Received: 31 July 2017 | Revised: 17 July 2018 | Accepted: 19 July 2018
DOI: 10.1002/ajp.22909

RESEARCH ARTICLE

WILEY AMERICAN JOURNAL OF PRIMATOLOGY

Social play among black and gold howler monkey (*Alouatta caraya*) immatures during intergroup encounters

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Funding information
American Society of Mammalogists; Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina; Zoo of Barcelona; Idea Wild; International Primatological Society; Animal Behavior Society

We studied intergroup social play (IGSP) among immatures in wild black and gold howler monkeys (*Alouatta caraya*) in northeastern Argentina. IGSP events are one form of affiliative interaction that can occur during intergroup encounters. The main goal of this study was to analyze IGSP in *A. caraya* immatures and assess how intrinsic (e.g., age and sex) and extrinsic (e.g., seasonality) factors can influence the development of this type of social behavior. We followed 12 groups between 2008 and 2015 and recorded 182 encounters and 61 events of IGSP. Considering the composition of play partners, most IGSP events occurred among juveniles of both sexes (33%), followed by juveniles that were only-male (31%), and finally between mixed-sex juveniles and infants (20%) interactions. Additionally, most IGSP events occurred mainly in summer (56%), followed by spring (29%), with fewer events occurring in autumn (15%) and no IGSP events recorded in winter. Our results suggest that IGSP constitutes a beneficial activity in wild *A. caraya* that promotes behavioral flexibility, where immatures acquire social skills, such as tolerance, by interacting with unknown individuals. Moreover, the higher participation of young males in IGSP is consistent with the fact that adult black and gold howler males tend to be more actively involved in group encounters than females, supporting the hypothesis that social play provides benefits in the development of motor and social skills. Finally, seasonality in the frequencies of IGSP might be related to availability of foods with high and easily mobilized energy content in summer and spring.

KEYWORDS
Alouatta caraya, development, intergroup encounters, sex differences, social play

1 | INTRODUCTION

Play in mammals is a crucial activity for promoting the development of motor and social skills and fine-tuning a species-specific behavioral repertoire (Fagen, 1993; Montgomery, 2014). Play consists of repeated, seemingly non-functional behaviors initiated when the animal is in a relaxed, unstimulating, or low stress setting (Burghardt, 2014). High rates of play characterize late infancy and early juvenility in several primates (e.g., *Papio anubis:* Owens, 1975; *Papio hamadryas:* Leresche, 1976; *Pan troglodytes:* Hayaki, 1985; Lonsdorf et al., 2014; *Saimiri sciureus:* Baldwin, 1969). Several authors propose that there is an adaptive value to the time and energy spent during play (Baldwin & Baldwin, 1978; Bekoff, 1988; Byers & Walker, 1995; Montgomery, 2014; Špinka, Newberry, & Bekoff, 2001). For example, such activities have been shown to improve motor, social, and cognitive skills (Biben, 1998; Burghardt, 2005; Govindarajulu, Hunte, Vermeer, & Horrocks, 1993; Pellis, Pellis & Bell, 2010). The adaptive value of play has been supported with different arguments, one of which focuses on the association between the type and amount of play that juveniles engage in and the types of behaviors they manifest as adults (Burghardt, 2005).

