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Fine-tuning of Social Play in Juvenile Lowland Gorillas (*Gorilla gorilla gorilla*)

ABSTRACT: Social play, which involves cooperation, communication, and learning, may represent a suitable field for the investigation of cognitive ability in a given species. We collected data on a captive group of gorillas in order to evaluate the potential cognitive skill of juveniles in fine-tuning play behavior. This study revealed that juvenile gorillas are able to “place” the play session in a proper spatial/temporal context, thus evaluating a complex net of factors (e.g., play partner, play roughness, group activity, space availability). When animals play fight, they use patterns of agonistic functional contexts. Since these actions are not intrinsically different from their “serious” context, it may be hard to distinguish them. One of the most important function of play in the ontogeny of primate social cognition may be to recognize stimuli, which may indicate the intentions of conspecifics. Accordingly, we found that juvenile gorillas are able to use play signals appropriately when a clear statement of purpose is necessary (i.e., during male–male competitive play sessions and when the escape opportunities are limited). The ability to interpret such ambiguous features of social signaling could represent a central issue in the evolution of behavioral flexibility and intelligence in primates. © 2007 Wiley Periodicals, Inc. *Dev Psychobiol* 49: 433–445, 2007.

Keywords: social play; play signals; fine-tuning; play-partner preference; play roughness; prefeeding tension; high-density conditions; cognitive skills; western lowland gorillas; *Gorilla gorilla gorilla*

INTRODUCTION

Play can be defined as all activity that appears to an observer to have no obvious immediate benefits for the performer, but which involves motor patterns typical of serious functional contexts, such as agonistic, anti-predatory, and mating behavior (Bekoff, 2001; Martin & Caro, 1985; Pellis & Pellis, 1996). The difference between playful and serious contexts is not in the actual behavioral patterns performed, but in the way they are performed (Bekoff & Allen, 1998). In fact, there are many aspects in which playful activity differs from the serious functional contents (Fagen, 1981; Loizos, 1967; Martin

& Caro, 1985). During play sessions the sequences of movements have more variable order compared with those of other functional contexts (fragmentation or disordering), the movements are exaggerated, and repeated more often compared to nonplay interactions (absence of inhibition). Moreover, play sequences may lack some components found in nonplay contexts and may be relatively incomplete (e.g., a movement may be started, but not finished) or interrupted by higher-priority behaviors (i.e., anti-predatory behavior) (Fagen, 1981).

Play behavior is a feature of ontogeny in many mammalian species and is widely believed to have an important role in the assembly of adult behavior (Fagen, 1993; Martin & Caro, 1985). The consistence of play within species suggests that it may be critical in the mammalian development and the ubiquitous nature and diversity of play suggest that it may have multiple adaptive roles (Nunes, Muecke, Sanchez, Hoffmeier, & Lancaster, 2004a).

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Play might help to establish social relationships among individuals likely to interact to each other in the future (e.g., *social skill hypothesis*; Baldwin & Baldwin, 1974; Bekoff, 1974; Fagen, 1981; Holmes, 1994, 1995; Maestripieri & Ross, 2004; Palagi, 2006). A variety of effects on physical and motor development have been also hypothesized to result from social play (*motor training hypothesis*; Byers, 1998; Byers & Walker, 1995). For example, motor development related to social play might have immediate benefits to young animals such as providing important physical exercise that develops endurance, control of body movements, and/or perceptual-motor integration (Nunes, Muecke, Lancaster, Miller, Mueller, Muelhaus & Castro, 2004b). Another immediate benefit could include testing social roles and improving communication skills that contribute to current survival in the juvenile stage (Burghardt, 2005; Dugatkin & Bekoff, 2003; Palagi, Cordoni, & Borgognini Tarli, 2004; Palagi, Paoli, & Borgognini Tarli, 2006; Špinka, Newberry, & Bekoff, 2001). Such immediate benefits might be even more evident in play among adult animals, a phenomenon so often neglected in the research on animal play (Palagi, 2006; Pellis & Iwaniuk, 1999).

Whatever are the functions of social play, it is one of the most sophisticated types of social communication (Fagen, 1981, 1993). Recently, Lewis (2000) observed that social play is correlated with the proportion of the brain composed of neocortex in some primates, suggesting that this behavior might be implicated in the development of the social cognition competence typical of many primate species.

Individuals of different species appear to fine-tune ongoing play sequences to maintain a play mood and to prevent play from escalating into real aggressions (Bekoff & Byers, 1998; Power, 2000). In order to let play sessions occur, a recognition of those stimuli that might appear ambiguous is needed (e.g., intentions of other animals). The ability to interpret such ambiguous features of social signaling could represent a central issue in the evolution of behavioral flexibility and intelligence in animals (Bekoff, 1995; Fagen, 1981, 1993; Pellis & Pellis, 1996). In this perspective, investigating whether immature animals are able to finely modulate such activity according to the different social conditions and to the diverse playmate availability could give information on the social cognitive ability and help to hypothesize some possible roles of social play. The goal of this study was to evaluate whether such fine-tuning exists in juvenile lowland gorillas. We focused our attention on juveniles because infants are not yet completely locomotor independent from their mothers. We analyzed the frequency and modality of play according to age and gender of playmates and according to different social contexts (e.g., space availability and food distribution). Moreover, we tried to

assess whether there is a selective design in using play facial displays. To reach these goals we tested the following predictions.

Prediction 1

Research on who plays with whom has demonstrated that, when a choice is available, animals tend to play with partners similar to themselves (see for extensive reviews Fagen, 1993; Power, 2000). In this view, we expect that juvenile gorillas show a strong preference according to the age of the playmate, selecting preferentially those subjects that are close in age.

Prediction 2

A widely held assumption is that gender differences in play behavior are not always found, but tend to occur for those species where there are differences between males and females in the importance of fighting skills for adult roles (Byers, 1980; Fagen, 1993; Maestripieri & Ross, 2004; Power, 2000; Symons, 1978). Gorillas show a strong sexual dimorphism in size and external features (Meder, 1993) and a social system based on male and female dispersal (Harcourt, 1978, 1979; Robbins & Robbins, 2005; Stokes, 2004; Watts, 1990, 1994). Male–male relationships are characterized by strong physical competition and confrontation (Watts, 1996). Relationships among females are ephemeral, with friendly contacts and agonistic support extremely uncommon (Watts, 1994, 1995, 1996).

