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Beyond the Canopy: Social Play Behavior in Wild Spider Monkeys (*Ateles geoffroyi*)

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Abstract

Play is a multifunctional behavior that may confer different advantages depending on the context, the species, sex, and age of the players. Despite numerous studies of social play in primates, we know little about this behavior in platyrrhines. This study was designed to provide a systematic description of social play in a wild group of Geoffroy's spider monkeys (*Ateles geoffroyi*). We conducted behavioral observations of acrobatic social play, object social play, cuddling play, and rough-and-tumble play in a large group of spider monkeys (N = 54) in Yucatan, Mexico. Over 5 months, we recorded and analyzed 104 play sessions. The probability of engaging in social play was higher for infants and juveniles than for subadults and adults, and it did not differ between sexes. Moreover, the probability of engaging in different types of social play did not vary across individuals based on their sex and age, nor on the frequency of play faces. Play sessions lasted longer when both players were younger and with a higher number of players, but there was no significant variation in session length associated with the frequency of play faces or players' sex. Overall, our study revealed patterns of play behavior that suggest substantial flexibility in play in this species, in line with the high levels of tolerance that characterize spider monkeys.

Keywords Acrobatic play · Object play · Cuddling play · Rough-and-tumble play · Play faces · Platyrrhine species

Introduction

Play has been defined as a spontaneous, repeated, self-rewarding, and seemingly nonfunctional behavior that differs from nonplayful behaviors either structurally, contextually, or developmentally and mostly occurs in relaxed, nonstressful contexts (Burghardt, 2014; Nathan & Pellegrini, 2012). When playing, individuals require

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Extended author information available on the last page of the article energy and time that often is diverted from other activities (De Almeida Rocha et al., 2014; Palagi, 2007, 2018), leading researchers to speculate about the adaptive function of this behavior (Bekoff & Allen, 1998; Burghardt, 2005).

Play is considered a multifunctional behavior (Palagi, et al., 2016a), which can confer different advantages depending on the context in which it occurs: the species, sex, and age of the individuals involved, and their physiological and emotional states (Palagi, et al., 2016a). The benefits that play provides can either be immediate (Palagi et al., 2004, 2006) or delayed (Berghänel et al., 2015; Blumstein et al., 2013; Nunes, 2014). Social play (i.e., play that involves at least two individuals) provides immediate advantages as a buffer during stressful events (Palagi et al., 2004, 2006), and in the longer term, it can facilitate the acquisition of new motor, cognitive, and social skills (Burghardt, 2006; Lewis, 2000; Špinka et al., 2001). In particular, social play can allow individuals to acquire information about other group members, foster the acquisition of social skills, strengthen and facilitate the creation of social bonds, and provide individuals with the opportunity to acquire novel behavioral patterns that may be useful in the future (Beltrán Francés et al., 2020; Heintz et al., 2017; Paquette, 1994; Pellegrini et al., 2007; Pelletier et al., 2017; Pellis et al., 2010a, 2010b; Pellis & Pellis, 2012).

Play occurs sporadically across animal taxa; it is present in some fish, bird, and reptile species (Burghardt, 2006), and it is quite common in mammals (e.g., brown bears, *Ursus arctos*: Clapham & Kitchin, 2016; wolves, *Canis lupus*: Cordoni & Palagi, 2016; deers, *Odocoileus spp.*: Carter et al., 2019; rats, *Rattus norvegicus*: Pellis & Pellis, 2007). In nonhuman primates (hereafter, primates), play is especially widespread (Burghardt, 2006). Compared with other taxa, for instance, primates spend a large percentage of their daily activity budget in play, up to 18% in infants and 10% in juveniles (Berghänel et al., 2015; Iki & Hasegawa, 2020; Palagi et al., 2004). Some authors hypothesize that this is because play, by fostering the acquisition of new motor, cognitive, and social skills (Burghardt, 2006; Lewis, 2000; Špinka et al., 2001), might be especially relevant for primates to develop the complex cognitive and behavioral skills that characterize them (Iwaniuk et al., 2001; Kerney et al., 2017; Montgomery, 2014). Indeed, there is a positive association between the amount of play shown by primate species and both the occurrence of complex behaviors (e.g., innovation, extractive foraging, tool use; Montgomery, 2014) and the relative size of the corticocerebellar system, which has been linked to primate complex cognition and behavior (Kerney et al., 2017).

