI index (for the definition of each variable see Table S2).

We tested the models involving the fixed factors of interest (Table S2), spanning a null model (only intercept) and a model including all the fixed factors (full model). To select the best model, we used the Akaike's corrected information criterion (AICc). To measure how much better the best model is comparing to the next best models, we calculated the difference (ΔAICc) between the AICc value of the best model and the AICc value for each of the other models. As a coarse guide, models with ΔAICc values less than 2 are considered to be essentially as good as the best model ("substantial", Burnham and Anderson, 2002). Moreover, to assess the relative strength of each candidate model, we employed ΔAICc to calculate the evidence ratio and the Akaike weight (*w*i). The *w*i (ranging from 0 to 1) is the weight of evidence or probability that a given model is the best model, taking into account the data and set of candidate models (Symonds and Moussalli, 2011).

3. Results

3.1. Play frequencies and OMU membership

The randomization paired-sample t-test revealed that the frequency of play between subjects belonging to the same OMU (intra-OMU) or to different OMUs (inter-OMU) did not differ in each of the three conditions analysed: 2-4 OMUs present in the video ($t_{(72)}=0.074$, $p=0.457$; Cohen's $d=0.071$; $\text{mean}_{\text{intra-OMU}}$ 1.863 ± 0.291 SE; $\text{mean}_{\text{inter-OMU}}$ 2.137 ± 0.565 SE), 5-7 OMUs present in the video ($t_{(23)}=-0.962$, $p=0.379$; Cohen's $d=0.327$; $\text{mean}_{\text{intra-OMU}}$ 2.333 ± 0.745 SE; $\text{mean}_{\text{inter-OMU}}$ 1.296 ± 0.436 SE) and >7 OMUs present in the video ($t_{(14)}=-0.076$, $p=0.958$, Cohen's $d= 0.031$; $\text{mean}_{\text{intra-OMU}}$ 2.666 ± 1.240 SE; $\text{mean}_{\text{inter-OMU}}$ 2.866 ± 2.069 SE) (Figure 1) (*Prediction 1a supported*).

3.2. Play modality and OMU membership

3.2.1. Play Asymmetry Index

We conducted a descriptive statistical analysis on Play Asymmetry Index (PAI) to investigate the level of competitive/cooperative balance characterizing the gelada play sessions. The mean PAI value (±SE) was 0.095 ± 0.025. Being this value extremely close to the perfect symmetry represented by the 0 value, the play sessions in this species seem to be characterized by low levels of competition. For the inter-OMU play, the mean value was 0.157 ± 0.038 SE (Figure 2a) and for the intra-OMU play the mean value was 0.047 ± 0.034 SE (Figure 2b).

Due to the diverse PAI values obtained for inter- and intra-OMU play sessions, we applied a LMM analysis to test which variables affected the Play Asymmetry Index (PAI, dependent variable) characterizing each play session (Table 1). We found two competing best models: the first model included the variable *OMU* (AICc = 307.205, *w*i = 0.401) with the probability of 40.01% to be the best model (F=4.389, df_1=1, df_2=266, p=0.037). The second best model (ΔAICc = 0.294) was the null model (AICc = 307.499, *w*i = 0.346) with the 34.6% of probability to be the second best model. In the first model, the variable OMU was significant (p=0.037) (Table 1), with the inter-OMU play scoring higher levels of asymmetry (Figure 3) (*Prediction 2b supported*).

3.2.2. Play duration

We applied a LMM analysis to test which variables affected the Play Duration (PD, dependent variable) characterizing each play session (Table 2). We found two best competing models. The first best model included the variable *OMU* (AICc=258.612, *w*i = 0.380) with the 38.00% of probability to be the first best model (F=8.137, df_1=1, df_2=2.66, p=0.005). The second best model (AICc=259.771, *w*i = 0.210) included the variable ‘OMU’ (F=9.164, df_1=1, df_2=265, p=0.003) and the variable ‘season’ (F=1.917, df_1=1, df_2=265, p=0.167) with the 21.00% of probability to be the second best model. The variable season did not reach the statistical significance. In both models, the variable OMU was always significant (first model, p=0.005; second model, p=0.003) with the intra-OMU play sessions lasting longer than those involving subjects belonging to different OMUs (Table 2, Figure 4) (*Prediction 2b supported*).