In this perspective, sex differences in gorilla social play are expected to occur. Specifically, we predict that female–female dyads show lower levels of play compared to male–male and male–female dyads.

Prediction 3

In most species, including primates, the social response to the introduction of food consists almost exclusively of competitive and aggressive behavior (de Waal, 1992). On the contrary, some species respond with a much wider range of social behaviors, including friendly contacts. Several studies showed that the rate of grooming, kissing, embracing, and playing increased drastically when food was introduced into the enclosure (de Waal, 1987, 1989a,b, 1992; Koyama & Dunbar, 1996; Palagi et al., 2004, 2006). The flurry of such friendly contacts has been defined “celebration.” By celebration animals appear to cope actively with competitive tendencies through mechanisms of tension reduction (de Waal, 1987). For example, a comparison of feeding sessions preceded by celebration and sessions with little opportunity to engage in celebration confirmed that sessions preceded by such

phenomenon involved less aggressive contacts (de Waal, 1992).

Therefore, play appears to be involved in the celebration processes used to reduce tension and prevent the escalation of conflict in high excitement contexts (immediate benefits). If gorillas employ a similar strategy, we expect to find a peak level of social play in the prefeeding period.

Prediction 4

Several studies on primates highlighted different kinds of behavioral response to diverse spatial conditions (Judge, 2000). Therefore, the study of the variation in the behavioral response to spatial density can provide very important clues about the role of environmental parameters (both physical and social) in the way that primates manage their social relationships and, ultimately, cope with potentially stressful conditions (Cordoni & Palagi, in press). For instance, under temporary space reduction Aureli and de Waal (1997) found that adult chimpanzees decreased their allogrooming, submissive greeting, and aggressive behavior, on the contrary juvenile social play increased. Accordingly, we predict that juvenile gorillas may increase their social play interactions under spatial reduction.

Prediction 5

The *play face* and the *full play face* are the typical play signals used by primates during social play (Loizos, 1967; Van Lawick-Goodall, 1968). They are often characterized by slightly lowered eyelids, open mouth with lower (play

face) and/or upper teeth (full play face) exposed, although some authors suggest that they can vary markedly among species, and also within the same species (Pellis & Pellis, 1996; van Hooff & Preuschoft, 2003; Waller & Dunbar, 2005). Such meta-communicatory signals give the following messages: “what follows is play” or “I am still playing with you” (Bekoff & Allen, 1998; Pellis & Pellis, 1996). Accordingly, we predict that play facial displays are more frequent when the risk of escalating into a conflict is elevated such as (i) during those play sessions particularly vigorous generally occurring among juvenile males and (ii) during the play sessions occurring when the escape opportunities are limited.

METHODS

The Study Group

We collected behavioral data during a period of four months of observation (May–September 2003) on the group of *Gorilla gorilla gorilla* hosted at the Apenheul Primate Park (Apeldoorn, The Netherlands). The colony was composed by 16 individuals belonging to all age-sex classes (see Tab. 1). The animals were housed in indoor (10 rooms connected by sliding doors) and outdoor (an island surrounded by a boundary ditch of 4–5 m wide) facilities of about 330 m² and 10,000 m², respectively. These environments were equipped with everything necessary for allowing the gorillas to move freely in all three dimensions. The animals were able to avoid each other in both facilities. The group received abundant food (fruits, vegetables, sunflower seeds, pellets, tree branches) four times a day in May and September and five times a day in June, July, and August. The food was often spread out to simulate normal foraging behavior.

Table 1. The *Gorilla gorilla gorilla* Colony Hosted at the Apenheul Primate Park (Apeldoorn, The Netherlands)

Individual	Age and Sex Categories	Date of Birth	Origin and Arrival Date	Observation Time Per Focal Animal (Hours)
Bongo (BO)	Adult male	1973, wild	Cameroon, 1974	45
Lobo (LO)	Adult female	1973, wild	Cameroon, 1975	51
Minta (MI)	Adult female	1974, wild	Cameroon, 1975	50
Mandji (MA)	Adult female	1975, wild	Cameroon, 1975	44
Dalila (DA)	Adult female	1972, wild	Copenhagen-unk, 1991	43
Irala (IR)	Adult female	1985, captivity	Krefeld-3438/1, 1997	45
Uzuri (UZ)	Juvenile male	1994, captivity, MA's son	Apenheul Primate Park	50
Miliki (MK)	Juvenile female	1994, captivity, DA's daughter	Apenheul Primate Park	49
Bibi (BI)	Juvenile female	1997, captivity, LO's daughter	Apenheul Primate Park	47
Kisiwa (KW)	Juvenile female	1997, captivity, DA's daughter	Apenheul Primate Park	45
M'bewe (MB)	Juvenile male	1997, captivity, MI's son	Apenheul Primate Park	47
Kidogo (KI)	Juvenile male	1998, captivity, MA's son	Apenheul Primate Park	48
M'kono (MN)	Juvenile male	1998, captivity, IR's son	Apenheul Primate Park	45
Zoezi (ZO)	Infant female	2000, captivity, LO's daughter	Apenheul Primate Park	40
Nemsi (NE)	Infant female	2001, captivity, MA's daughter	Apenheul Primate Park	38
Gyasi (GY)	Infant female	2002, captivity, DA's daughter	Apenheul Primate Park	38

Data Collection

We followed the gorilla colony recording all play behaviors (see Tab. 2) via sampling methods suggested by Altmann (1974). To evaluate play intensity (rough and gentle play sessions) we used similar parameters applied by Flack, Jeannotte, and de Waal (2004) and Palagi (2006).

By focal animal sampling we recorded also the avoidance behavior (an animal avoids to interact with a conspecific by moving away when the latter is approaching) performed by the animals in the two different conditions of space availability (for definitions see below).