In some primate species, social play appears to be more frequent in males than females from the beginning of their lives (e.g., blue monkeys, *Cercopithecus mitis stuhlmanni*: Förster & Cords, 2005; rhesus macaques, *Macaca mulatta*: Kulik et al., 2015; olive baboons, *Papio anubis*: Owens, 1975; Western lowland gorillas, *Gorilla gorilla gorilla*: Maestripieri & Ross, 2004). In other species, sex differences in social play emerge through development. In chimpanzees (*Pan troglodytes*), males reach a peak in social play earlier than females (Lonsdorf et al., 2014), whereas in Japanese macaques (*Macaca fuscata*) the time spent playing decreases through development more slowly in males than in females (Eaton et al., 1986; Nakamichi, 1989). Because sex differences in primate play are common and often emerge early during development, they often are considered to be genetically encoded or determined by environmental effects that act very early during primate life (Cords et al., 2010; Lonsdorf et al., 2014). In other species, however, there are no clear sex-differences in patterns of social play (see Marley et al., 2022, for a review). For some authors, this interspecific variation is explained by the extent of behavioral and morphological differences between male and female adults that characterize the species, with sex differences in play behavior only emerging when primates show marked behavioral dimorphism as adults (Palagi, 2018; Paukner & Suomi, 2008; Watts & Pusey, 1993). If adult males are more likely than adult females to engage in fights and conflicts, males also may engage more often in play (and especially in play fighting behavior) from a young age (Paukner & Suomi, 2008). When behavioral and morphological dimorphism is minimal, in contrast, there may be no sex differences in social play (Cleveland & Snowdon, 1984; Maestripieri & Ross, 2004; Stevenson & Poole, 1982; Watts & Pusey, 1993).

When playing, primates use a variety of different behaviors. Social play, for instance, may entail behaviors that imply no physical contact between players, as in acrobatic play (i.e., two or more individuals perform pirouettes and chasing) and object play (i.e., two or more individuals play with an object). However, social play can imply physical contact, such as cuddling play (i.e., one individual kicks *softly* while being *gently* grabbed by the other) and in rough-and-tumble play (i.e., also known as wrestling or play fighting, in which two or more individuals are in close body contact and use patterns typical of real fight, such as bites, kicks, or slaps; see Ciani et al., 2012; Petit et al., 2008). Depending on their individual characteristics, primates may preferentially engage in different play behaviors, because this might provide them with specific selective advantages (Palagi, 2018). For instance, rough-and-tumble play is usually the most common type of social play (Burghardt, 2005), especially in juveniles (Bekoff & Fagen, 1981), whereas acrobatic play is more common in younger individuals (Palagi & Cordoni, 2012). These differences might reflect variation in the selective advantages that these types of play provide. Acrobatic play and object play provide vestibular stimulation and information about objects and might thus especially foster motor development—something especially important in very young primates. In contrast, cuddling play and rough-and-tumble play provide individuals with information about other group members' strength and competitive skills—something that may be more important as primates approach adulthood and more often engage in affiliative and aggressive interactions (Fagen, 2011; Palagi & Cordoni, 2018; Pellis & Pellis, 2009).

Social play is a risky behavior, especially when it involves physical contact, because it may easily escalate into serious fighting (Palagi, 2007, 2018; Waller & Dunbar, 2005). To reduce this risk, primates have evolved communicative tools that may prevent aggressive escalations and increase the duration of social play (Flack & de Waal, 2004; Mancini et al., 2013; Palagi & Mancini, 2011; Scopa & Palagi, 2016; Špinka et al., 2016; Yanagi & Berman, 2014). Play faces (i.e., relaxed open mouth facial expressions), for instance, are spontaneous emotional expressions (Scopa & Palagi, 2016) that convey a playful meaning to behaviors that may otherwise appear agonistic (Bekoff & Allen, 1998; Palagi, 2008, 2009; Pellis & Pellis, 1996). By decreasing the risk of misinterpreting the meaning of the interaction, play faces are expected to be especially frequent when misinterpretation is particularly likely or costly. In line with this, primates appeared to more frequently use play faces with a higher number of players (Palagi, 2008), when play involved physical contact (Chevalier-Skolnikoff, 1974; Demuru et al., 2015; Fedigan, 1972; Palagi, 2007; Palagi & Paoli, 2007) and under space reduction (Tacconi & Palagi, 2009). Moreover, a higher frequency of play faces increased the duration of play sessions (Palagi, 2007; Špinka et al., 2016; Waller & Cherry, 2012), so that play faces might be crucial not only to decrease the risk of aggressive escalations but also to sustain play behavior (Demuru et al., 2015).

Play duration may be affected by the number and identity of the individuals involved. When many individuals play together, the risk of aggressive escalations may increase, and play sessions are more likely to abruptly come to an end (Palagi, 2018; Petit et al., 2008; Reinhart et al., 2010). Play sessions may last longer when individuals are better matched in terms of sex and age and thus are more likely to play in a similar way. According to Thompson (1998), for instance, play provides immediate feedback on the development of players' locomotor and social skills, especially during competitive play sessions with equally matched partners (i.e., having similar age sex or rank). Indeed, there is some evidence that, at least in some species, individuals preferentially play with group members that are similar in terms of sex, age, and/or rank (Lutz et al., 2019).