4. Discussion

In this study, we tested two main hypotheses on the roles of immature play by exploring this activity in a wild population of geladas. As previously observed by Dunbar and Dunbar (wild population, 1975) and Palagi and Mancini (captive population, 2011), we found that geladas engage in play at a similar frequency independently from the group membership of the playmates and the number of the players available (Figure 1; Table 3) (Prediction 1a supported). This result agrees with the *Social Skill Hypothesis* and underlines not only the importance of the inter-group playful interactions in a multi-level society, but also the high tolerance levels typical of geladas (Snyder-Mackler et al., 2012). The tolerant relationships in play are also evident by the generally low absolute values of Play Asymmetry Index (PAI) calculated for both inter- and intra-OMU playful sessions (Figure 2a-2b). Despite the low competitive elements characterizing play fighting in our groups of immature subjects, we found that OMU membership had an effect on play modality, being the inter-OMU play sessions more asymmetric than the intra-OMU sessions (Prediction 2b supported; Table 3). OMU membership also affected the duration of the play sessions which generally lasted longer between subjects belonging to the same OMU (Prediction 2b supported; Table 3). In agreement with the *Social Skill Hypothesis*, we did not find any effect of the sex and age of the players in either the asymmetry or the duration of the playful sessions (Prediction 1c and 1d supported).

Immature geladas seem to maintain an equilibrium in the engagement of playful interactions with the subjects belonging to their own or different OMUs. The amount of intra- and inter-OMU play sessions did not differ as a function of the availability of players indicated by the number of OMUs present (Figure 1). The formation of "play units" can provide benefits at different levels. By engaging in play with fellows belonging to a different group, immature subjects expand their social network thus developing relationships that can be useful in the future. At a group level, "play units" can increase the levels of tolerance necessary for the band, which represents an "ecological unit" (Snyder-Mackler et al., 2012) whose OMUs need to share the home range while avoiding strong conflicts. The linkage between social tolerance and little discrimination in selecting play mates has been reported for other primate species. In Tonkean macaques (*Macaca tonkeana*) play occurs between related and unrelated individuals at similar rates (Ciani et al., 2012). Fröhlich et al. (2020) found that in orang-utans, infants interact differently with different social partners depending on the interaction type. Behncke (2015) showed that bonobos (*Pan paniscus*) belonging to different communities play together during their encounters in the Congo river basin. e Humans (*Homo sapiens*) living in tolerant hunter-gatherer societies do not select their playmates as a function of sex, age or family membership (Gray, 2009; Lew-Levy et al., 2019). More despotic species, whose relationships are based on strong competition, generally select their playmates following several criteria such as age, sex, group membership and affiliation. For example, in the most despotic species of macaques, immature play occurs almost exclusively between related subjects (*Macaca fuscata*, Ciani et al., 2012; *Macaca mulatta*, Symons, 1978). Also hamadryas baboons (*Papio hamadryas*) show a strong selection of playmates. The highest frequency of play has been recorded between subjects of similar age (Abegglen, 1984) and sharing strong social bonds and high level of familiarity (Lutz et al., 2019). The linkage between playmate selection and despotic social style is also evident outside the primate order. For example, South American sea lions (*Otaria flavescens*), a highly despotic species, are highly selective in their choice of playmates by limiting the number of players with which they interact and by playing frequently with age-matched companions and friends (Llamazares-Martìn et al., 2016).