We collected 725 hr of observation by focal animal sampling (108 hr in the indoor facility and 617 hr in the island). Each animal was followed every day and at different times in order to obtain data covering the entire day in balanced proportions as much as possible. Moreover, concomitantly for the whole group, we recorded play sessions by using the scan animal sampling method (5-min interval between subsequent scans) obtaining 378 hr of observation with this technique (4,536 scans for each individual of the group).

Data were collected by speaking into a tape-recorder and the records were subsequently computer-transcribed. Systematic data collection was preceded by a training period (approximately 70 hr) that lasted until the observations by the four observers (three of them were the authors) matched in 95% of cases (Martin & Bateson, 1986).

The observations, carried out both in the indoor and outdoor facilities, took place daily over 6-hr periods, that spanned morning and afternoon, including feeding times after 8.30 a.m. As there were sections of the indoor and outdoor facilities out of sight, we stopped the observation until we could see the focal animal again.

Definition of Prefeeding, Feeding, Postfeeding, and Baseline Conditions

We distinguished four different periods by preliminary observations:

- Prefeeding time (*Pre*): the last 30 min block before food provisioning.
- Feeding time (*Feed*): the 30 min block starting from food provisioning.
- Postfeeding time (*Post*): the 30 min block following feeding time as defined above.
- Baseline (*BI*): the entire time block not included in the period “around food” (*Pre* plus *Feed* plus *Post*).

The parameter for delimiting the three periods linked to feeding activity was the usual time span necessary for complete food consumption (i.e., 30 min).

We were able to collect data on 160 feeding sessions. For prefeeding, feeding, and postfeeding periods we recorded 864, 960, and 780 scans, respectively.

Table 2. Play Behavioral Patterns Recorded during the Observation Sessions

Gentle Play Patterns	
Gentle wrestling	Limbs entwined while sitting or laying; gorillas roll/twist together placing open mouths on each other
Grab gentle	An animal massages gently another
Jump	An animal jumps on object or equipment present in its environment
Play bite	An animal gently bites a playmate
Play manipulation	An animal manipulates and investigates objects found in the environment
Play push	An animal gently pushes a playmate either with its hands or feet
Play slap	An animal slaps any part of a playmate's body
Slide down	An animal slides down from hill, tree or other external equipment
Tickle	The partner's body is contacted either with the mouth or with the hands
Rough Play Patterns	
Acrobatic play	One (solitary play) or more animals (social play) climb, jump and dangle from supports of the environment (e.g. branches)
Pirouetting	An animal turns, somersaults or rolls over either on the ground or on vertical supports
Play brusque rush	An animal jumps with its four limbs on a playmate
Play pull	An animal pulls a playmate
Play recovering a thing	An animal chases a playmate and attempts to grab an object carried by it
Play retrieve	An animal holds a playmate to avoid its flight
Play run	An animal runs alone (solitary play) or chases a play partner (social play)
Play stamping	An animal jumps on a play partner with its feet
Rough and tumble	Two animals (or more) grasp, slap, and bite each other. This pattern is typical of immature individuals
Other Play Patterns	
Chest beating	An animal repetitively strikes the chest or belly area with outstretched or cupped hands (used generally to invite to play)
Full play face	Playful facial display: the mouth is opened with the upper and lower teeth exposed
Play face	Playful facial display: the mouth is opened with only the lower teeth exposed
Play invitation	An animal approaches a possible play partner, pats it and then goes away. This display is used to start a play session

Definition of Crowding Condition

We considered crowding condition as a state during which the space availability for each individual is reduced (Judge, 2000). It is possible to distinguish two different situations: short-term crowding (from a few hours to a few days) and long-term crowding (many years or generation) (Aureli & de Waal, 1997; Caws & Aureli, 2003; de Waal, 1989b).

The gorillas under study were exposed to repeated and predictable periods of reduced space availability (a few hours during night and early morning): this condition does not completely fit either with short-term or with long-term crowding conditions. However, we opportunistically used such temporary change in the daily routine of the management of the group to test the influence of this periodic and peculiar increased spatial density on the gorilla behavioral patterns. We used the data recorded only when all the group-members were closed inside (Cordoni & Palagi, in press).

Data Analysis

Data analysis, carried out on the whole data set, focused mainly on the seven juvenile gorillas (age range: 5–8 years). We considered all the play sessions performed by such juveniles with unrelated group-members: infants (3), other juveniles (6), and adults (6). When the analyses were carried out at the individual level, in order to avoid the bias due to the different number of individuals available for each age-class (i.e., for a juvenile the chance to interact with another juvenile is twice compared to the chance to interact with an infant), all the frequencies recorded were normalized on the number of individuals belonging to the specific age category. These data were subsequently analyzed by nonparametric statistics (Lehner, 1996; Siegel & Castellan, 1988; Zar, 1999). Particularly, the Friedman two-way analysis of variance was used to determine whether several (three or more) samples with blocked measurements or repeated measures on the same individuals were significantly different (i.e., to test for difference in play frequencies across four conditions: Pre, Feed, Post, and BI). When the obtained value of Friedman was significant, in order to determine what pairs of samples differed significantly we used the Dunnett's multiple comparison test suggested by Lehner (1996) and Zar (1999). The Wilcoxon matched-pair signed-ranks test (corrected for ties) (Siegel and Castellan) was employed to assess differences in play rates between two diverse conditions (e.g., indoor and outdoor condition). We made use of exact tests according to the threshold values suggested by Mundry and Fisher (1998). Statistical analyses were performed using Microsoft Excel, SPSS 9.05.

When the analyses were carried out at the dyadic level, we employed randomization tests with a number of 10,000 shuffles to avoid errors due to nonindependence of the data (Manly, 1997). We used the software Resampling Procedures 1.3 by David C. Howell (freeware), that provides a F -value when comparing more than two independent groups and a t -value (difference between the means of the samples, standardized by the standard error) when comparing two independent groups, with the probability to obtain such values under the null hypothesis.

All the analyses were two tailed and the level of significance was set at 5%. Conventional p -values were marked with an asterisk when significant ($p < .05$), a double asterisk ($p < .01$) and a triple asterisk ($p < .001$) when highly significant.

RESULTS

Play Partner Preference According to Age and Sex

The overall individual mean frequencies of play interactions performed by juveniles with peers (JJ), infants (JI), and adults (JA), differed significantly (Friedman $\chi_r^2 = 10.286$, $df = 2$, $N = 7$, $p = .004$).