Although many studies have investigated social play in primates, we know much less about this behavior in platyrrhines. In squirrel monkeys (*Saimiri* spp.), for instance, individuals strongly differ in how frequently they engage in social play (Baldwin & Baldwin, 1973, 1974) and flexibly adjust their play behavior to the specific characteristics of the partners, more often reversing roles when playing with partners differing in sex and/or age (Biben, 1986, 1989). Other studies in platyrrhines suggest sex- and age-variation in play behavior, with social play being higher in juvenile males than females (tufted capuchins, *Sapajus apella*: Fragaszy et al., 2004; Paukner & Suomi, 2008) and peaking in early juveniles (mantled howler monkeys, *Alouatta palliata*: Baldwin & Baldwin, 1978; Zucker & Clarke, 1992). In spider monkeys (*Ateles* spp.), groups are characterized by high levels of fission–fusion dynamics (i.e., frequent changes in subgroup size and composition; Aureli et al., 2008) and play may be especially important to maintain and reinforce social bonds across group members (Antonacci et al., 2010; Palagi, 2023), as the frequent fission and fusion events may generate social uncertainty (Pellis & Pellis, 2009). In this species, most play faces during rough-and-tumble play occur before play bites to reaffirm the playful context when the risk of escalation is very high and partially to promote play behavior, although head shakes also are used for this purpose (Pellis & Pellis, 1997, 2011).

In this study, we provide a systematic description of social play in wild Geoffroy's spider monkeys (*Ateles geoffroyi*), a platyrrhine species characterized by low sexual dimorphism (Aureli & Schaffner, 2010; di Fiore & Campbell, 2007) and high levels of fission–fusion dynamics (Aureli & Schaffner, 2008). We examined the influence of age, sex, and play face use on patterns of play and tested five hypotheses. First, if immatures rely on play to acquire novel motor, cognitive, and social skills (Burghardt, 2006; Lewis, 2000; Špinka et al., 2001), we predicted that social play will be overall more likely in immatures than adults (Prediction 1). Second, if sex differences in play occur in sexually dimorphic species (Palagi, 2018; Paukner & Suomi, 2008; Watts & Pusey, 1993), then male and female spider monkeys will not differ in their likelihood of engaging in social play (Prediction 2a), nor in the play types they engage in (Prediction 2b), because they are not sexually dimorphic. Third, if play is important for infants to practice their motor skills, but for juveniles and subadults to acquire social information about potential partners (Fagen, 2011; Palagi & Cordoni, 2018; Pellis & Pellis, 2009), then we predicted that play behaviors with no physical contact between players (i.e., acrobatic play and object play) will be more likely in infants (Prediction 3a), whereas cuddling play and rough-and-tumble play will be more likely in juveniles and subadults (Prediction 3b). Fourth, if play faces serve to avoid escalation, then we predicted that play faces will more likely occur during cuddling play and rough-and-tumble play, because cuddling play and rough-and-tumble play involve physical contact and are thus more likely to escalate in aggressive interactions (Chevalier-Skolnikoff, 1974; Demuru et al., 2015; Fedigan, 1972; Palagi, 2007; Palagi & Paoli, 2007) (Prediction 4). Finally, if play faces reaffirm the playful intention of the interaction and sustain play behavior (Demuru et al., 2015), then we predicted that play sessions will last longer with a higher frequency of play faces (Prediction 5a) in the presence of fewer players (Prediction 5b), because the presence of many players may increase the risk of aggressive escalations (Palagi, 2018; Petit et al., 2008; Reinhart et al., 2010), and when players are matched in terms of sex (Prediction 5c) or age (Prediction 5d), because they are more likely to play in a similar way and play sessions may thus last longer (Lutz et al., 2019; Thompson, 1998).

Methods

Ethical note

We conducted a purely observational study, after obtaining the permits by the CONANP (Comisión Nacional de Áreas Naturales Protegidas) and SEMARNAT (Secretaría de Medio Ambiente y Recursos Naturales). During the study, we followed the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Nonhuman Primates and the Code of Best Practices for Field Primatology by the American Society of Primatologists. The authors declare that they have no conflict of interest.

Data availability The dataset resulting from the focal observations we analysed is provided as supplementary material. More data and information are available from the corresponding author on reasonable request.

Study site and study subjects

We conducted our study in the Yucatan Peninsula, Mexico, in the protected area of Otoch Ma’ax Yetel Kooh (20° 38’ N, 87° 38’ W), which includes an undisturbed fragment of semi-evergreen medium forest, successional forest, regenerating forest and lakes (Ramos-Fernández & Ayala-Orozco, 2003). The area hosts a group of wild Geoffroy's spider monkeys that has been followed longitudinally for more than 20 years, so that demographic records were available for all group members. Individuals were fully habituated to human observers and individually recognizable from their facial and body characteristics. At the onset of the study, the group included 54 subjects (i.e., 13 adult females, 10 adult males, 3 subadult females, 1 subadult male, 9 juvenile females, 6 juvenile males, 3 infant females, 8 infant males, and 1 infant of unknown sex; see Shimooka et al., 2008 and Table I, for age categories).