In agreement with the *Motor Training Hypothesis*, we found that the playful sessions involving subjects of different OMUs were more unbalanced compared to those involving immatures belonging to the same OMU (Figure 3). The highest degree of competition characterizing inter-OMU play suggests that less familiar animals can engage in lower levels of self-handicapping. Less familiar players may use this tactic to assess and develop their own motor abilities in relation to the abilities of future competitors. In the long term, the abilities acquired during competitive play can translate into improved physical skills and motor control during real contests and confrontations which can occur later in life (Byers and Walker, 1995).

The inter-OMU playful interactions were shorter than the intra-OMU ones (Figure 4). This can be a strategy adopted by less familiar subjects to limit the risk of escalation into real fighting. A similar strategy is also present in other mammalian species which tend to shorten the session when it is characterized by higher levels of competition (*Canis lupus familiaris*, Cordoni et al., 2016; *Otaria* *flavescens*, Llamazares-Martìn et al., 2016). This interpretation is also supported by data coming from meerkats (*Suricata suricatta*), a cooperative and highly tolerant social species. In meerkats, subjects sharing weak social bonds engage in shorter playful sessions compared to strongly bonded subjects thus suggesting that the quality of relationship can impact play modality even when the players belong to the same group (Palagi et al., 2019).

In conclusion, the gelada 'play units' have provided the opportunity to test hypotheses on the potential benefits of social play. The absence of any kind of playmate selection reflects the tolerant nature of the species as suggested by the similar amount of inter- and intra-OMU play. Moreover, play in geladas does not seem to suffer social canalization being similarly distributed across age, sex and group membership. These findings are in agreement with the *Social Skill Hypothesis* which predicts that play is a tool at the basis of the development of social relationships, especially in the tolerant species. However, in agreement with the *Motor Training Hypothesis*, the higher levels of competition of the play session characterizing the inter-OMU play indicate that this behaviour can also be a tool to train the physical skills that will be useful to increase the ability to cope with future real competitive situations. As a whole, being that some of our results are in agreement with the *Social Skill Hypothesis* and others with the *Motor Training Hypothesis* (Table 3)*,* it is clear that the two hypotheses are difficult to be disentangled thus suggesting the multiple and interconnected potential benefits of social play in geladas.

Ethical Statement

This study was approved by University of Pisa (Animal Care and Use Board) (Italy), the University of Turin (Italy) and the Ethiopian Wildlife Conservation Authority (EWCA). Since the study was purely observational the committee waived the need for a permit. The study was conducted with no manipulation of animals.

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Declarations of interests

The authors declare that there are no conflicts of interest.

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Table 1

Description of the coefficient values of the two best models explaining the distribution of the Play Asymmetry Index. AICc=Akaike's Corrected Information Criterion. (* $p < 0.05$). OMU=One-Male Unit

MODELS (dependent variable = Play Asymmetry Index)						
Fixed Variables (AICc = 307.205)	***Coefficient***	***Error Deviation***	***t***	***p***	***Confidence Interval (95%)***	
intercept	0.048	0.0347	1.395	0.164	-0.020	0.117
OMU = inter	0.110	0.0524	2.095	0.037	0.007	0.213
OMU[a] = intra	0	-	-	-	-	-
Fixed Variables (AICc = 307.499)						
intercept	0.097	0.0263	3.694	0.000	0.045	0.149

[a] redundant coefficient

Table 2

Description of the coefficient values of the two best models explaining the distribution of the LOGduration variable. AICc=Akaike's Corrected Information Criterion. (* $p < 0.05$). OMU=One-Male Unit. LOGduration= duration of each play session in logarithmic scale.