In this regard, time invested in social play could differ between males and females, suggesting that there might be a relationship between social play during immature periods and the characteristics of adult behaviors and group social structure (Kulik, Amici, Langos, & Widdig, 2015; Lonsdorf et al., 2014; Maestripieri & Ross, 2004; Paukner & Suomi, 2008). In several species, males tend to play more frequently than females (*P. anubis:* Owens, 1975; *Erythrocebus patas:* Rowell & Chism, 1986; *Macaca mulatta:* Kulik et al., 2015; Maestripieri & Hoffman, 2012; *S. sciureus:* Baldwin, 1971; *Cebus apella*: Paukner & Suomi, 2008; *P. troglodytes:* Hayaki, 1985; Lonsdorf et al., 2014; *Gorilla gorilla gorilla:* Maestripieri & Ross, 2004), which may be related to sex difference in behavior among older animals, such as the more active participation of adult males in group defense (Paukner & Suomi, 2008) and mate choice, where reproductive success is largely dependent on fighting skills (Maestripieri & Ross, 2004). In addition, the age class of the play partners also tends to be an important aspect of the play interaction (Cheney, 1978; Fagen, 1993). In this sense, choosing a similarly aged partner for play may be important because their approximately equal weight and strength might allow both animals to participate productively in the playful interaction, resulting in a play bout that is less likely to break down (Fairbanks, 1993; Maestripieri & Ross, 2004).

Another approach to studying the adaptive value of play focuses on the cost of engaging in playing activities, which must be countered by corresponding benefits; otherwise, play would be eliminated by natural selection (Burghardt, 2005). Although social play seems to provide advantages to the individuals involved (development motor, social, and cognitive skills), some studies conducted in captivity suggest that play has energetic costs related to the use of metabolic sources and time that could be devoted to more "important" activities (i.e., foraging, resting, thermoregulation) (Baldwin & Baldwin, 1978; Miller & Byers, 1991; Sharpe, Clutton-Brock, Brotherton, Cameron, & Cherry, 2002; Siviy & Atrens, 1992). Fagen (1981) suggested that play can be influenced by seasonality in habitat quality. Studies in different primate species showed that the fraction of time dedicated to play declines in periods of nutritional stress, suggesting that this social activity has some energetic cost (O'Meara, Graham, Pellis, & Burghardt, 2015; Stone, 2008). For example, studies in *Chlorocebus aethiops* (Lee, 1984), *Rhinopithecus roxellana* (Li et al., 2011), *S. sciureus* (Stone, 2008), and *G. gorilla* (Grueter et al., 2016) have demonstrated that increased playing rates are associated with the availability of high quality food (i.e., fruits with high contents of sugar, such as bamboo shoots).

Several authors have proposed that social play facilitates tolerance and behavioral flexibility (i.e., animals that play adapt better to new requirements or situation in their social environment) (Antonacci, Norscia, & Palagi, 2010; Fagen, 1993; Montgomery, 2014; Palagi, Paoli, & Tarli, 2006; Špinka et al., 2001). In this regard, Špinka et al. (2001) proposed the "training for the unexpected" hypothesis in which play results in increased versatility of movements used to recover from "positional" shocks, such as losing ground underfoot and falling over. Play can also enhance the ability of animals to cope emotionally with unexpected situations. Furthermore, social play allows participating individuals to assess characteristics of others (i.e., strength, motor skills) and to recognize possible future mates or individuals for affiliative interactions (Pellis & Iwaniuk, 2000a).

Although social play has been an important aspect of the behavior of immature primates, intergroup social play (IGSP)—that is, play that occurs between members of different groups in the context of intergroup encounters—has not been studied extensively (but see Antonacci et al. (2010)). In many species, adult individuals of both groups perform different kinds of displays during intergroup encounters, involving vocalizations, aggressive chases, and contact aggression, which in some cases can result in serious injuries or death (Korstjens, Nijssen, & Noë, 2005; Palombit, 1993; Pavé et al., 2012; Watts, MulleR, Amsler, Mbabazi, & Mitani 2006). However, other encounters are characterized by peaceful intermingling and can involve grooming, copulation, and social play among members of different groups or with solitary males (Antonacci et al., 2010; Fashing, 2001; Korstjens et al., 2005; Kowalewski, 2007). An important function of a group encounter is that individuals gain information about different aspects of neighboring groups, such as group composition (age and sex of individuals), reproductive state of adult individuals and future breeding vacancies (Kowalewski & GarbeR, 2010; Lazaro-Perea, 2001; Wilson, Kahlenberg, Wells, & Wrangham, 2012). For example, studies in *P. verreauxi* reported that most of male social play is directed toward unfamiliar males, and therefore, play can be considered as a tool for increasing tolerance toward strangers (Antonacci et al., 2010).