Data collection and coding

Two observers (SCR and EMCS) collected data between November 2022 and March 2023, 5 days a week, between 6.30 and 14.00 {AU: Is this time of day?}, using two different methods. First, we conducted 10-min focal samples on 46 individuals (i.e., all group members, except for 7 infants that were born few weeks before/after we started data collection, and one subadult female that joined the group when we were about to end data collection). We conducted a total of 1019 samples (mean ± *SD* 3.7 ± 1.14 h per focal subject), selecting focal subjects on a pseudorandomized basis (i.e., prioritizing those that had been more rarely sampled). During focal samples, one observer observed the focal subject and dictated information (i.e., observation day, focal subject, occurrence, and duration of social play, play partner, time spent out of view) to the other observer, who entered it on a tablet using CyberTracker. Second, whenever a social play session started during a focal sample, the observer dictating information also video-recorded the play session with a camera (Panasonic FULL-HD HC-V180), recording until the session came to an end. We considered a play session as starting when at least one subject approached at least one other group member and directed a playful behaviour (i.e., acrobatic play, cuddling play, rough-and-tumble play, play face, play bite) toward the latter, and to end either when the composition of the players changed (in which case, we started recording a new play session with different players), or when the players showed no play behaviour for at least 10 s (Gallo et al., 2021).

From the videos, we later coded 1) the number and 2) identity of the players. For each player, we also coded the occurrence and exact duration of 3) acrobatic play, 4) cuddling play, and 5) rough-and-tumble play; the occurrence and number of 6) play faces, 7) play bite, and 8) aggressive interactions; and 9) play session duration. We never observed object play. Social play occurred in 77 focal samples and a total of 155 play sessions across the 6 months. Of these 155 sessions, we discarded 51, because players were not clearly visible on the video and we could not code their play behaviour reliably (i.e., they were too high on the canopy, covered by dense foliage). Therefore, our final sample consisted of 104 video-recorded play sessions.

To ensure interobserver reliability, we started data collection only on reaching 80% interobserver reliability during focal observations. We assessed interobserver reliability during five focal observations with individuals of different sex and age classes, based on the occurrence of social play, proximity to other group members,

Table I For each member of our study group (which consisted of a wild group of spider monkeys, *Ateles geoffroyi*, in the Otoch Ma'ax Yetel Kooh protected area in Yucatán, Mexico, from November 2022 to March 2023), sex and age class (i.e., infants: < 2 years; juveniles: 2–5 years; subadults: 5–8 years; adults: > 8 years), number of 10-min focal samples conducted and number of play sessions in which they were involved (study subjects who were not the subject of focal samples could be involved in play sessions if they played with the subject of a focal sample)

Study subject	Sex	Age class	No. focal samples	No. play sessions
Alamo	Male	Infant	25	8
Antena	Female	Adult	25	1
Apolo	Male	Adult	23	0
Aura	Female	Juvenile	25	16
Bekech	Female	Subadult	25	0
Boxhuevo	Male	Adult	24	1
Braga	Female	Juvenile	24	37
Cacao	Male	Infant	26	16
Canela	Female	Juvenile	25	11
Casper	Male	Infant	0	0
Chaac	Male	Juvenile	4	0
Chickich	Female	Juvenile	24	22
China	Female	Adult	26	0
Colis	Male	Infant	0	3
Covid	Male	Infant	25	29
Cria Mich	Female	Infant	0	0
Cria Rwanda	Male	Infant	0	0
Cria Tanga	Unknown	Infant	0	0
Digit	Male	Adult	15	2
Dobby	Male	Infant	0	1
Erbse	Male	Adult	4	1
Eulogio	Male	Adult	25	0
Fabrizio	Male	Juvenile	25	19
Ikil	Female	Adult	4	0
Ixchel 2	Female	Subadult	0	0
Joane	Female	Adult	26	0
Juan	Male	Adult	19	0
Lola	Female	Adult	25	0
Luna	Female	Juvenile	25	10
Luz	Female	Juvenile	25	9
Mandibula	Female	Adult	26	0
Marcos	Male	Adult	13	0
Marylin	Female	Adult	25	0
Mich	Female	Adult	26	0
Nacho	Male	Adult	23	1
Nit	Female	Subadult	20	0
Pancha	Female	Adult	26	1
Pekin	Male	Juvenile	26	14
Poncho	Male	Juvenile	26	9
Puma	Male	Juvenile	25	22
Rwanda	Female	Adult	25	0
Sacbe	Female	Juvenile	25	3

Table I (continued)

