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Socioecological correlates of social play in adult mantled howler monkeys

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The study of animal play is highly complex since its potential functions vary with social and environmental circumstances. Although play is generally characteristic of immature animals, it may persist in adults in its social form, particularly when interacting with young individuals, and less often with other adult playmates. We measured the amount of social play in 62 wild adult howler monkeys, *Alouatta palliata*, belonging to seven different groups in Mexico and Costa Rica. Overall, adult play represented a small mean proportion of observation time across all groups, but it was present in all study groups. Generalized linear mixed models revealed that group size correlated with both adult–adult and adult–immature play, supporting the hypothesis that more individuals provide more play opportunities. While play between adults decreased with increases in the immature to adult ratio, we did not find a clear preference for adults to play with immatures, emphasizing the importance of playing with other adult peers. Conversely, adults played more with immatures as the immature to adult ratio increased, which may correspond with the role adult–immature play may have in the socialization process of young individuals. More time dedicated to foraging on fruits corresponded with more adult–adult play. This finding, aside from being associated with more energy being available to engage in play, supports the hypothesis that play is a mechanism for solving conflicts associated with contest competition by either reducing social tension and/or fighting for a limited resource. The range of factors affecting social play indicates that this behaviour in adult howler monkeys is facultative, having affiliative, socializing and competitive roles, depending on the socioecological context.

The perennial question of why animals play has been debated since the earliest detailed studies of behaviour began (Darwin, 1871; Groos, 1898; Spencer, 1872). Darwin (1871 p39) wrote 'happiness is never better exhibited than by young animals, such as puppies, kittens, lambs, and company, when playing together, like our own children'. Spencer (1872) believed that play occurs when excess energy builds up in an animal's brain. He thought that this could lead to the imitation of more functional behaviours through play. Since play has elements from other behaviours, including aggression and affiliation, it can have a wide variety of causes and functions (Bekoff & Byers, 1998; Breuggeman, 1978; Pellis et al., 2019; Smith, 1982). Accordingly, the role of play might respond to specific social and environmental circumstances that fluctuate across contexts. This makes the study of play highly complex and many questions remain unanswered about the evolution and function of this intriguing behaviour (Cenni & Fawcett, 2018; Graham & Burghardt, 2010; Pellis et al., 2015; Richter et al., 2016; Schank et al., 2018).

For many species, including humans, play is a conspicuous phenomenon in young individuals (hereinafter 'immatures'), which spend large proportions of their time playing (Bekoff & Byers, 1981; Fagen, 1981; 1992; Fairbanks, 2000; Martin & Caro, 1985). Accordingly, the main function given to explain animal play is the rehearsal of behaviours individuals will assume later in adult life. These behaviours include mating, foraging and fighting (Burghardt, 2010; Fagen, 1981; Groos, 1898; Naples & Rothschild, 2015;

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Lafreniere, 2011; Palagi & Mancini, 2011; Pellis et al., 2015) in addition to facilitating the development of relationships with other group members (Bekoff, 1984; Cafazzo et al., 2018; Cordoni et al., 2018; Eifermann, 1971; Mackey et al., 2014; Merrick, 1977; Paquette, 1994; Pellis et al., 2010; Poirier & Smith, 1974; Shimada & Sueur, 2018). Nevertheless, play can also endure beyond sexual maturity in many species (e.g. otters: Beckel, 1991; birds: Diamond & Bond, 2003; wolves: Essler et al., 2016; kangaroos: Ganslosser, 1993; humans: Johnson et al., 2015; nonhuman primates: Pellis & Iwaniuk, 2000a), suggesting that it may be a relevant functional behaviour across the entire life span of social animals.

Studies suggest that when adults participate in social play (i.e. an interaction in which two or more individuals play with each other), the behaviour can serve multiple compatible functions depending on the nature of the context and the participants (Bekoff & Byers, 1981; Dolhinow, 1999; Yamanashi et al., 2018). In this sense, when adults play with immatures (the most frequent type of adult play described; Fagen, 1981, 1992), it might serve as a means to 'educate' them about the social rules that govern groups (Bekoff & Byers, 1998; Carpenter, 1934; Fagen, 1992; Pellegrini & Smith, 2005; Poirier & Smith, 1974; Zahavi, 1977). During play, adults aid immatures with forming existing relationships, creating new ones, and allowing them to test social boundaries via pulling, biting, tugging or hitting, which in other contexts would not be tolerated by others. Social play only among adults may have similar roles, that is, strengthening social networks and promoting cooperation between participants (Baldwin, 1982; Pellis et al., 1993). In primates in particular, play between adults might have an affiliative function similar to grooming as it provides ways to interact with others (Merrick, 1977; Palagi et al., 2006). That is, it allows individuals to establish and maintain social bonds (Baldwin & Baldwin, 1973; Enomoto, 1990; Goodall, 1986) and limit aggression, reduce tension and increase tolerance when stressful situations, such as food competition, arise (Breuggeman, 1978; Gray, 2009; Martin & Caro, 1985; Norscia & Palagi, 2011). For example, play among adult bonobos, *Pan paniscus*, is more frequent before and during feeding than in any other context, which supports the idea that adults use it to cope with competition and social tension (Palagi et al., 2006).

As social play is a particularly elaborate and energy-consuming behaviour that often resembles fighting (Aldis, 1975), it can also assume a competitive function, assessing the abilities, the strengths and the weaknesses of playmates as well as showing competitive skills in a 'safe' context (Breuggeman, 1978; Montgomery, 2014; Palagi, 2018; Paquette, 1994; Pellis & Iwaniuk, 2000a, 2000b, 2002; Palagi et al., 2004, 2006, 2007; Cordoni, 2009; Smuts, 2014). This function becomes particularly important in social species without rigid dominance hierarchies or with social uncertainty (Ciani et al., 2012; Palagi et al., 2016; Pellis & Iwaniuk, 2000a). Thus, adult individuals can use play as a tool to negotiate social relationships, maintain alliances, reduce social tension and foster cooperation between group members (Antonacci et al., 2010; Ciani et al., 2012; Norscia & Palagi, 2011; Palagi et al., 2016).