Pairwise comparisons revealed that juveniles played most with other juveniles (compared with infants, $q = 3.9$, $p = .01$, $n = 7$ and compared with adults, $q = 3.9$, $p = .01$) and juveniles played more with infants than with adults, $q = 3.9$, $p = .01$, $n = 7$ (Fig. 1). The frequency of play invitations did not follow a random distribution according to the age-classes (mean hourly frequency of play invitations JA $.15 \pm .064$ SE, JJ $2.10 \pm .44$ SE, JI

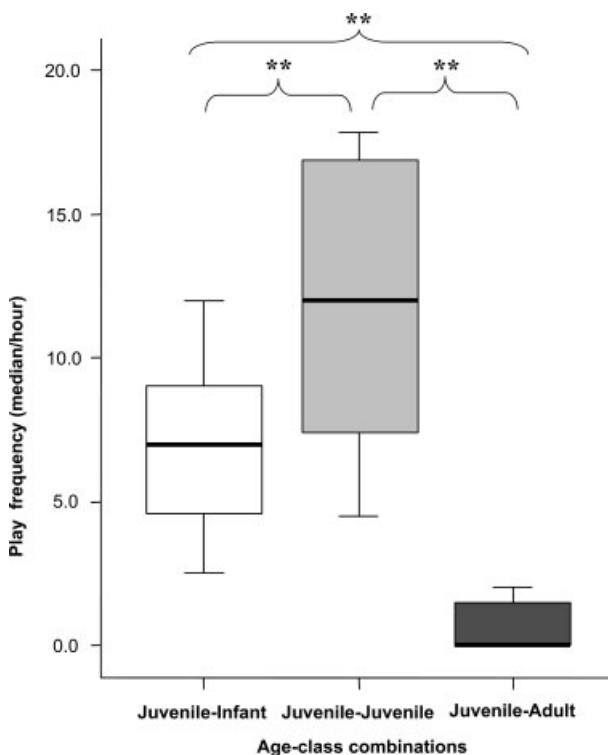


FIGURE 1 Hourly frequency of play interactions performed by juveniles with peers, infants, and adults normalized for the number of individuals available for each age-class. Solid horizontal lines indicate medians; length of the gray boxes corresponds to interquartile range; thin horizontal lines indicate range of the observed values (minimum and maximum). Only significant results are reported.

.28 ± .10 SE; Friedman $\chi_r^2 = 14$, $df = 2$, $N = 7$, $p = .0001$). Moreover, we found that juveniles invited to play more frequently other juveniles compared to the other age-classes (Posthoc tests: JJ vs. JI $q = 4.6$, $p = .01$, $N = 7$; JJ vs. JA $q = 5.29$, $p = .01$, $N = 7$).

The rates of successful play invitations on the total of play invitations performed by juveniles differed across the age-class combinations (mean successful play invitations/total play invitations JA .2 ± .14 SE, JJ .54 ± .04 SE, JI .57 ± .12 SE; Friedman $\chi_r^2 = 5.846$, $df = 2$, $N = 7$, $p = .048$). Posthoc tests revealed that the most frequent unsuccessful play invitation rates occurred between juveniles and adults (JJ vs. JA $q = 4.58$, $p = .01$, $N = 7$; JJ vs. JI $q = .64$, n.s., $N = 7$; JA vs. JI $q = 3.02$, $p = .01$, $N = 7$) (Fig. 2).

Among juvenile gorillas, play frequencies did not follow a random distribution in relation to the partners' sex (randomization ANOVA, one-way: $F = 10.353$, $p = .003$). The randomization test for two independent samples revealed two significant differences: male–male (MM) versus male–female (MF) (MM > MF: $t = 4.174$, $p = .0005$) and MM versus female–female (FF) (MM > FF: $t = 2.515$, $p = .0123$). Particularly, we found no significant difference in the gentle play distribution according to sex (mean hourly frequency: MM .67 ± .15 SE; MF .32 ± .068 SE; FF .33 ± .082 SE;

randomization ANOVA, one-way: $F = 3.530$, n.s.) (Fig. 3a). On the other hand, rough play distribution revealed a statistical significance (mean hourly frequency: MM 1.26 ± .19 SE; MF .40 ± .064 SE; FF .36 ± .076 SE; randomization ANOVA, one-way: $F = 17.62$, $p = .0001$) with higher levels of play among males compared to the other sex-class combinations (FF vs. MF, $t = .36$, n.s.; MF vs. MM $t = 5.408$, $p = .0001$; MM vs. FF, $t = 3.197$, $p = .0113$) (Fig. 3b).

Finally, we analyzed the use of play signals (play face and full play face) in gentle and rough play sessions among juveniles as a function of their sex-combinations. Considering gentle play sessions, we did not find any significant difference (mean of play signals/session: MM .35 ± .09 SE; MF .32 ± .05 SE; FF .37 ± .08 SE; randomization ANOVA, one-way: $F = 1.97$, n.s.). On the contrary, as for rough play sessions we found a statistical difference (mean of play signals/session: MM .76 ± .02 SE; MF .33 ± .06 SE; FF .25 ± .06 SE; randomization ANOVA, one-way: $F = 8.20$, $p = .004$); MM dyads performed higher frequency of play signals compared to MF and FF dyads (MM vs. MF: $t = 3.53$, $p = .005$; MM vs. FF: $t = 6.36$, $p = .01$; MF vs. FF: $t = .62$, n.s.) (Fig. 4).

Play Behavior and the Presence of Food

We analyzed the distribution of play of juveniles with peers, infants, and adults in the four conditions (Prefeeding, Feeding, Postfeeding, and Baseline).

The rates of play that juveniles performed with infants differed significantly across the four periods (Friedman $\chi_r^2 = 7.629$, $df = 3$, $N = 7$, $p = .047$). Pairwise comparisons revealed the following results: Pre vs. Feed $q = 3.3$, $p = .01$, $N = 7$; Pre vs. Post $q = 1.93$, n.s., $N = 7$; Pre vs. Bl $q = 3.02$, $p = .01$, $N = 7$; Feed vs. Post $q = 3.02$, $p = .01$, $N = 7$; Feed vs. Bl $q = 3.48$, $p = .01$, $N = 7$; Post vs. Bl $q = 3.3$, $p = .01$, $N = 7$ (Fig. 5a).