Study subject	Sex	Age class	No. focal samples	No. play sessions
Sancho	Male	Adult	7	0
Selva	Female	Infant	25	18
Sol	Male	Infant	26	17
Tanga	Female	Adult	25	0
Valentin	Male	Subadult	24	7
Veronica	Female	Adult	26	1
Voldemort	Male	Juvenile	26	38
Wiguiberto	Male	Adult	3	0
Wishona	Female	Infant	0	0
Xibalba	Female	Adult	26	1
Yalit	Female	Juvenile	26	11
Yuli	Female	Juvenile	25	14

individual identities of the focal and the partners, occurrence of vocalizations, gestures, and vigilance (i.e., all the behaviors we recorded during the focal observations and that we used for this or other studies). Moreover, a second rater recoded all the behaviors coded from the videos in 20% of the play sessions (N = 31), showing very good reliability (i.e., Spearman's correlation for duration of play sessions: $\rho = 0.92$; Cohen's k for probability of acrobatic play: $k = 1.00$; for probability of cuddling play: $k = 0.87$; for probability of rough-and-tumble play: $k = 0.85$; for number of players: $k = 1.00$; for number of play faces: $k = 0.71$; for number of play bites: $k = 0.85$; for number of aggressive interactions: $k = 1.00$; all N = 31, all $p < 0.001$).

Statistics

We ran five generalized linear mixed models (Baayen et al., 2008) in R (R Core Team, 2020) with the glmmTMB package (Brooks et al., 2017), using two different datasets. The first dataset was based on the focal observations and contained one line for each focal sample (N = 1019), including focal subject identity, sex and age class (i.e., infant, juvenile, subadult, adult), observation day, time the focal spent in social play, and observational effort (i.e., the duration of the focal sample, subtracted the time out of view). We then modelled (Model 1) whether the probability of engaging in social play during the focal sample varied depending on the interaction of subject's sex and age class, including observational effort as offset term, and observation day and players' identity as random factors.

The second dataset included one line for each play session observed (N = 104), with players' identity, sex and age class, number of players, whether players engaged in acrobatic play, cuddling play and rough-and-tumble play, observational effort, whether players produced play faces, and how frequently (i.e., number of play faces produced during the play session). Originally, we aimed to model the proportion of time players spent in acrobatic play, cuddling play, and rough-and-tumble play. However, models with proportions as responses failed to meet the model predictions and led to serious convergence problems. Therefore, we opted to use binomial distributions instead. In particular, we modelled whether the probability of players engaging in acrobatic play (Model 2), cuddling play (Model 3), and rough-and-tumble play (Model 4) varied depending on players' sex combination, age combination, and occurrence of play faces (as test predictors), with observational effort as offset term and players' identity as random factor. However, we had to simplify Model 2, because it otherwise failed to converge due to complete separation in the data. We removed occurrence of play faces from the predictors (as no play faces were produced during acrobatic play), and we did not differentiate between infant-adult and juvenile-adult play sessions (i.e., merging the two levels of age combination, as there were no infant-adult sessions with acrobatic play). Finally, we modeled (Model 5) whether play session duration varied depending on the number of players, the frequency of play faces in the session (both *z*-transformed), players' sex combination, and age combination (as test predictors), including players' identity as random factor.

For each model, we used the "performance" package (Lüdecke et al., 2021) and the "DHARMa" package (Hartig, 2022) to check model assumptions, including residual distribution, convergence, overdispersion, and multicollinearity (max VIF: 1.86; Miles, 2005). None of the models presented showed any issues, except for Model 5, which showed a significant deviation in the Kolmogorov–Smirnov test, but plotting residuals against all predictors revealed no clear pattern in their distribution. We then compared each of the full models above to a null model (i.e., containing the same random factors and offsets, but no test predictors) using chi-square tests, and then used the drop1 function to assess the significance of single test predictors. If the interaction was not significant, we reran the model only including the terms of the interaction as main terms. If significant predictors were categorical predictors with more than two categories, we used the emmeans package for post-hoc analyses (Lenth et al., 2023).

Results

Occurrence of social play

Focal subjects engaged in social play in 77 of 1019 focal samples. In Model 1, the full model significantly differed from the null model (GLMM, $\chi^2 = 52.91$, $df = 7$, $p < 0.001$), with age having a significant effect on the probability of playing (Table II). Post-hoc tests showed that the probability of social play was highest in infants, intermediate in juveniles, and lowest in subadults and adults (Fig. 1).

Variation in play behavior

Spider monkeys engaged in acrobatic play in 25 of 104 play sessions, in cuddle play in 26 of 104 sessions, and in rough-and-tumble play in 65 of 104 sessions. On

Table II Results of significant full models testing the influence of sex and age on play in a wild group of spider monkeys (*Ateles geoffroyi*) in the Otoch Ma'ax Yetel Kooh protected area in Yucatán, Mexico, from November 2022 to March 2023. Reference categories are in parentheses, and significant predictors are marked with an asterisk