Previous research on social play in howler monkeys (genus *Alouatta*) has mostly described developmental aspects of infants and juveniles of the mantled howler monkey, *A. palliata* (Baldwin & Baldwin, 1978; Gennuso et al., 2018; Jasso del Toro et al., 2020; Zucker & Clarke, 1992). Play in howler monkeys starts around the age of 3 months, when the infant starts moving more autonomously, peaks during the juvenile period (between 12 and 36 months), then drastically reduces as they approach adulthood (>40 months). Adult howler monkeys have a highly folivorous diet, which makes them comparatively inactive primates, spending most of their time resting for cellulose digestion (Cristóbal-Azkarate & Arroyo-Rodríguez, 2007; Dunn et al., 2010; Milton, 1980; 1998). Howler play decreases with age according to increasing demand for energy in digestion as mothers wean juveniles (Baldwin & Baldwin, 1978). Correspondingly, in a review of play by Pellis and Iwaniuk (2000b), *A. palliata* adults were reported not to engage in social play. Nevertheless, several authors have observed social play in adult howler monkeys (Fontaine, 1994; Garcia, 2001; Zucker & Clarke, 1992). Zucker and Clarke (1992) further suggesting that social play should be more common in *A. palliata* than in other howler species (e.g. *A. seniculus*), as they live in groups with several adult males and females. Correspondingly, Garcia (2001) observed 59 dyadic interactions of social play in adult *A. p. mexicana* males in Agaltepec island, Mexico, during 840 h of focal observations.

The objective of the present study was to examine the social and ecological variables affecting adult social play in howler monkeys and shed further light on the potential function of this behaviour in natural populations. This study encompassed two subspecies of howler monkeys, from seven different groups in Mexico (*A. p. mexicana*) and Costa Rica (*A. p. palliata*). We first examined how social play varied with age. Then, we tested the effect of several socioecological factors on the amount of time adult howler monkeys spend playing with other adults (adult–adult play) and immatures (adult–immature play), including group size, immature to adult ratio, sex, howler density, study area, percentage of time dedicated to foraging on fruit and percentage of time dedicated to travelling.

METHODS

Study Sites

We studied social play in howler monkeys at two sites: Los Tuxtlas Biosphere Reserve, Mexico, where the subspecies *A. p. mexicana* lives, and the Sector Santa Rosa in Guanacaste Conservation Area in Costa Rica where *A. p. palliata* lives (Table 1).

The vegetation in the Los Tuxtlas Biosphere Reserve consists of tropical forest fragments that vary in size and degree of isolation (Arroyo-Rodríguez and Asensio et al., 2008, Arroyo-Rodríguez and Mandujano et al., 2008; Cristóbal-Azkarate et al., 2005). The climate is warm and humid, with a mean annual temperature of 25 °C and rainfall between 3000 and 4600 mm (Estrada et al., 1997). The vegetation in Santa Rosa comprises relatively continuous tropical dry forest with patches of semievergreen forest at various stages of succession and an annual rainfall of approximately 1500 mm (Fedigan & Jack, 2012). In the Los Tuxtlas Biosphere Reserve, we studied three howler monkey groups inhabiting three forest fragments of different size, whereas in Santa Rosa we studied four groups that lived in a continuous dry forest (Table 1). We could identify all individuals by natural markings (skin pigmentation on the hands and feet and sometimes scars).

We classified individuals as adult males, adult females, juveniles and infants following Domingo-Balcells and Veà (2009), which we validated based on the behaviour and appearance of 37 individuals (20 adults and 17 immatures) for which we knew the exact age. To simplify analyses, we grouped juveniles and infants into a single category of immatures (Table 1).

Behavioural Data Sampling

Observations covered the whole day from dawn to dusk when possible. However, the total observation time and sampling period (month/year) varied between groups and study sites (Table 1). While following howler monkeys, we continuously recorded all occurrences and durations (s) of social play using a stopwatch, along with the identities of the individuals involved. Observations occurred at distances between 20 and 30 m using both naked eye

Table 1
Group composition, observation time and sampling periods at study sites

Site and subspecies	Group ID	Group composition	Observation time (h)	Sampling period	Geographical coordinates	Study area (ha)	Howler density (individuals/ha)
Los Tuxtlas Biosphere Reserve, Mexico	AGA	21F 19M 19I	415	Aug 1997–Jun 1998	18°27N, 95°02W	8.3	9.5
	LIZ	2F 2M 1I	300	Aug 2000–Jun 2001	18°41N, 95°11W	1.3	4.6
A. p. mexicana	PLA	2F 2M 3I	300	Aug 1997–Jun 1998	18°27N, 95°03W	40	0.48[a]
Santa Rosa Sector, Guanacaste Conservation Area, Costa Rica	CH	9F 4M 6I	274	Apr–Oct 2005	10°50'N, 85°38'W	10 800	0.56[b]
A. p. palliata	CP	11F 2M 4I	207	Apr–Oct 2005	10°50'N, 85°38'W	10 800	0.56[b]
	SN	5F 2M 2I	278	Apr–Oct 2005	10°50'N, 85°38'W	10 800	0.56[b]
	SE	4F 1M	110	Apr–Oct 2005	10°50'N, 85°38'W	10 800	0.56[b]

AGA: Agaltepec Island; LIZ: Arrollo Liza; PLA: Playa Escondida; CH: Charly; CP: Cerco de Piedra;SN: Sendero Natural; SE: San Emilio. F: adult female; M: adult male; I: immature (infant >3 months and juveniles).
[a] Serio-Silva & Rico-Gray, 2002.
[b] Fedigan & Jack, 2012.

and binoculars. We recorded field data in a notebook at the moment of observation, and later transcribed these into a database. The total observation time was 1884 h across the seven groups (Table 1). We could usually observe all the individuals of the study groups simultaneously, except for group AGA, as this group has atypical dynamics for the species, i.e. fission–fusion dynamics by which individuals often separate into subgroups (Dias & Rodriguez-Luna, 2006). Therefore, although the total observation time in group AGA was 415 h, the observation time for each individual was not equal for all members, because we never observed all individuals together simultaneously. Thus, to estimate play percentages at AGA, we divided the time spent playing per individual by its individual observation time to control for variation in individual observation effort. We did this by recording the individuals' presence in the observed subgroup at 30 min scan intervals. Mean observation time (±SD) of individuals in group AGA was 82.2 (±38.5 h) per adult individual.