Even for play among juveniles, we found a statistical difference (Friedman $\chi_r^2 = 19.286$, $df = 3$, $N = 7$, $p = .0001$). Posthoc test showed several significant differences: Pre vs. Feed $q = 5.61$, $p = .01$, $N = 7$; Pre vs. Post $q = 4.53$, $p = .01$, $N = 7$; Pre vs. Bl $q = 3.97$, $p = .01$, $N = 7$; Feed vs. Post $q = 5.94$, $p = .01$, $N = 7$; Feed vs. Bl $q = 4.53$, $p = .01$, $N = 7$; Post vs. Bl $q = 1.93$, n.s., $N = 7$ (Fig. 5b).

Finally, also in the juvenile–adult combination we obtained a significant difference (Friedman $\chi_r^2 = 10.385$, $df = 3$, $N = 7$, $p = .009$). Pairwise comparisons revealed the following results: Pre vs. Feed $q = 3.97$, $p = .01$, $N = 7$; Pre vs. Post $q = 3.87$, $p = .01$, $N = 7$; Pre vs. Bl $q = 5.9$, $p = .01$, $N = 7$; Feed vs. Post $q = 2.62$, $p = .05$, $N = 7$; Feed vs. Bl $q = 1.01$, n.s., $N = 7$; Post vs. Bl $q = 2.09$, n.s., $N = 7$ (Fig. 5c).

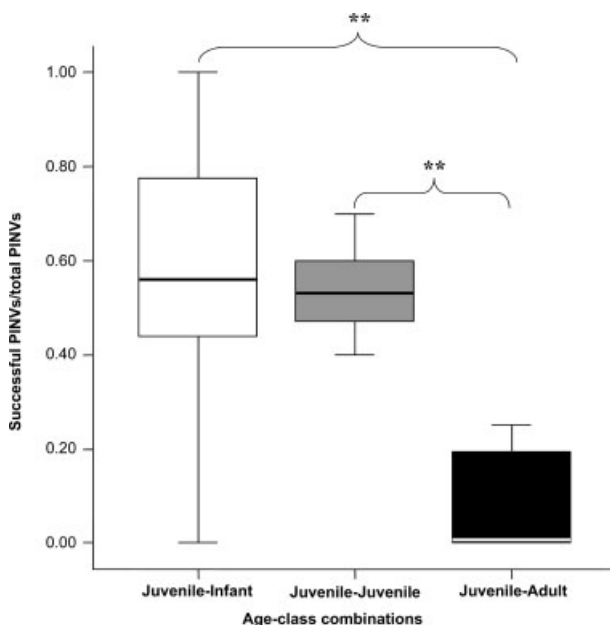


FIGURE 2 The levels of successful play invitations on the total of play invitations performed by juveniles toward peers, infants, and adults normalized for the number of individuals available for each age-class. Solid horizontal lines indicate medians; length of the gray boxes corresponds to interquartile range; thin horizontal lines indicate range of the observed values (minimum and maximum). Only significant results are reported.

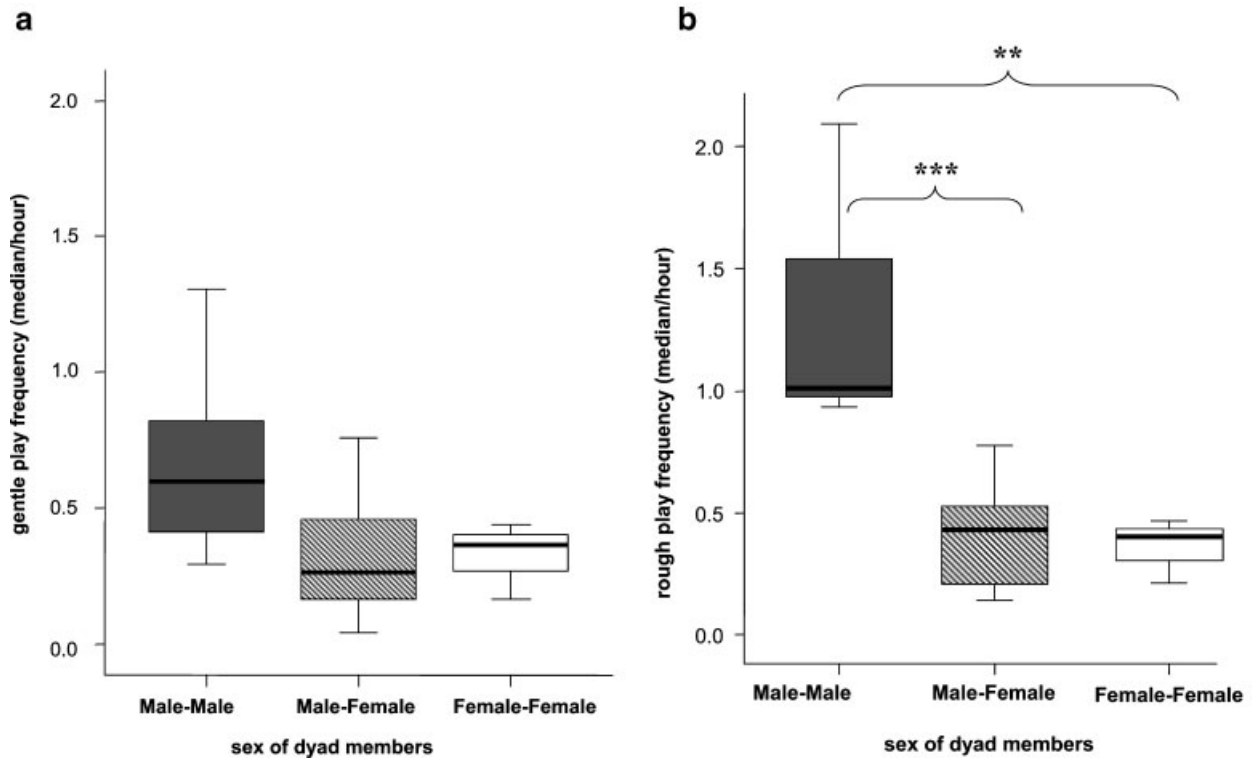


FIGURE 3 The overall level of gentle (a) and rough (b) play among juveniles according to pair-mate sex combinations. Solid horizontal lines indicate medians; length of the gray boxes corresponds to interquartile range; thin horizontal lines indicate range of the observed values (minimum and maximum). Only significant results are reported.