In this study, we explore IGSP by *Alouatta caraya* immatures in the context of intergroup encounters. This howler species lives in cohesive unimale/multimale-multifemale social groups with members of all age classes (infants, juveniles, subadults, adults) (Kowalewski & Zunino, 2004; Zunino, Kowalewski, Oklander, & Gonzalez, 2007). The species is characterized by frequent intergroup encounters (between 1 and 2 encounters/day) (Garber & Kowalewski, 2011). In *A. caraya*, non-agonistic interactions (i.e., mating, grooming, and play) occur in 41% of these group encounters (Kowalewski, 2007). During adulthood, black and gold howler monkeys are sexually dimorphic (i.e., males are, on average, 2 kg heavier than females) (Rumiz, 1990) and dichromatic (males have black pelage while females' fur is golden; Crockett, 1987). Both sexes disperse from their natal groups between juvenility and early adulthood (Pavé et al., 2012; Rumiz, 1990) but female philopatry often occurs across populations (Calegaro-Marques & Bicca-Marques, 1996; Kowalewski, 2007; OklandeR, Kowalewski, & Corach, 2010). In adulthood, this howler species expresses sex-specific behaviors; for example, the social behavior of adult females consists mainly of parental care and grooming, whereas adult males play active roles in context of intergroup encounters and fights (Holzmann, Agostini, & Di Bitetti, 2012; Kowalewski & Garbe, 2010). *A. caraya* shows seasonal variation in birth patterns, diet, activity budget, and daily path length, all of which are potentially influenced by food availability (Kowalewski & Zunino, 2004; Pavé et al., 2012; Raño, Kowalewski, Cerezo, & GarbeR, 2016; Zunino, Pavé, Brividoro, & Kowalewski, 2017). These characteristics make *A. caraya* a good model to explore social play among immatures in the context of group encounters. We predicted that aspects of IGSP should be influenced both by the sex and age of participating individuals (as intrinsic factors) and by seasonality as an extrinsic factor. Specifically, we aimed to answer the following

questions: How common are IGSP events among wild groups of *A. caraya*? Does IGSP involve same sex and similar age individuals? Does IGSP vary according to different seasons of the year?

2 | METHODS

2.1 | Study site

We conducted this study at two nearby sites in northeastern Argentina. One site is Isla Brasilera (IB) (27° 18′ S, 58° 38′ W) in Chaco Province, with an area of 292 ha near the confluence of the Paraná and Paraguay Rivers. This site is characterized by a continuous flooded forest with an ecological density of howlers of 3.25ind/ha (Kowalewski & Zunino, 2004). The other site is a mainland and fragmented forest around Biological Field Station Corrientes (EBCo) and Provincial Park San Cayetano (27° 30′ S, 58° 41′ W) in Corrientes Province, with an area of approximately 160 ha. The ecological density of howlers at this site is 1.04ind/ha (Zunino et al., 2007). The sites are located 27 km from each other, and they do not vary substantively in temperature, precipitation, or photoperiod (Rumiz, 1990). The climate is subtropical at both sites, with an average annual temperature of 21.7 °C and an average annual rainfall of 1,230 mm (National Weather Service at the Aero Corrientes Station). Seasonality is characterized by marked differences in temperature, with average of 27 °C during summer (December–February) and an average of 16 °C during winter (June–August). Rains occur throughout the year with a small decline in precipitation during winter (Rumiz, 1990; Zunino, 1986). In general, the forests of IB and EBCo provide howlers with a stable year-round supply of food items (leaves, flowers, and fruits), but food availability declines in the austral winter (approximately 40% decrease with respect to the austral summer, which is the time of year with the highest food availability) (Kowalewski & Zunino, 2004; Pavé et al., 2012; Zunino et al., 2017).