We followed Burghardt's five criteria (2005) to identify social play in howler monkeys. First, play was functionally incomplete as there was no evident logical survival outcome for players in the context in which it appeared. Second, social play was spontaneous and voluntary, and it was perceived by observers as pleasurable to the players. Third, social play was different from other more 'serious' behaviours such as aggression which included severe contact and had a clear role of attacker and defender. Instead, during a single play bout, there were frequent role reversals among play partners. Fourth, it was repeated, but not stereotyped, i.e. it did not repeatedly occur in the same sequence of actions. Fifth, to our knowledge, it never occurred in the presence of severe stress, such as a loud noise or during threats from conspecifics or predators. We further defined social play as a nonaggressive interaction between two or more individuals through an unordered combination of one or more of the following actions, which were never preceded or followed by any sign of social distress: biting, chasing, wrestling/grappling, pushing, pulling, baring teeth and/or chasing (Braza, 1980). A play bout could occur with individuals hanging from their tails and often included typical play signals such as 'shaking the head' or 'play face' (Fagen, 1981). We identified an adult–adult play bout as when two or more adult individuals played together without any immature being involved, an adult–immature play bout as when at least one adult played with at least one immature individual and, finally, mixed play as when two or more adults played with at least one immature. We recorded that an individual had stopped playing when the activity was discontinued for at least 10 s. Thus, a play bout ended when all players stopped playing for at least 10 s. We also recorded the time spent foraging on fruit, resting and travelling using scan sampling at 5 min intervals. Data were collected by one observer in Mexico and five observers in Costa Rica. During the first 2 weeks in Costa Rica, field observers undertook a training period to become skilled at individual identification and distinguishing social play in howler monkeys. This allowed data collection to be comparable between sites and increased interobserver reliability. Only when there was a consensus between observers identifying social play during training was an observer deemed to be independent and allowed to collect data in the field.

Statistical Analyses

We used the R platform (R Core Team, 2021) for all statistical analyses. A nonparametric analysis of variance (Kruskal–Wallis ANOVA) was used to test for significant differences in the amount of social play (s) among the 62 individuals across age classes (infants = 18, juveniles = 10, subadults = 5, adults = 57), the seven groups, and the two subspecies. We also used a Friedman test to examine whether adults played differently across the three social play types (adult–adult, adult–immature or mixed play). In addition, we fitted a generalized linear model (GLM) adjusted for a binomial distribution to determine the influence of age in months on the percentage of social play of 37 individuals (infants = 11, juveniles = 6, adults = 21) with known age in months. The GLM included 'cbind (seconds playing, seconds not playing)' in the formula to normalize the response variable by observation time (Gardener, 2012). That is, the seconds playing and the seconds not playing were entered in the GLM as a two-vector response variable (e.g. Ceccarelli et al., 2020; Dias et al., 2020). We introduced the quadratic term of age (months^2) in the GLM to test for its nonlinear effect on play.

We ran two generalized linear mixed-effects models (GLMMs) that assessed the influence of all predictors (i.e. we ran two full models) on both adult–adult play and adult–immature play ($N = 62$: 40 adult females, 22 adult males): group size, howler monkey density (individuals/ha), percentage of observation time spent foraging on fruit and travelling, study area (ha), sex and immature to adult ratio (number of immatures/number of adults of both sexes). Instead of total group size, we only entered the number of adults in the group when modelling adult–adult play. If subspecies or study group significantly affected adult–adult play via the Kruskal–Wallis ANOVA, then we controlled for these effects by

setting these variables as random factors in the model selection analyses described below. The time spent by adults in social play was entered as the response variable (normalized by observation time by including the 'cbind' function in the GLMM formula), adjusted for a binomial distribution. We transformed study area to its natural logarithm, and all continuous factors were standardized by subtracting the mean of each observation and dividing it by the standard deviation before GLMM analyses. We implemented GLMMs using the 'glmer' function in the 'lme4' package (Bates et al., 2015). We calculated the variance inflation factor (VIF) to check potential multicollinearity among parameters for the two full models (Miles, 2014), which revealed no concerns (VIF < 3). Models conformed to assumption of normality of residuals when inspecting quantile–quantile plots, and to homogeneity when residuals were plotted against predicted values.

Adult Play Preferences

To analyse the preference of adults to play with other adults versus play with immatures, we calculated the play preference using log ratios (Elston et al., 1996) for each adult individual:

$$\text{play preference ratio} = \ln\left(\frac{A_o/I_o}{A_a/I_a}\right)$$

where A_o and I_o are the observed numbers of times focal adults played with other adult individuals and immature individuals, respectively, considering all play bouts each adult participated in, and A_a and I_a correspond to the number of available adult and immature players. Play preference ratios > 0 indicate a preference towards playing with other adults, whereas ratios < 0 indicate a preference towards immatures, and values around 0 indicate no preference towards either of the two age classes. We performed *t* tests to determine whether preference ratios were significantly different from zero; that is, whether individual choices to play with other adults or immatures were nonrandom concerning the available number of adult and immature individuals in the corresponding group. The available number of adult and immature individuals for each adult of group AGA corresponded to the total number of adult and immature individuals observed in the group scans, respectively. We removed the individuals from the SE group from the preference analysis as the only immature in the group disappeared during the sampling period.

Ethical Note

Our study was noninvasive and exclusively observational, carried out with the permission of the corresponding authorities in Mexico and Costa Rica. The research adheres to the ASAB/ABS Guidelines for the Use of Animals in Research, the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates and follows the American Society of Mammologists' Guidelines on wild mammals in research.

RESULTS

Age and Play

We observed social play in all age classes of howler monkeys (Fig. 1), although infants (mean±SD = 1.4±1.27%) and juveniles (2.16±1.19%) had larger percentages of observation time playing than subadults (0.84±0.48%) and adults (0.62±0.55%). Both the ANOVA across age classes (Kruskal–Wallis $H_3 = 18.9$, $P < 0.001$; Fig. 1a) and the GLM (Fig. 1b) as the predictor confirmed that social play decreased in adulthood in howler monkeys. Both the linear ($\beta = 4.57\text{e-}03$, SE = 3.26e-04, $P < 0.001$) and quadratic ($\beta = -2.773\text{e-}04$, SE = 3.681e-06, $P < 0.001$) age GLM terms were significant. However, even the oldest individuals still engaged in some social play (Fig. 1).