Play Behavior under High-Density Condition

To test for the influence of high-density condition on play behavior we compared the frequency of playful interactions in the indoor and outdoor facilities.

Both for juvenile–infant and juvenile–adult pairs, we found no significant difference in the play rates performed in the two enclosures (JI mean hourly frequency INDOOR $.33 \pm .16$ SE, OUTDOOR $.36 \pm .10$ SE, Wilcoxon's $T = 12$, ties = 0, $N = 7$, n.s.; JA mean hourly frequency INDOOR $.07 \pm .04$ SE, OUTDOOR $.012 \pm .01$ SE, Wilcoxon's $T = 0$, ties = 4, $N = 7$, n.s.) (Fig. 6).

On the other hand, we observed a significant increase of play rates among juveniles in the indoor facility compared to the island (JJ mean hourly frequency INDOOR 13.0 ± 2.60 SE, OUTDOOR $4.36 \pm .84$ SE, Wilcoxon's $T = 0$, ties = 0, $N = 7$, $p = .015$) (Fig. 6).

Furthermore, considering play signals *per* play session, we found that these facial displays were performed to a greater extent in the indoor facility (JJ mean play signals/session INDOOR $.30 \pm .05$ SE, OUTDOOR $.16 \pm .03$ SE, Wilcoxon's $T = 0$, ties = 1, $N = 7$, $p = .03$).

We took into account avoiding behavior performed by juveniles toward peers and adults in the indoor and

outdoor facilities. Juveniles avoided their age-mates with comparable frequency in the two enclosures (JJ mean hourly frequency INDOOR $.77 \pm .23$ SE, OUTDOOR $.35 \pm .07$ SE, Wilcoxon's $T = 1$, ties = 0, $N = 6$, n.s.); whereas, they avoided adults with higher frequency in the indoor compared to outdoor facility (JA mean hourly frequency INDOOR $1.48 \pm .33$ SE, OUTDOOR $.35 \pm .06$ SE, Wilcoxon's $T = 0$, ties = 0, $N = 7$, $p = .016$).

DISCUSSION

According to the social intelligence hypothesis, intelligence is an adaptation for social living (cf. Byrne & Whiten, 1988; Humphrey, 1976; Jolly, 1966). In this perspective, social play, which involves cooperation, communication, and learning (especially in youngsters) may represent a suitable field for the investigation of cognitive ability development (Bekoff & Allen, 2002; Pellis, 2002).

Social play sessions were common among juvenile gorillas, which invited to play each others more frequently compared to adults and infants (Prediction 1 confirmed).

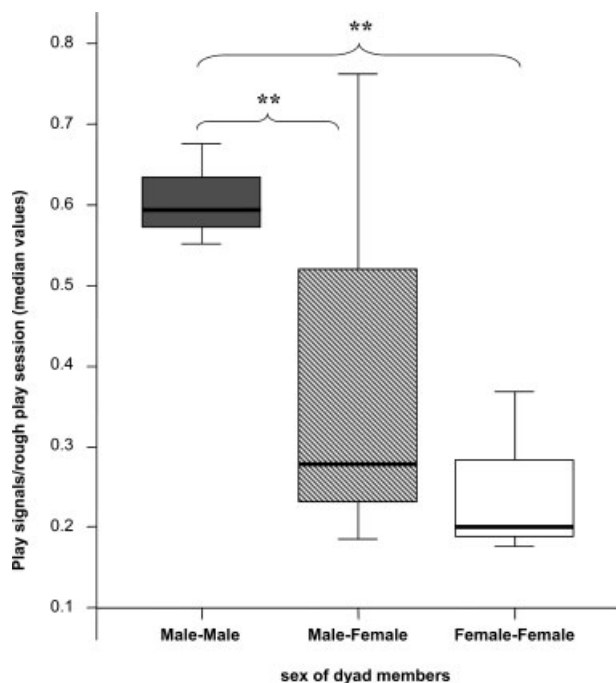


FIGURE 4 The rate of play signals *per* rough play session performed among juveniles according to pair-mate sex combinations. Solid horizontal lines indicate medians; length of the gray boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values (minimum and maximum). Only significant results are reported.

In a play fight it is useful to practice against a well-matched partner and this tendency is evident in many mammalian species (Nunes et al., 2004a for ground squirrels; Miller & Byers, 1998 for pronghorns; Owens, 1975; Cheney, 1978 for baboons; Brueggeman, 1978; Fady, 1976 for macaques; Hayaki, 1985; Mendoza-Granados & Sommer, 1995 for chimpanzees; Brown, 1988 for infant gorillas). Probably, symmetry characterizing play sessions among size-matched partners gives playmates the possibility to compete, practice, and strategize in a safer context (Dolhinow, 1999). In this view, for juvenile gorillas playing with infants might not be challenging enough to test and improve their strength and motor ability due to the physical asymmetry characterizing the two playmates (Power, 2000). On the other hand, even though juvenile gorillas rarely solicited play with adults, the latter usually refused playing with the former by ignoring their invitation attempts.

Partner choice in juvenile primates often means a partner of the appropriate gender (Fagen, 1981). Our results confirmed only partly the Prediction 2. In fact, play sessions among females were less frequent compared to those among males, but no difference emerged between female–female and male–female play frequency. This last finding may be explained with the peculiar

relationships existing between male and female gorillas. In fact, adult females limit their “social interactions” with the dominant male to spatial proximity searching for his protection. A consequence of this closeness to males is the reduction of inter-female distances. In fact females never engage in cooperation and coalition with males and females (Robbins, 1996; Sicotte, 2002; Stoinski, Kuhar, Lukas, & Maple, 2004; Watts, 1995).