2.2 | Study groups

We present data collected from 12 groups studied between October 2007 and March 2015 (Table 1). We considered infants to be animals from birth to 1 year old, juveniles to be between 1 and 3 years for females and 1 to 4 years for males, and subadults to be between 3 and 4.5 for females and 4 to 5 for males (Rumiz, 1990). At IB, we studied five groups with a mean home range (±SD) of

TABLE 1 Group composition, observation periods, and hours of the groups studied at both sites in Argentina

Site	Gr	Period	Hours	IF	IM	JF	JM	SAF	SAM	AF	AM	Total
IB	XE	Oct 2008–Oct 2009	156.05	0–1	2–2	2–0	3–2	3–0	2–0	2	1	13
	MA	Oct 2008–Oct 2009	110	1	2	2	2	0	0	3	2	12
		Aug–Nov 2010		1	0	2	1	1	4	1	2	12
	GR	Oct 2008–Oct 2009	123.7	0	1	0	3	0	0	3	1	8
		Aug–Nov 2010		1	2	0	1	0	2	3	1	10
	EM	Oct 2008–Oct 2009	166.75	0	2	1	3	0	0	3	2	11
		Aug–Nov 2010		1	0	0	1	1	0	2	1	6
	CQ	Sept 2008–Nov 2010	53.65	0	2	3	0	1	1	3	3	13
		IB Total	**610.15**									**85**
EBCo	SE	Sept 2008–July 2009	75.31	1	0	0	2	1	1	1	1	7
		June 2012–June 2013	489.5	0	0	3	1	0	0	2	2	8
	AL	Sept 2008–June 2010	312.27	2	0–2	2–3	2–4	0	0	4	2	14–15
		June 2012–June 2013	422	0	0	3	2	0	0	4	2	11
		Aug 2014–March 2015	362	2	2	4	2	0	0	4	1	15
	CN	June 2012 – June 2013	498	0	2	1	1	0	0	2	1	7
		Aug2014–March 2015	362	2	0	0	2	0	0	2	2	8
	HN	Aug 2014–March 2015	342	2	0	2	1	1	0	3	1	10
	HU	Nov 2008–Sept2010	329.11	0–1	0–2	2–3	1	2	0	2	1–2	10–13
		Aug 2014–March 2015	362	2	0	2	2	0	1	6	2	15
	TA	Nov 2009–June 2010	75.31	1	0	0	0	1	0	2	1–2	5–6
		Oct 2007–Feb 2008	232	1	0	1	1	0	0	2	1	6
		June 2012–June 2013	473	0	0	0	1	0	0	4	2	7
	ML	Nov 2009– June 2010	89.01	1	1	1	2	1	0	3	1	9
		EBCo Total	**4,423.51**									**132-137**

Gr, study group; IF, infant female; IM, infant male; JF, juvenile female; JM, juvenile male; SAF, subadult female; SAM, subadult male; AF, adult female; AM, adult male. Line (–) represents changes in the number of individuals across the study in the age–sex class indicated.

4.08 ± 1.13 ha; all these groups overlapped in their home range (range = 25–77%) with 2–3 neighboring groups. At EBCo, we studied seven groups with a mean home range of 9.13 ± 3.38 ha; these groups overlapped their home range (range = 20–75%) with 1–3 neighboring groups. The geographic location of each group was noted every hour during the observation day using a handheld GPS. A total of approximately 470 location records were obtained at the IB site and 4,060 locations for the EBCo site. With these spatial data, we determined home range size using the minimum convex polygon method (Anderson, 1982) with the free software Quantum GIS 2.0.1.