Social Play Categories Across Groups and Subspecies

Overall, adults played for a mean (±SD) of 0.61 (±0.55) percentage of observation time. There were differences in the percentage of time adults dedicated to social play across study sites (Fig. 2a), but these were not significant (Kruskal–Wallis $H_6 = 10.5$, $P = 0.103$). There were differences between subspecies in adult social play (Kruskal–Wallis $H_1 = 13.8$, $P < 0.001$; Fig. 2b).

Adults spent more time playing with other adults (adult–adult play), followed by adults playing with immatures (adult–immature

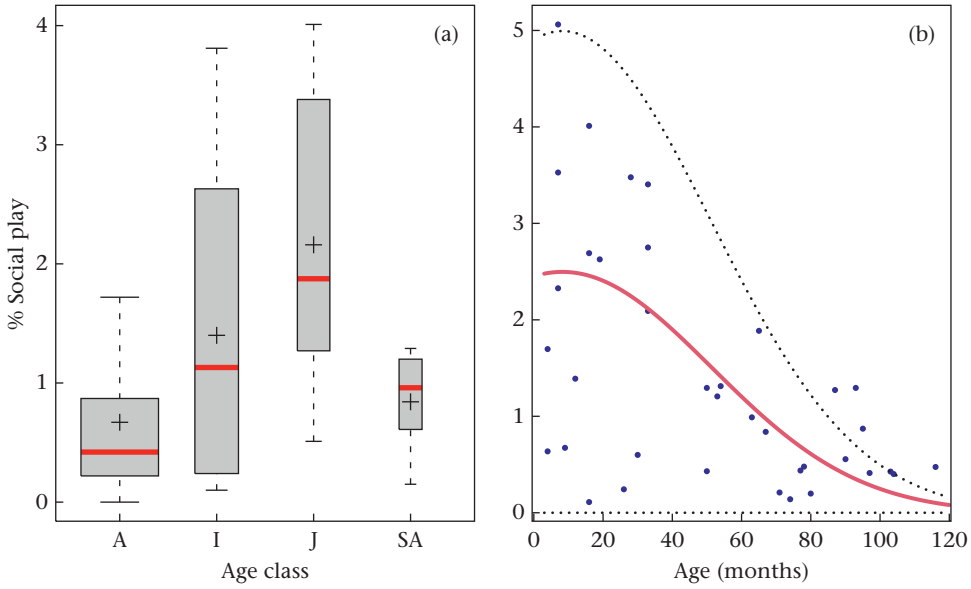

Figure 1. (a) Changes in social play in howler monkeys according to age class (A: adults; I: immatures; J: juveniles; SA: subadults). Solid lines and crosses within the box indicate the median and mean, respectively. The edges of the box indicate the 25th and 75th percentiles and the whiskers indicate the values within 1.5 times the interquartile range. (b) Relationship between age (months) and social play; 95% confidence intervals are shown in grey dotted lines around the solid regression line.

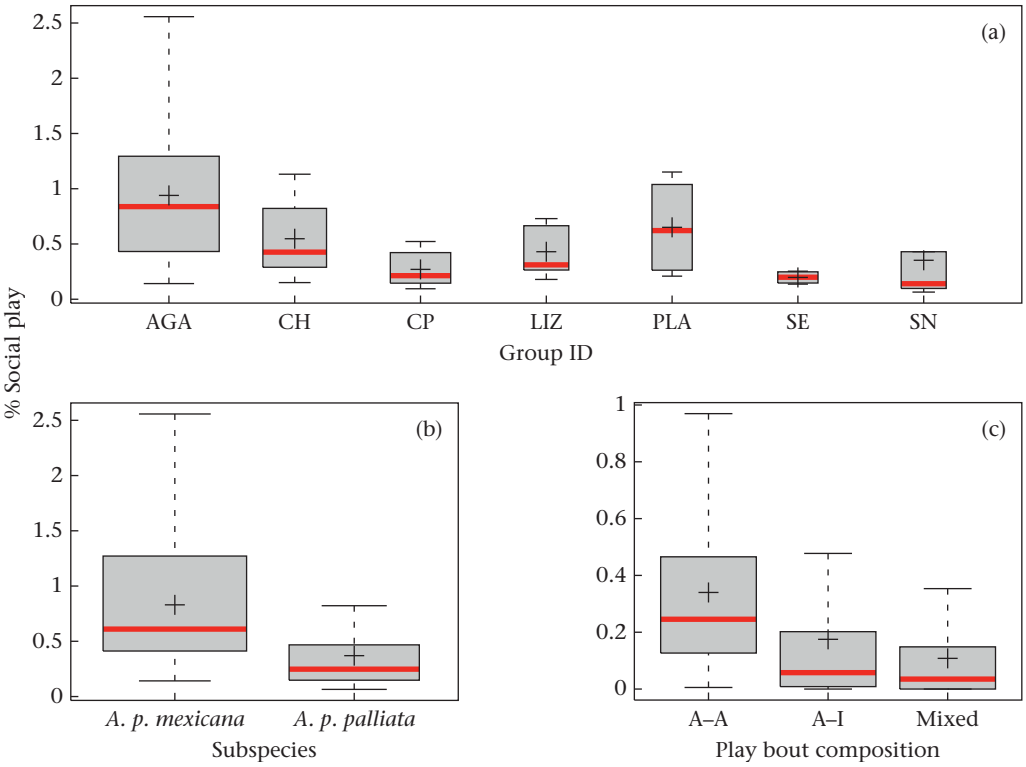

Figure 2. Percentage of observation time in social play by adult howler monkey individuals across (a) study groups (AGA: Agaltepec Island; CH: Charlie; CP: Cerco de piedra; LIZ: Arroyo Liza; PLA: Playa Escondida; SE: San Emilio; SN: Sendero Natural), (b) *Alouatta* subspecies and (c) play bout composition: adult–adult play (A-A), adult–immature play (A-I), mixed play (mixed). Solid lines and crosses within the box mark the median and mean, respectively. The edges of the box indicate the 25th and 75th percentiles and the whiskers indicate the values within 1.5 times the interquartile range.

play), and adults playing with other adults and immatures simultaneously (mixed play; Fig. 2c). These differences were significant (Friedman test: $\chi^2_1 = 39.9$, $P < 0.001$).