Considering gentle and rough play sessions separately, we found surprising results. The gentle sessions seem to be uniformly distributed across all the sex-class combinations, conversely, the most striking difference was found in the rough sessions (play fighting), which showed a peak level among males. This specific play practice could be particularly fruitful in providing an immediate feedback on physical skills of developing individuals (Nunes et al., 2004a,b). Such immediate feedback can be used to regulate future activities. The motor training hypothesis predicts that play fighting rehearses the ability to fight seriously later with conspecifics and that the frequency of juvenile rough play increases with the degree of adult intra-specific competition in a given species (Byers & Walker, 1995). In this view, juvenile males need to assess their own fighting skills with the best training partners and by the most convenient roughness.

When animals play fight, they use patterns of agonistic functional contexts. Since these actions are not intrinsically different from their “serious” context, it may be hard to distinguish them. Many animals solved this problem by evolving some *signals* that have the function of establishing and/or maintaining a playful mood (Bekoff, 2001; Bekoff & Allen, 1998; Loizos, 1967; Pellis & Pellis, 1996). The selective use of play signals (play face and full play face; see Tab. 2) by juvenile gorilla males in their rough play sessions might corroborate the hypothesis proposed by Pellis and Pellis (1996) on the retroactive function of play signals (e.g., to avoid escalating into a real conflict) (first part of Prediction 5 confirmed). In fact, even though play fighting provides safe practice for real fighting, it only does so if the playful convention is respected by both participants. During male–male play fighting, the most competitive form of play, signals seem to be extremely functional for juvenile gorillas (Bekoff & Allen, 1998).

Play generally occurs when an animal is free from social stressors (Fagen, 1981; Loizos, 1967; Martin & Caro, 1985). For example, De Oliveira, Ruiz-Miranda, Kleiman, and Beck (2003) found that both in wild and in food supplemented groups of golden lion tamarins, social play usually occurred after foraging. Accordingly, during the prefeeding period we recorded lower levels of social play between juveniles and infants, such play levels increased in the baseline condition. This finding was probably due to the tendency of adult females to

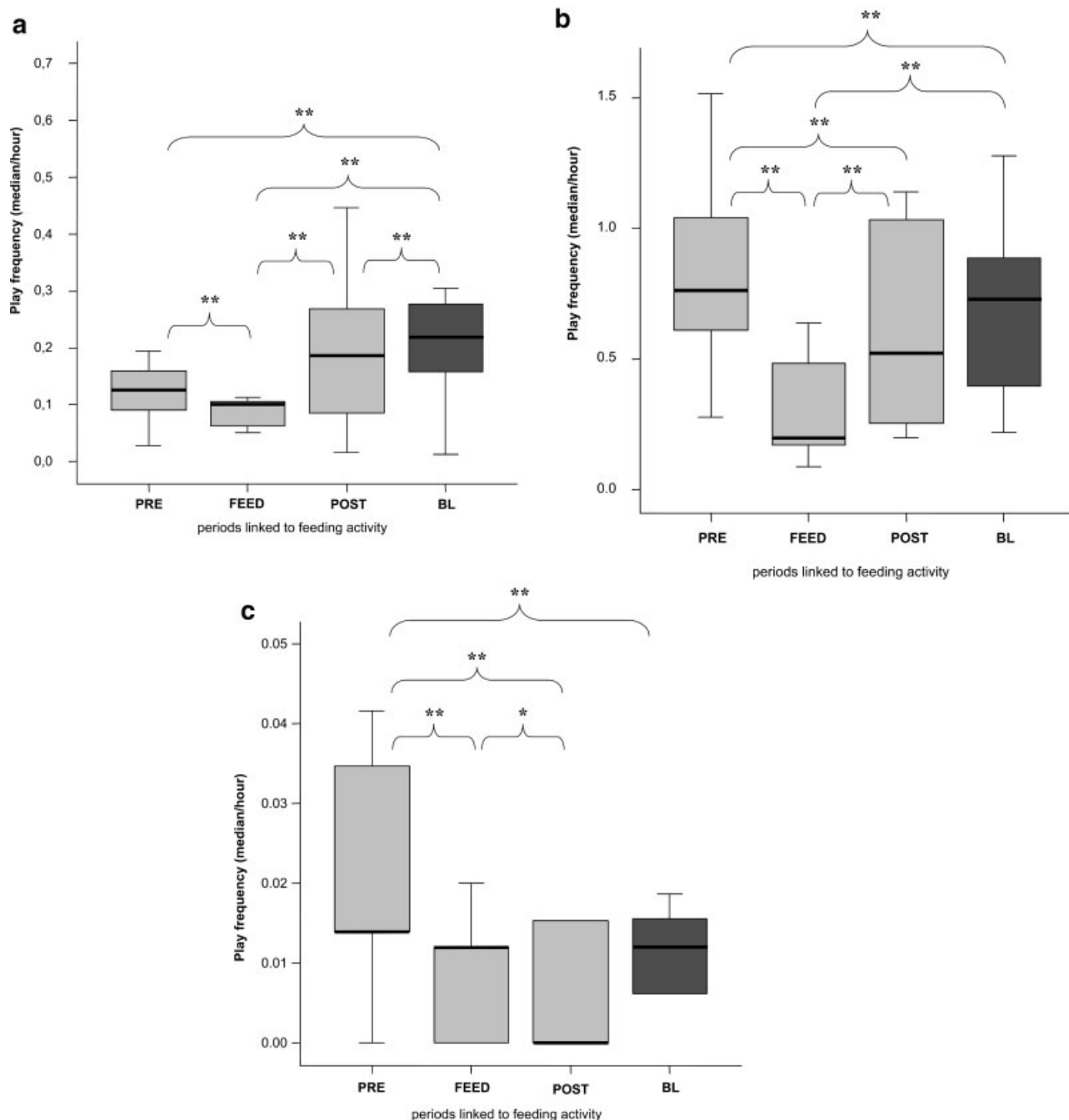


FIGURE 5 Play distribution across the four conditions (Preeating PRE, Feeding FEED, Postfeeding POST, and Baseline BL) in juvenile-infant (a), juvenile-juvenile (b), and juvenile-adult (c) dyads. Solid horizontal lines indicate medians; length of the gray boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values (minimum and maximum). Only significant results are reported.