On average (±SD), we obtained 122 ± 44.66 observation hours per study group at IB (range = 53.70–166.80 hr; $n = 5$ groups) and 613.60 ± 225.41 observation hours per study group at EBCo (range = 287.95–789.27 hr; $n = 7$ groups), with a total of 5212.60 observation hours collected across all groups (610.20 hr at IB and 4,602.50 hr at EBCo). Observation hours were distributed across seasons as follows: at IB, 249.50 hr in spring (September to November), 125.70 hr in summer (December to February), 110.10 hr in autumn (March to May), and 124.85 hr in winter (June to August); at EBCo, 1,431.17 hr in spring, 1,537.37 hr in summer, 768.90 hr in autumn, and 865.01 hr in winter.

2.3 | Data collection

We used the *all occurrences technique* (Altmann, 1974) to record group encounters and IGSP events occurring during these encounters. All authors recorded both types of events, mainly as part of their doctoral research projects in their respective study groups, and all followed the same standardized data collection protocol. Group encounters were defined as situations in which two or more groups were in visual contact and within a distance equal to or less than 30 m of one another for more than 10 min (Fernández, Pavé, Peker & Pérez-Rueda, 2017; Kowalewski & Garber, 2010). During each encounter, we recorded the date (season), the occurrence of IGSP, its duration (in seconds), and the sexes and ages of the individuals involved. A social play event was defined as a contact activity that involved two or more individuals that displayed at least one of the following behaviors: chasing and wrestling, tugging and holding, gentle bites, pulling the tail, pushing each other with their hands, and vocalizations that sound like "grr" (Baldwin & Baldwin, 1978; Burghardt, 2005; Holzmann, 2012).

2.4 | Data analyses

We calculated group encounter and IGSP rates for each group as the number of encounters/IGSP event occurring in 100 observation hours. We divided the number of encounters and IGSP events by 100 hr for comparative purposes because we followed the different groups for different hours throughout the different doctoral projects.

To analyze the potential effect of intrinsic factors (i.e., sex and age classes of the play participants) and the extrinsic factor (season) on the occurrence of IGSP, we used a general linear mixed model (GLMM) with binomial (link:*logit*) distribution fit by maximum likelihood [Laplace approximation] (Zuur, Ieno, WalkeR, Saveliev, & Smith, 2009) using the function *lmer* from the "lme4" package in R computing environment version 3.3.1 (R Core Team, 2016). We formulated the GLMM with occurrence/non-occurrence of IGSP as the dependent variable, sex and age classes of the participants, the interaction between sex and age and seasonality as independent variables (fixed effects), and with the group's identity as a random effect; additionally, total observation hours for each group was included as an offset in the model (Table 2). For all combinations of independent variables where IGSP was not observed, the dependent variable took on the value of zero; in contrast, for all combinations of independent variables where IGSP was recorded, the dependent variable took on the value of one. We considered a total of 1,620 combinations of the different levels of the three fixed effects (sex, age, and season). We based model evaluation on the information-theoretic approach using Akaike's information criterion (AIC) to infer the relative support for alternative (Akaike, 1973). We based the interpretation of GLMM results on model ΔAIC_i, that is, AIC of respective model—AIC of best model (Bolker et al., 2009). Following the guidelines published by Burnham and Anderson (2002), we considered models having ΔAICi ≤2 to receive substantial

TABLE 2 Summary of predictor variables included in GLMM analyses.

Variable	Definition
Dependent variable	
IGSP	Binomial (absence of IGSP = 0, presence of IGSP = 1)
Independent variables (fixed effects)	
Sex	Factor variable: Three levels (mixed-sex/only-females/only-males)
Age (combination of age categories in IGSP)	Factor variable: 6 levels (I.J; I.A, J.J, J.A, SA.A, I.J.SA)
Season	Factor variable: Four levels (summer, autumn, spring, winter)
Offset	
Observation hours (hr) per study group	Continuous variable (mean = 633.05 hr, min = 81.01 hr, max = 1097.27 hr)
Independent variables (random effects)	
Group	Factor variable: 12 Levels (Groups: XE, MA, GR, EM, CQ, SE, AL, CN, HN, HU, TA, ML)

Age variable includes the six possible combinations observed in this study. IJ, infants and juveniles; IA, infants and adults; JJ, all juveniles; JA, juveniles and adults; SAA, subadults and adults; IJSA, infants, juveniles and subadults. IGSP event includes from 2 to 6 participants.