Adult–Adult Play and Adult–Immature Play

There were no differences between subspecies in adult–adult play (Kruskal–Wallis $H_1 = 0.11$, $P = 0.73$) or adult–immature play (Kruskal–Wallis $H_1 = 0.51$, $P = 0.47$). There were, however, significant differences in the percentage of time that adults dedicated to adult–adult play (Kruskal–Wallis $H_6 = 28.9$, $P < 0.001$; Fig. 3a) and

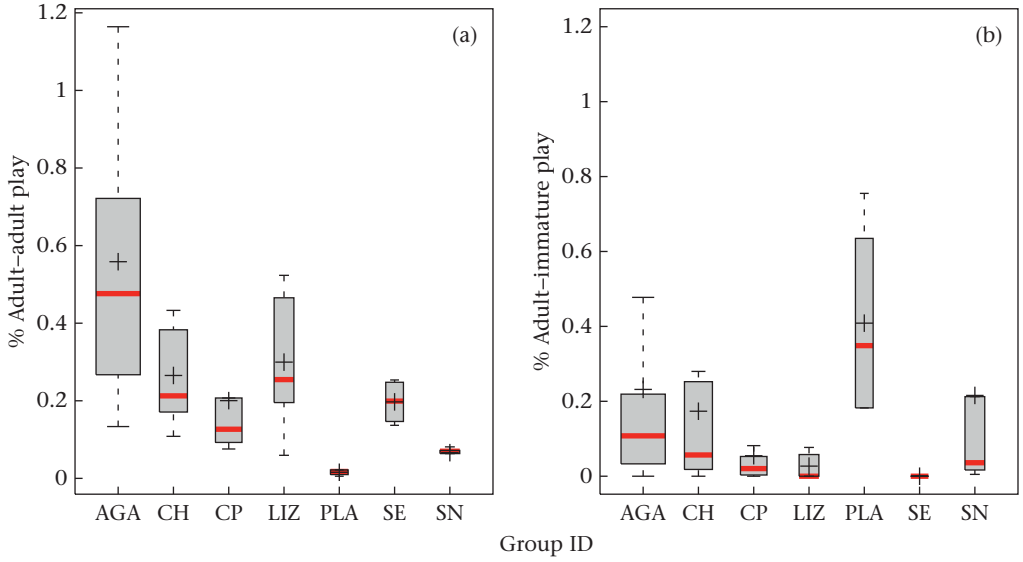

Figure 3. Percentage of observation time engaged in (a) adult–adult play and (b) adult–immature play by adult individuals across different groups (AGA: Agaltepec Island; CH: Charlie; CP: Cerco de piedra; LIZ: Arroyo Liza; PLA: Playa Escondida; SE: San Emilio; SN: Sendero Natural). Solid lines and crosses within the box mark the median and mean, respectively. The edges of the box indicate the 25th and 75th percentiles and the whiskers indicate the values within 1.5 times the interquartile range.

adult–immature play (Kruskal–Wallis $H_6 = 19.1$, $P < 0.005$; Fig. 3b) across study groups.

Factors Explaining Adult–Adult Social Play

The number of adults in the group and the percentage of time spent foraging on fruit both positively affected social play, whereas the immature-to-adult ratio affected it negatively (Table 2, Fig. 4). The percentage of time spent travelling had a positive effect on social play, but it had an estimate close to 0, and thus had a very weak effect. Adult females played more with other adults than adult males (Table 2). The density of howler monkeys and the study area did not have a significant effect on social play.

Factors Explaining Adult–Immature Social Play

Group size, the immature to adult ratio and the percentage of time spent travelling all positively affected adult–immature social play (Table 3, Fig. 5). The percentage of time spent foraging on fruit had a low negative estimate and a high standard error and the density of howler monkeys and study area did not have a significant effect on adult–immature play. Adult females played with immatures more than adult males.

Adult Social Play Preferences

We observed a total of 1261 social play bouts: 40% (499 bouts) occurred only between adults, whereas 60% (762 bouts) occurred between adults and immatures. However, adult howler monkeys did not show a significant preference to play with immatures over other adults ($t_{46} = 0.78$, $P = 0.44$; Fig. 6). Neither adult females ($t_{35} = 0.99$, $P = 0.47$) nor adult males ($t_{20} = 0.17$, $P = 0.86$) showed a preference to play with immatures over adults, as preference values were close to 0 (Fig. 6).

DISCUSSION

Despite play occupying a low proportion of overall observation time (0.61% of 1884 total observation hours) in adult howler monkeys in this study, it did not disappear during adulthood and even the oldest known individuals engaged in social play. The amount of time dedicated to social play in howler monkeys was negatively correlated with their age, which is the general rule among animals (Fagen, 1981). The peak in play occurred around the weaning age of howler monkeys (Baldwin & Baldwin, 1978) and was followed by a steady decline as they age (Fagen, 1981; Pellegrini & Smith, 2005). Adult play was sensitive to several socioecological factors, which offer insight into the role of this behaviour in adult howler monkeys.

Table 2
Summary of GLMM estimates explaining variation in adult–adult play among *Alouatta palliata* adult individuals

Parameter	Estimate	SE	*z*	*P*
(Intercept)	-6.43	0.42	-15.11	< 0.001
Immature to adult ratio	-1.32	0.029	-44.96	< 0.001
Number of adults	0.52	0.023	22.19	< 0.001
% Time feeding on fruit	0.15	0.014	10.74	< 0.001
% Time travelling	0.01	0.003	3.09	< 0.001
Howler density	-0.8	0.70	-1.19	0.231
Sex(male)	-0.37	0.008	-44.90	< 0.001
Study area	-0.64	0.53	-1.20	0.230

In terms of the social predictors of adult play, both adult–adult play and adult–immature play increased with the number of adults and overall group size, respectively. This is consistent with other studies showing that play increases with the number of potential playmates, and therefore there being more opportunities to play in a larger social group (Fagen, 1981). Our study also supports the notion that immatures constitute an important stimulus for adult play (Fagen, 1981, 1992) as adult–immature play increased with the proportion of immatures in the group. Play in this context has been discussed as having an educational/socialization function, helping immatures learn social rules and create and develop relationships (Bekoff, 1984; Enders & Carpenter, 1934; Fagen, 1992; Pellegrini & Smith, 2005; Poirier & Smith, 1974). However, we did not find a preference for adults to play with immatures, and adult–adult play was relatively common in the different study groups. This suggests that adult–adult play may fulfil important functions in howler monkey society.