recover and transport their offspring during such “exciting period.” Conversely, for juvenile-juvenile and juvenile-adult social play we found peak levels just before food distribution (preeating time; Prediction 3 confirmed). Several authors emphasized the great ape

cognitive ability in using anticipatory mechanisms of tension regulation due to the imminent presence of food (de Waal, 1992; Koyama & Dunbar, 1996; Palagi et al., 2004, 2006). Specifically, Palagi et al. (2004) found that among unrelated juvenile chimpanzees playful behavior

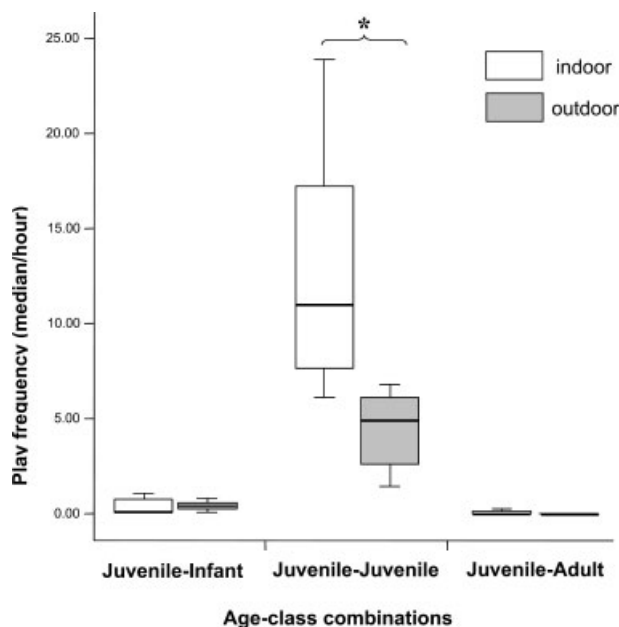


FIGURE 6 Play hourly frequency performed by juvenile–infant, juvenile–juvenile, and juvenile–adult dyads in indoor (white boxes) and outdoor conditions (gray boxes). Solid horizontal lines indicate medians; length of the gray boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values (minimum and maximum). Only significant results are reported.

occurred more frequently in the prefeeding (the last 25 min block before food provisioning) than in the control condition (the farthest time-block from the feeding-time). The same authors also found a play peak frequency at the prefeeding time between adults and unrelated immature subjects. Similar results were also found in bonobos with high rates of social play recorded during prefeeding in unrelated adult–adult and adult–immature dyads (Palagi et al., 2006). Our finding on play distribution according to prefeeding, feeding, and postfeeding conditions suggests that similar mechanisms are also present in juvenile gorillas, which may finely use social play to anticipate the forthcoming tension and dissipate the excitement associated with feeding. Nunes et al. (2004b) suggested that social play has immediate adaptive motor benefits for young animals; one possible immediate benefit of play is to increase the versatility of motor responses in individuals, thus preparing them to cope with novel, foreign or tense situations (Špinka et al., 2001). Moreover, as play is also a safe mechanism to test personal (self-assessment) and partner’s abilities (social assessment) (Loizos, 1967; Paquette, 1994; Poirier, Bellisari & Haines, 1978; Thompson, 1998), it could be most effective during periods of high social excitement (probable delayed benefits) (Palagi et al., 2004).

The investigation on environmental constraints revealed that social play among juveniles raised in condition of spatial reduction (Prediction 4 confirmed). Although this result may be also viewed as an increased interaction opportunity (reduction of inter-individual distances) (Aureli, van Panthaleon van Eck, & Veenema, 1995), it shows that juveniles are able to finely modulate their behaviors by selecting age/size-matched playmates. In fact, in high-density conditions juveniles avoid to interact with the adults. Specifically, adult avoidance fits with the “coping-model,” which predicts that individuals stay away from risky partners, especially when escape opportunities are limited (de Waal, 1989b; Judge, 2000; Judge & de Waal, 1993; Cordoni & Palagi, in press). Among juvenile Yerkes chimpanzees, Aureli and de Waal (1997) found an increase of play behavior under high-density conditions. These authors supposed that the increase of juvenile play might be strongly promoted by the reduced levels of adult activity. This interpretation could also explain our findings; in fact, in the indoor facility adult gorillas tended to stay more spatially dispersed to fellows (Cordoni & Palagi, in press). However, play fighting in a condition of reduced escape opportunities and high population density can be a risky affair; under such conditions it becomes essential for individuals to avoid aggressive escalation by signaling an honest statement of purpose making it clear what is serious from what is not (Bekoff, 1995; Bekoff & Allen, 1998; Pellis & Pellis, 1996). Our data on the use of play signals under space reduction confirm this assumption; in fact, juvenile gorillas increased their play facial displays during indoor play sessions (the last part of the Prediction 5 confirmed) thus confirming the strategic use of fine-tuning in play communication.

Many authors agree that play is one of the most sophisticated types of social communication (Bekoff, 1995; Fagen, 1981, 1993; Pellis & Pellis, 1996). The function of play in the ontogeny of primate social cognition may be to recognize stimuli, which may indicate the intentions of conspecifics. The ability to interpret such ambiguous features of social signaling could represent a central issue in the evolution of behavioral flexibility and intelligence in primates. In fact, several studies carried out on the timing of play in primates support the theories that play evolved to influence neural selection during early brain development (*neural selection model*, Fairbanks 2000).

In summary, the evidence presented here suggests that juvenile gorillas are able to fine-tune their play behavior depending on playmates, social contexts, and environmental conditions. They are not only able to maintain a play session by using play signals appropriately (thus revealing the cognitive ability of balancing cooperation and competition as it has been suggested by many

authors both for primate and nonprimate species: Bekoff, 1995, 2001; Bekoff & Allen, 1998; Flack et al., 2004; Pellis, 2002), but they have also the cognitive ability to “place” the session in a proper spatial/temporal context, thus evaluating a complex net of factors (e.g., play partner, play roughness, group activity, space availability).

NOTES

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