MODELS and test predictors	Estimate	SE	2.5% to 97.5% CIs	Likelihood ratio tests	*df*	*p*
Model 1: Probability that focal subjects engaged in social play during the focal sample						
Intercept	−11.75	0.56	−12.84 to −10.66	-	-	-
Sex (male)	0.37	0.30	−0.21 to 0.95	1.55	1	0.214
Age (infant)	3.28	0.55	2.20 to 4.35	47.42	3	<0.001*
Age (juvenile)	2.85	0.50	1.87 to 3.83			
Age (subadult)	0.37	1.12	−1.83 to 2.57			
Model 5: Duration of play sessions						
Intercept	86.44	39.72	8.58 to 164.29	-	-	-
Sex combination (male—female)	−32.62	17.72	−67.36 to 2.11	5.29	2	0.071
Sex combination (male—male)	−5.06	18.81	−41.93 to 31.80			
Age combination (infant—infant)	34.09	38.48	−41.33 to 109.52	9.98	4	0.041*
Age combination (infant—juvenile)	29.76	38.71	−46.10 to 105.62			
Age combination (juvenile—adult)	−32.03	41.71	−113.79 to 49.73			
Age combination (juvenile—juvenile)	−6.74	37.48	−80.21 to 66.73			
Frequency of play faces in the session	−3.90	6.37	−16.38 to 8.58	0.37	1	0.540
No. players	27.43	6.57	14.56 to 40.31	16.12	1	<0.001*

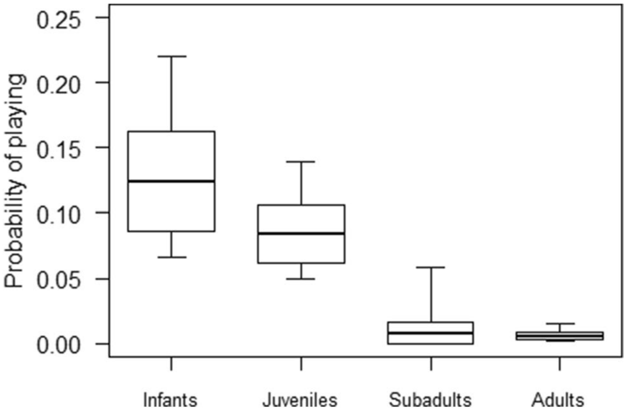

Fig. 1 Probability of engaging in social play during focal observations, as a function of the focal subject's age class in a wild group of spider monkeys (*Ateles geoffroyi*), in the Otoch Ma'ax Yetel Kooh protected area in Yucatán, Mexico, from November 2022 to March 2023. The thick lines of the box plots represent the mean probabilities as estimated by the fitted model (i.e., Model 1, but unconditional on the other categorical variables that were standardized, so that the values reported here are slightly different from the ones reported in the text). The ends of the boxes represent the estimated standard errors, and the ends of the whiskers represent the 95% confidence intervals

average (mean ± SD), they spent 22 ± 41% of play session time in acrobatic play, 22 ± 40% in cuddling play, and 55 ± 48% in rough-and-tumble play. Most play sessions involved young players (i.e., only juveniles: 52/104; only infants: 20/104; infants and juveniles: 19/104), with few sessions also including adults (i.e., with infants: 3/104; with juveniles: 10/104). Most play sessions included both female and male players (51/104) or only male players (34/104); a minority only included female players (19/104). Play faces occurred in 25 play sessions; none of these sessions included acrobatic play, 9 of 25 included cuddle play, and 16 of 25 included rough-and-tumble play. We found no significant difference between the full and null models for Models 2 to 4 (GLMM, Model 2: $\chi^2 = 6.26$, $df = 5$, $p = 0.281$; Model 3: $\chi^2 = 9.50$, $df = 7$, $p = 0.219$; Model 4: $\chi^2 = 12.58$, $df = 7$, $p = 0.083$), which modeled whether the probability of players engaging in acrobatic play, cuddling play, and rough-and-tumble play varied depending on players' sex combination, age combination, and occurrence of play faces.

Duration of play sessions

Play sessions lasted on average 74 ± 70 s (mean ± SD), ranging from four to 333 s. Most sessions included only two players (77/104) or three players (17/104), with five of 104 sessions, including four players; three of 104, including five; one of 104, including six; and one of 104, including seven players. The frequency of play faces was on average 0.41 ± 1.03 per min, ranging from 0 to 5.13 play faces/min. Moreover, 24% of the play faces observed were followed (i.e., within 3 s) by play bites produced either by the signaler (19%) or by another player (5%). Across all play sessions, there was only one instance of aggressive behavior, with two female juvenile players only engaging in rough-and-tumble play and producing no play faces. In Model 5, the full model significantly differed from the null model (GLMM, $\chi^2 = 24.21$, $df = 8$, $p = 0.002$), with number of players and age combination having a significant effect on the duration of play sessions. In particular, sessions were longer when more players were involved (Table II; Fig. 2). Moreover, post-hoc tests showed that play session duration was longest when players were all infants, or infants and juveniles, intermediate when players were all juveniles, or infants and adults, and lowest when players were juveniles and adults (Fig. 3).