Having more individuals in a group may favour play as a mechanism to facilitate both group cohesiveness and tension reduction (Palagi et al., 2006; Shimada & Sueur, 2018; Yamanashi et al., 2018) in the same way grooming behaviour does (Grueter et al., 2013; Kudo & Dunbar, 2001). It is noteworthy that individuals of *A. palliata* very rarely groom each other (Crockett & Eisenberg, 1987). Moreover, both male and female howler monkeys disperse and groups are thus usually formed of unfamiliar individuals that immigrated from other groups (Arroyo-Rodríguez and Asensio et al., 2008, Arroyo-Rodríguez and Mandujano et al., 2008; Clarke & Glander, 2010; Cristóbal Azkarate et al., 2015). This may increase the necessity of interacting with other members of the group to strengthen group cohesion. Therefore, in the absence of other obvious affiliative behaviours in howler monkeys, play may be occupying at least part of the role that grooming would in other primate species. This idea is supported by the observation that the percentage of time dedicated to foraging on fruits was positively correlated with adult–adult play. Fruit is a defensible resource that generates contest competition (Clutton-Brock & Harvey, 1977; Emlen & Oring, 1977) and Palagi et al. (2004) found a peak in the frequencies of both grooming and social play time among adult chimpanzees, *Pan troglodytes*, particularly before feeding, a period that creates high stress in the species. These behavioural peaks during an apprehensive context suggest that play and grooming share a mechanism to deal with social conflicts. Although predominantly folivorous, howler monkeys can be frugivorous when fruit are available (Asensio et al., 2007; Cristóbal-Azkarate & Arroyo-Rodríguez, 2007; Dunn et al., 2010), and Bergman et al. (2016) suggested that across *Alouatta* species, *A. palliata* has the highest levels of intragroup contest competition. However, howler monkeys do not possess a fixed social hierarchy to navigate this potential competitive setting and rarely show aggression to each other (but see Cristóbal-Azkarate et al., 2004), and Pellis and Iwaniuk (2000a) argued that social play is a substitute for codified and structured social rules. This aligns with the possibility that in species with social uncertainty, social play could serve to assess social relationships (Ciani et al., 2012; Palagi et al., 2016). Garcia (2001) suggested that social play among howler monkeys in the AGA group is used as a way of testing and establishing social hierarchies without engaging in an open fight. Regardless of whether play has a competitive or an affiliative role in adult howler monkeys (or both), our findings support the idea that adult social play might be used as a tool for regulating social relationships within howler monkey groups.

An alternative hypothesis for the positive effect of fruit consumption on adult–adult play could be that a fruit-based diet