MODELS (dependent variable = LOGduration)						
Fixed Variables (AICc = 258.612)	***Coefficient***	***Error Deviation***	***t***	***p***	***Confidence Interval (95%)***	
intercept	1.118	0.0324	34.482	0.000	1.054	1.182
OMU = inter	-0.139	0.0486	-2.853	0.005	-0.234	-0.043
OMU[a] = intra	0	-	-	-	-	-
Fixed Variables (AICc = 259.771)						
intercept	1.133	0.0339	33.401	0.000	1.066	1.200
OMU = inter	-0.148	0.0488	-3.027	0.003	-0.244	-0.052
OMU[a] = intra	0	-	-	-	-	-
Season = dry	-0.119	0.0862	-1.385	0.167	-0.289	0.050
Season[a] = early wet	0	-	-	-	-	--

[a] redundant coefficient

Table 3

Scheme of the Hypotheses and Predictions tested in the study (✓= Prediction supported; × = Prediction not supported).

PREDICTION	1. SOCIAL SKILL HP	2. MOTOR TRAINING HP	RESULTS	
a	Similar frequencies between inter- and intra-OMU playmates	Different frequencies between inter- and intra-OMU playmates	1a ✓	2a ×
b	Similar asymmetry and duration between inter- and intra-OMU play	Different asymmetry and duration between inter- and intra-OMU play	1b ×	2b ✓
c	Similar asymmetry and duration between same- and mixed-sex dyads	Different asymmetry and duration between same- and mixed-sex dyads	1c ✓	2c ×
d	Similar asymmetry and duration between age-matched and age-mismatched dyads	Different asymmetry and duration between age-matched and age-mismatched dyads	1d ✓	2d ×

Figures

Fig. 1

Mean (±SE) frequency of inter-OMU (grey bar) and intra-OMU (black bar) play sessions as a function of the three clusters of OMUs considered. Each cluster of OMU is defined as the number of OMUs (2-4; 5-7; >7) present in a range of 50 meters from the play session. The number of clusters is an indirect measure of the different number of possible players that could be involved in play

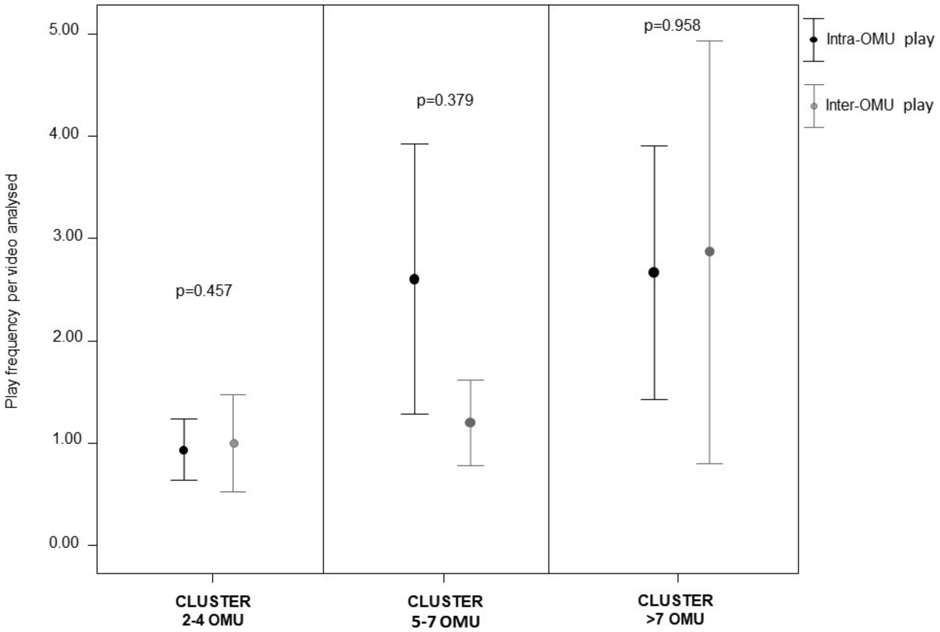

Fig. 2

Mean values of Play Asymmetry Index calculated for each play session categorized in inter-OMU (a) and intra-OMU (b) play conditions. The values range from -1 to 1. The 0 value indicates a completely symmetric play session; while the extreme values (-1 and 1) represent a completely asymmetric play session