Discussion

Our results partially supported our hypotheses, which were largely based on literature concerning other species. In particular, play was more likely in infants and juveniles than in subadults and adults (in line with Prediction 1). Moreover, the probability of engaging in social play did not significantly differ between males and females, neither overall (in line with Prediction 2a), nor in terms of the play types they engaged in (in line with Prediction 2b). However, in contrast to our predictions, the probability of engaging in acrobatic play, cuddling play, and rough-and-tumble play did not vary across individuals depending on their age (Predictions 3a and 3b),

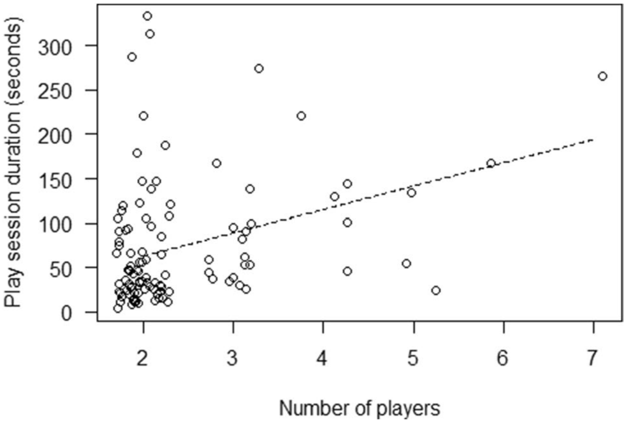

Fig. 2 Play session duration (in seconds) as a function of the number of players in the session in a wild group of spider monkeys (*Ateles geoffroyi*) in the Otoch Ma'ax Yetel Kooh protected area in Yucatán, Mexico, from November 2022 to March 2023. Circles represent the individual play sessions and are slightly jittered on the x axis to increase visual clarity. The line represents the fitted model, which was like Model 5 but unconditional on the other categorical variables that were standardized

nor it was linked to differences in the frequency of play faces observed (Prediction 4). Finally, play session duration did not increase with a higher frequency of play faces (in contrast to Prediction 5a) or depending on the players' sex (in contrast to Prediction 5c). However, it increased with a higher number of players (in contrast to Prediction 5b) and when players had a similar age (in line with Prediction 5d).

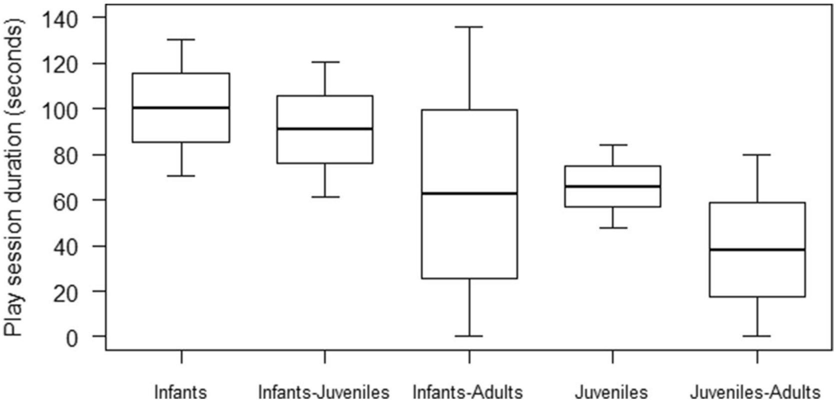

Fig. 3 Play session duration (in seconds) as a function of players' age classes in a wild group of spider monkeys (*Ateles geoffroyi*) in the Otoch Ma'ax Yetel Kooh protected area in Yucatán, Mexico, from November 2022 to March 2023. The thick lines of the box plots represent the mean probabilities as estimated by the fitted model (i.e., Model 5, but unconditional on the other categorical variables that were standardized, so that the values reported here are slightly different from the ones reported in the text). The ends of the boxes represent the estimated standard errors, and the ends of the whiskers represent the 95% confidence intervals

Play was more likely in younger (i.e., infants and juveniles) than older (i.e., subadults and adults) individuals, in line with abundant literature showing that immatures are more likely to play than older individuals, especially in species that are characterized by prolonged immaturity and extended parental care, such as primates (Cordoni et al., 2019; Pellegrini, 2010; Pellis & Pellis, 2009). During the infant and juvenile stages, play may be crucial to acquire and practice social skills that may be useful during adulthood (Lewis, 2000; Pellis et al., 2010a, 2010b) and to foster the development of flexible motor, behavioral, and emotional responses, especially in unpredictable contexts (Antonacci et al., 2010; Palagi, 2012; Špinka et al., 2001).