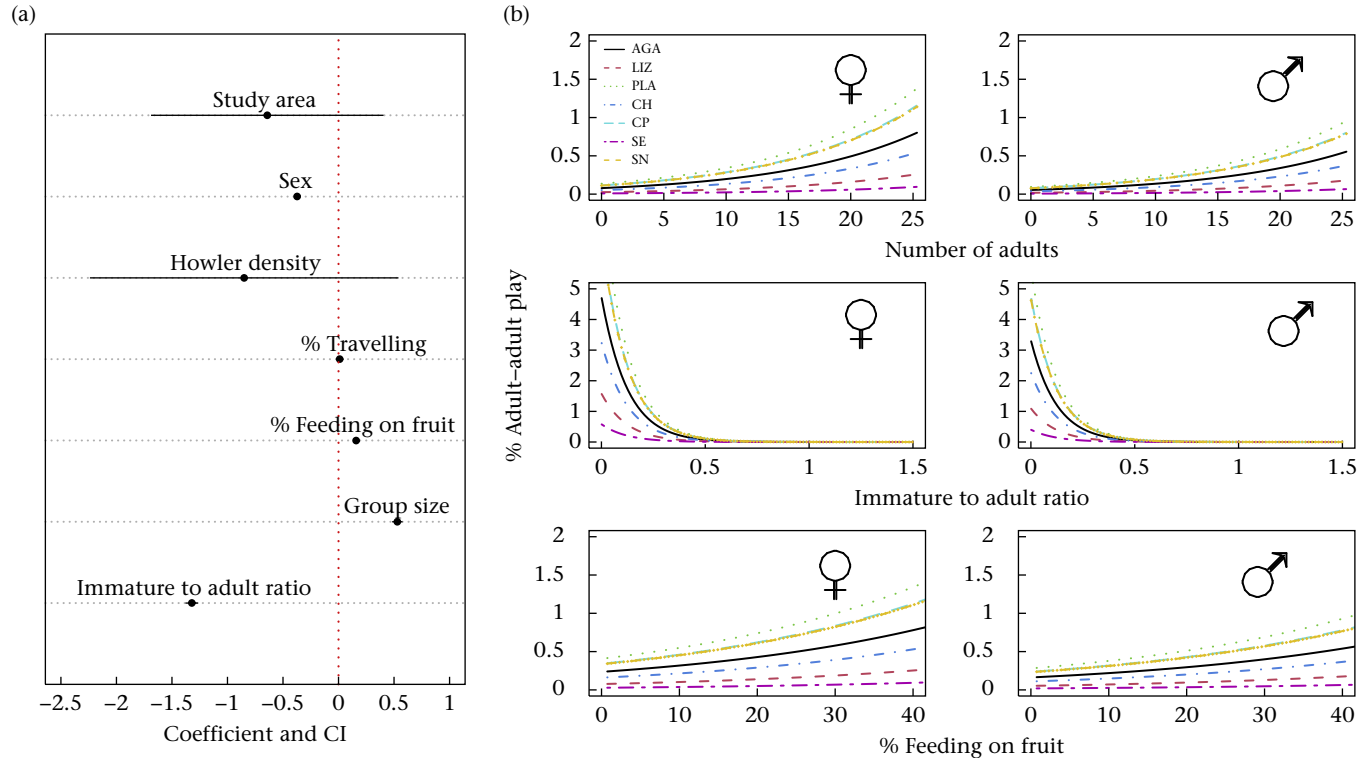

Figure 4. (a) Coefficients (dots) and 95% confidence intervals (horizontal lines) of the GLMM explaining adult–adult play. (b) Mean fitted responses for the time engaged in adult–adult social play (expressed as percentage of observation time) by howler monkeys according to sex, the number of adults in the group, the immature to adult ratio and the percentage of time spent feeding on fruit. Group ID was a random factor: AGA: Agaltepec Island; LIZ: Arroyo Liza; PLA: Playa Escondida; CH: Charlie; CP: Cerco de piedra; SE: San Emilio; SN: Sendero Natural.

provides more energy than a leaf-based one (Milton, 1980). However, if this was the case, we should have also observed a positive effect of time dedicated to foraging on fruits over adult–immature play. Such a difference is likely to be due to immature animals not being direct competitors of adults at fruit trees yet, as they are not fully dependent on plant eating to obtain energy (Baldwin & Baldwin, 1978). In contrast, the proportion of time dedicated to travelling did not affect adult–adult play but was unexpectedly positively correlated with adult–immature play. Perhaps more movement in the group as a result of travelling creates opportunities for adults to encounter immatures, and vice versa (Dunn et al., 2010, 2013) and, thus, this situation triggers adult–immature play. However, the same effect was not found in adult–adult play, for which we could not find another reasonable explanation.

Adult females played more with both other adults and immatures than adult males did. In principle, adult females are predicted to play less overall, as they are more constrained by the energy requirements of reproduction (Fagen, 1981). This effect might be particularly strong in energy-conservative howler monkeys (Milton, 1998). However, this gives further weight to the possibility that females, which are more vulnerable to within-group food competition than males (Isbell, 1991), may use play to solve conflicts over access to food resources (Palagi et al., 2004).

Two of the study groups (SE and AGA) live in very small forest fragments with high howler density and are exposed to the strong negative effects of fragmentation, such as edge effects and low fruit availability (Marsh, 2003). In other studies, play behaviour has been shown to decrease or disappear entirely under food shortage or other stressful situations (Held & Špinka, 2011; Sharpe et al., 2002; Sommer & Mendoza-Granados, 1995). However, neither the size of the study area nor howler density was correlated with adult social play. Adults from SE and AGA groups exhibited play at similar or higher percentages than adults living in larger study sites and under lower howler densities. Perhaps the known plasticity of howler monkeys to adjust to the negative conditions of fragmentation, such as associated energetic constraints (Bicca-Marques et al., 2020), did not put them in an extreme situation that exempts them from engaging in play. Moreover, in the case of the AGA group, due to virtually living in complete isolation on an island, there exists socioecological circumstances that might trigger adult play for other reasons. The lack of ability to emigrate elsewhere for AGA individuals has also created a particularly large and related group, which provides more playmate availability and higher chances of playing with kin. Animals tend to play most frequently with kin and allies (Fagen, 1981; Pellegrini & Smith, 2005; Tomasello et al., 1990), and the unusual familiarity among individuals in group AGA may boost the

Table 3
Summary of GLMM estimates explaining variation in adult–immature play among *Alouatta palliata* adult individuals

Parameter	Estimate	SE	*z*	*P*
(Intercept)	-7.39	1.02	-7.23	< 0.001
Immature to adult ratio	0.35	0.03	10.79	< 0.001
Number of adults	0.63	0.04	12.72	< 0.001
% Time feeding on fruit	-0.22	0.02	-9.34	< 0.001
% Time travelling	0.51	0.004	108.23	< 0.001
Howler density	-0.85	1.68	-0.50	0.613
Sex (male)	-0.33	0.009	-35.07	< 0.001
Study area	-1.07	1.27	-0.84	0.400