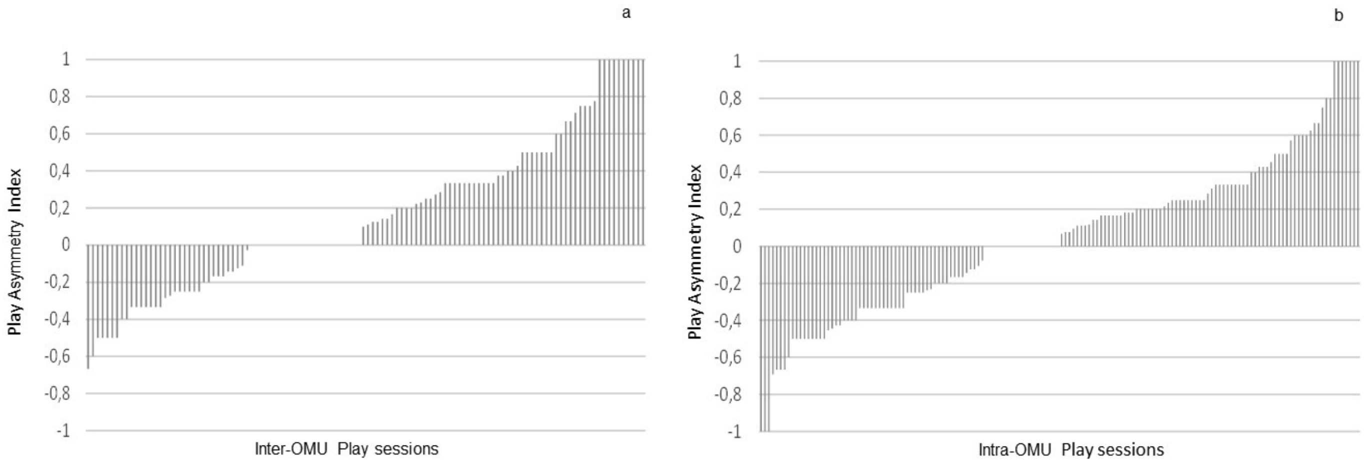

Fig. 3

Mean (±SE) of Play Asymmetry Index characterizing inter-OMU (grey bar) and intra-OMU (black bar) play sessions

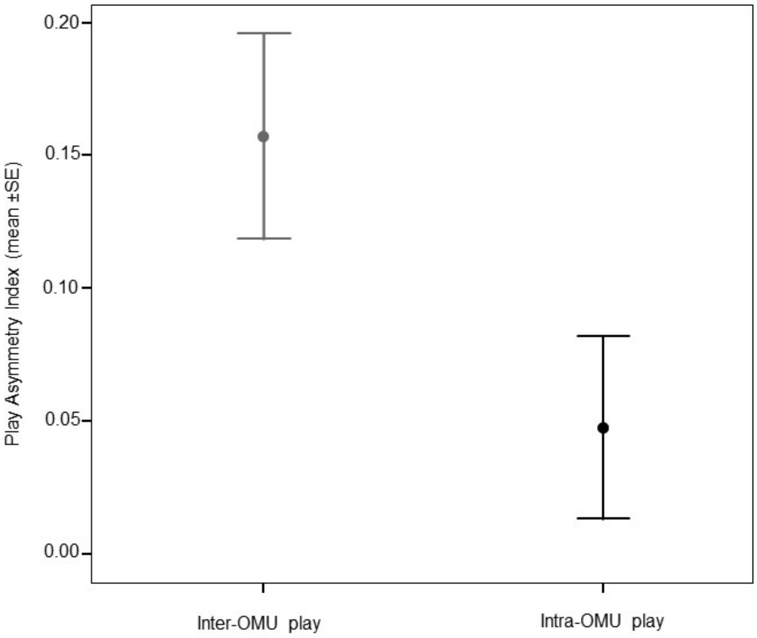

Fig. 4

Mean (±SE) of LOGduration of inter-OMU (grey bar) and intra-OMU (black bar) play sessions