Males and females did not differ in their probability of engaging in social play, nor in the play types they engaged in. These results support the lack of consistent sex differences in primate patterns of social play (see Marley et al., 2022, for a review) and support the hypothesis that sex differences in play behavior may only emerge when adults show marked behavioral dimorphism and sex differences in play patterns are thus adaptive to foster the acquisition of sex-specific motor, cognitive, and social skills (Palagi, 2018; Paukner & Suomi, 2008; Watts & Pusey, 1993). The lack of clear sex-differences in spider monkey play behavior is well in line with the fact that this species shows low sexual dimorphism (Aureli & Schaffner, 2010; di Fiore & Campbell, 2007). Moreover, these findings are in line with studies in other species that found no clear sex differences not only in the frequency of play behavior, but also in the occurrence of specific play types, such as rough-and-tumble play (e.g., red titi monkeys, *Callicebus cupreus*: Chau et al., 2008; yellow baboons, *Papio cynocephalus*: Young & Hankins, 1979; red colobus monkeys, *Procolobus rufomitratus*: Worch, 2010; Western lowland gorillas: Palagi et al., 2007).

The probability of engaging in acrobatic play, cuddling play, and rough-and-tumble play did not differ significantly across individuals based on their age. In addition, we never observed social object play, although Carpenter (1935) described solitary object play with sticks and other objects in this species. Possibly, for arboreal species, it may be physically too challenging to engage in social play while dangling from the trees with objects in their hands, as suggested by other studies in arboreal species that showed no evidence of social object play (Baldwin et al., 1974; Baldwin & Baldwin, 1973, 1978).

Play faces did not have the crucial role we had expected. Play faces occurred in only 22 of 104 play sessions, and their occurrence did not increase session duration. These findings are contrast with studies of other species showing a link between the frequency of play faces and play session duration (Palagi, 2007; Špinka et al., 2016; Waller & Cherry, 2012; but see Beltrán Francés et al., 2020). However, they are partially in line with the other study on play faces in this species, which showed that spider monkeys may not use play faces to increase the duration of play, but rather to reaffirm the playful context when the risk of escalation is especially high (e.g., before play bites; Pellis & Pellis, 1997). Nonetheless, in our study, only 24% of play faces were followed by play bites, mostly by the same player that had produced the play face. Further studies are needed to better understand the function of play faces in spider monkeys.

The probabilities of engaging in acrobatic play, cuddling play and rough-and-tumble play were not linked to differences in the frequency of play faces. However, we never observed play faces during acrobatic play, although they occurred during cuddle play and rough-and-tumble play. These results are largely in line with the hypothesis that play faces are produced mostly during ambiguous contact situations to reaffirm the playful context and prevent the situation from escalating into real aggression (Mancini et al., 2013; Palagi et al., 2014; Pellis & Pellis, 2009). Interestingly, we only observed aggressive escalations once, suggesting that the use of communicative tools to convey the playful intention may be very effective in this species (see Aureli et al., 2008).

Play session duration did not increase depending on the players' sex, but it increased when players were younger. These results do not support the hypothesis that individuals play preferentially with partners that match their age and are thus more similar in body size (Govindarajulu et al., 1993; Lutz et al., 2019). Whereas play sessions were longest when players included only infants, or both infants and juveniles, their duration decreased when players included only juveniles or both infants and adults, and even more when players were juveniles and adults. Therefore, it is likely that longer play sessions were linked to the presence of younger individuals, rather than to the presence of players of similar age. Finally, play session duration in our study increased with the number of players. When play sessions include more players, they can be harder to maintain because of the higher number of parties that need to regulate and communicate their behavioral intentions (Palagi et al., 2016b). However, play sessions with multiple players may be especially important to foster the acquisition of new social partners and enlarge individuals' social networks (Cordoni et al., 2019; Palagi, 2018), and effective communication tools might allow spider monkeys to engage in these more complex forms of social play.

Our study had several limitations. First, we only observed one group of spider monkeys, which clearly limits the generalizability of our findings. Moreover, our study lasted only a few months and may not capture seasonal variation in play frequency and behavior. Finally, the setting of our study did not allow us to capture other behaviors that may be very important during social play, such as head shakes and mimicking of facial expressions, as it is hard to observe these behaviors when individuals are high in the canopy. In the future, it will be important to include these behaviors to understand the communicative function that they might have within and without the social play context (Pellis & Pellis, 1997, 2011). These limitations emphasize the need for caution when extrapolating from our results to the entire species and highlight potential avenues for future research, including larger study samples and the use of more detailed ethograms.

Overall, this study provides a preliminary overview of social play in a wild group of spider monkeys. Our findings reveal patterns of play behavior that are in line with the low sexual dimorphism of this species and that are suggestive of substantial flexibility in how social play is instantiated, mirroring the high levels of tolerance that characterize this species (Aureli & Schaffner, 2008, 2010). Males and females did not differ clearly in their play behavior, sex and age did not predict the play style of individuals, and play faces seemed to have a limited function during play sessions, although they were more common when play implied body contact. The fact that our hypotheses, which were mostly based on literature on other species, were only partially supported, suggests high variation across species in their play behavior and calls for more studies of spider monkeys and other platyrrhines to better understand the mechanisms and functions of social play.

Inclusion and diversity statement While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list.

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