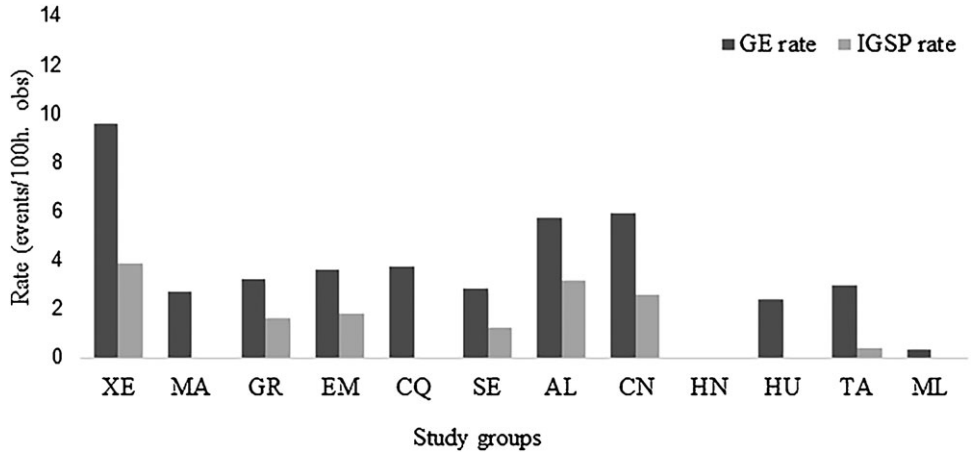

FIGURE 1 Rates of group encounters (GE) and intergroup social play (IGSP) per group

support, those having Δ AICi within 2–10 to receive considerably less support, and models with ΔAICi>10 to have essentially no support. We calculated marginal and conditional R^2 of the model using the function *r.squaredGLMM* from the "MuMIn" package. Post-hoc analyses of categorical independent variables were tested by conducting a Bonferroni- type multiple-testing procedure, adjusted method: control of the false discovery rate (FDR) (Verhoeven, Simonsen, & McIntyre, 2005) using the function *glht* from the "multcomp" package. Graphical analyses of deviance residuals, using the function *simulateResiduals* from the "DHARMa" package, validated the fitting of the final model.

This research complied with the current laws and regulations of Argentina and was conducted with permission from the National Resources Board, Fauna and Flora Department, Corrientes Province, Argentina. This research also adhered to the American Society of Primatologists Principles for the Ethical Treatment of Primates (https://www.asp.org/society/resolutions/EthicalTreatmentOfNonHumanPrimates.cfm).

3 | RESULTS

In 479 days of field work, we recorded a total of 182 group encounters (3.59 ± 2.58 GE/100 hr) involving 11 of the 12 study groups (in all except the HN group from EBCo site) (range = 0–56 encounters per group). In 51 (28%) of these encounters, we recorded IGSP events (1.22 ± 1.39 IGSP/100 hr). Considering only those encounters in which IGSP events occurred, we recorded 1.33 ± 0.97 IGSP events per group encounter (range = 1–7; $N = 61$). These events involved seven of the groups studied (three groups from IB and four groups from EBCo) (Figure 1). The duration of group encounters was variable, with a mean duration (±SD) of 74.10 ± 74.54 min (range = 2–380 min). The duration of IGSP events was also variable; 7.41 ± 8.24 min (range = 0.13–25 min). On average, the time invested in IGSP events corresponded to 14% (range = 0.38–100%) of the total time invested in each group encounter. GLMM analysis and AIC model selection indicated that sex, age, and season were significant predictors of occurrence of IGSP (R^2m = 91.98%, R^2c = 96.04%, df = 13). Models that excluded any of the fixed effects were not significant (Table 3), and the interaction of sex and age did not add significantly to the explanatory power of the models.