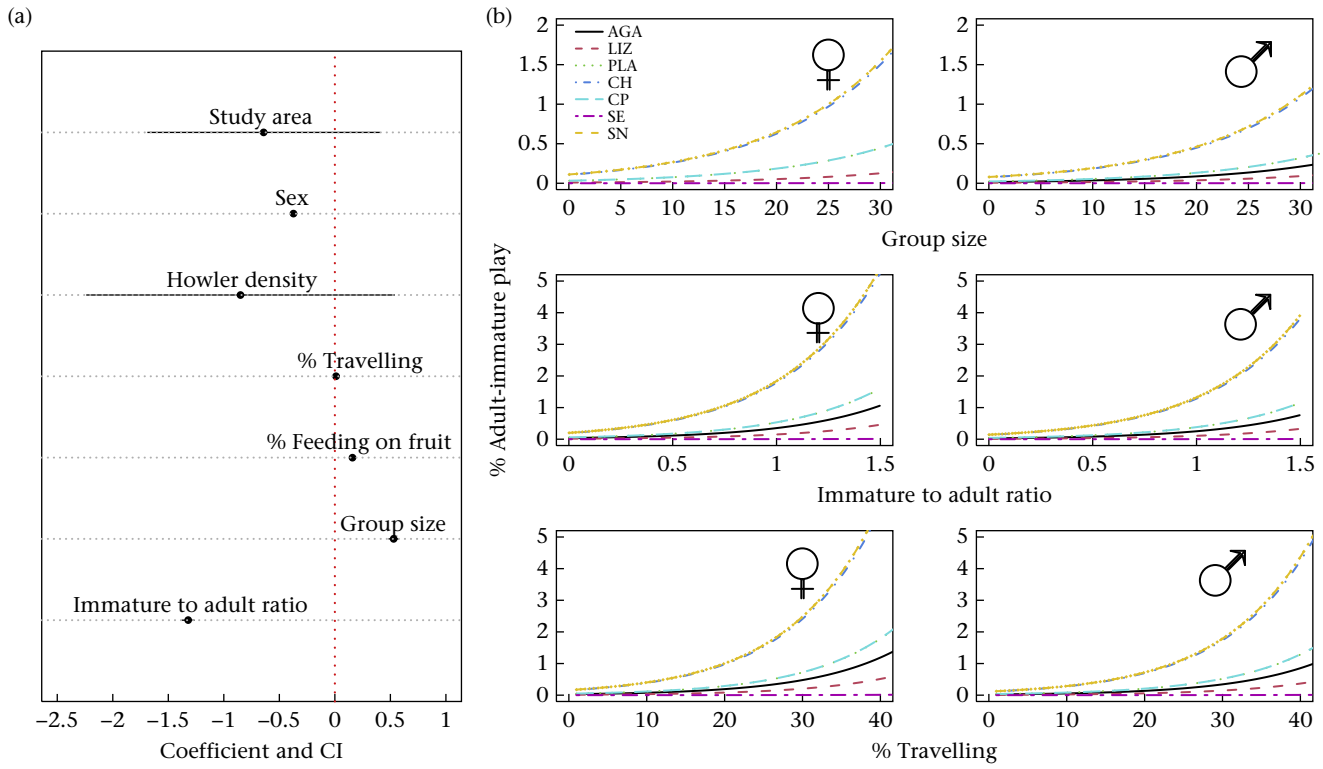

Figure 5. (a) Coefficients (dots) and 95% confidence intervals (horizontal lines) of the GLMM explaining adult–immature play. (b) Averaged fitted responses for time engaged in adult–immature social play (expressed as percentage of observation time) by howler monkeys according to sex, group size, the immature to adult ratio and the percentage of time spent travelling. Group ID was a random factor: AGA: Agaltepec Island; LIZ: Arroyo Liza; PLA: Playa Escondida; CH: Charlie; CP: Cerco de piedra; SE: San Emilio; SN: Sendero Natural.

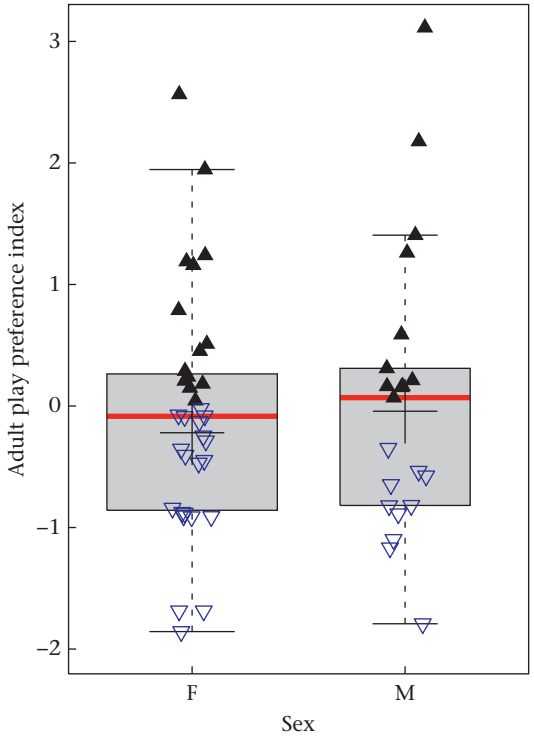

Figure 6. Play preference index of adult female (F) and male (M) howler monkeys for other adults and immatures. Values over 0 (solid point-up triangles) indicate a preference to play with adults whereas those under 0 (empty point-down triangles) a preference to play with immatures. Solid lines and crosses within the box mark the median and mean, respectively. The edges of the box indicate the 25th and 75th percentiles and the whiskers indicate the values within 1.5 times the interquartile range. Points outside this range are outliers.

largest adult–adult play percentages of all study sites (but see Biben, 2010). Moreover, AGA's fission–fusion dynamics (Dias & Rodríguez-Luna, 2006), highly atypical for the species, may have created the necessity to regulate social relationships through play at the potentially tense subgroup fusions. This possibility suggests further research studying whether play occurs at fusion events in this group.

Conclusions

Howler monkeys generally have an inactive lifestyle to save the energy needed for plant digestion from their highly folivorous diet (Milton, 1998). Thus, our results of adult social play seem to align with the expectations of how an energy-conservative species should behave regarding an energy-costly activity such as play (Martin & Caro, 1985), and the idea that social play is mainly present in primate species with a dynamic social organization such as *Ateles*, *Cacajao* and *Pan*, but not *Alouatta* (Pellis & Iwaniuk, 2000a). Still, our findings indicate that adult play in howler monkeys is not atypical in their social behavioural repertoire.

We found that several socioecological parameters structure social play in adult howler monkeys: age, sex, group size, immature to adult ratios, travelling and frugivory. Moreover, the effect of immature to adult ratios and frugivory varied depending on whether adults played with other adults or immatures in a group. When adult play is directed to immatures, it should reasonably have the function of socializing/educating them. However, when play is directed towards adults, this suggests that it may act as a tool that regulates social relationships, which may be either competitive or affiliative.

These findings imply that play is a behaviour that may have a role that varies depending on the sex of the adult, the context adults face in each group, and whether the interaction is with other adults or immatures. Considering the potential variation in both

contextual use and function of play, and its cooperative and competitive elements (Bateson & Barrett, 2008; Bauer & Smuts, 2007; Breuggeman, 1978; Cordoni et al., 2021), it seems likely that the same social behaviour has the facultative role of adjusting to different situations, and thus functions, 'disguised' in the same behavioural structure.

We suggest that despite its overall form, and the general perception of what play means, this behaviour may not necessarily be associated with education, joy or frivolity, but it may serve other roles that are not so obvious, such as reducing social tension during competition.

Author Contributions

Norberto Asensio: Study design, data collection, data curation, data analyses and writing; **Eugenia Zandona**: Study design, data collection, data curation and writing; **Jurgi Cristobal-Azkarate**: Methodology, writing, review, editing; **Jacob C. Dunn**: Methodology, writing, review, editing.

Data Availability

The data sets in CSV (comma separated values) and reproducible R scripts used for this study are available at https://github.com/norberello/social-play-in-adult-howler-monkeys or from the corresponding author on reasonable request.

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