3.1 | Age and sex of play participants

Age and sex classes were significant predictors of play participants in IGSP (Table 3). The number of participants varied from 2 to 6 (2.79 ± 0.91 individuals) for each IGSP event. The most frequent age and sex composition of play participants was mixed-sex juveniles

TABLE 3 Ranking of the best GLMM model to explain variation in intergroup social play among *Alouatta caraya* individuals using AIC

Model	AIC	ΔAIC	Log likelihood	Deviance	Akaike weight
Age + sex + season	299.48	0	−136.74	273.48	0.979
Age*sex + season	307.19	7.71	−128.6	257.2	0.021
Sex + age	344.36	44.88	−136.74	324.36	0
Age + season	349.08	49.6	−163.54	327.08	0
Sex + season	390.53	91.05	−189.27	376.53	0
Age	391.17	91.69	−163.54	327.08	0
Season	434.99	135.51	−212.5	424.99	0
Sex	435.96	136.48	−213.98	427.96	0
Null model	479.28	197.8	−237.64	475.28	0

TABLE 4 GLMM results, estimates of fixed effects that have an effect in the occurrence of intergroup social play in *Alouatta caraya*

Fixed effect	Code	Estimate	Std. Error	Z value	*P*-value
Intercept		−10.23	1.48	−6.92	<0.001***
Age classes of individuals (df = 6)					
Adult + Juvenile	A.J	−0.74	1.31	−0.56	0.57
Adult + Subadult	A.SA	−0.74	1.31	−0.57	0.57
Juveniles + Infants	J.I	2.23	0.84	2.66	<0.01**
All Juveniles	J.J	3.56	0.81	4.4	<0.001***
Subadult + Juvenile + Infant	SA.J.I	−0.74	1.31	−0.56	0.57
Subadult + Juvenile	SA.J	0.65	0.94	0.69	0.49
Sex composition (df = 2)					
Mixed-sex		4.38	1.09	4.01	<0.001***
All males		3.06	1.1	2.78	<0.001***
Season (df = 3)					
Spring		0.99	0.5	1.99	<0.05*
Sumer		1.62	0.47	3.47	<0.001***
Winter		−20.45	8278.8	−0.002	0.99
Standard deviation of random effects: 1.83					

Intercept: Adult + infant/all females/autumn.

(33%), followed by only-male juveniles (31%) and mixed-sex infants and juveniles (20%).

Considering only age composition, two combinations were significantly ($p < 0.01$) higher in their participation in IGSP events: 64% ($N = 39$) of IGSP events occurred among juveniles (mostly only-males or mixed-sex partners) and 21% ($N = 13$) of IGSP events involved juveniles and infants (Table 4). We did not observe IGSP events exclusively among infants, among subadults, or among adults. Only 7% ($N = 4$) of IGSP events occurred between a juvenile and a subadult and only 3% ($N = 2$) were between infants and adults. Additionally, we recorded a small number of IGSP events for some cases, specifically between juveniles and one adult, juveniles and infants, juveniles and one subadult, and between one adult and subadult (1% of IGSPs for each event). Post hoc analysis exhibited differences only in the comparison of all-juvenile IGSPs to those of other combinations of ages (Figure 2, Table 5).

Regarding the sex of IGSP participants, 64% ($N = 39$) of the IGSP events involved both males and females (mixed-sex), 34% ($N = 21$) involved only-males (Table 4), and 2% ($N = 1$) involved only-females (Figure 3, Table 4). Post hoc analyses exhibited differences between the three levels (Figure 3, Table 5).

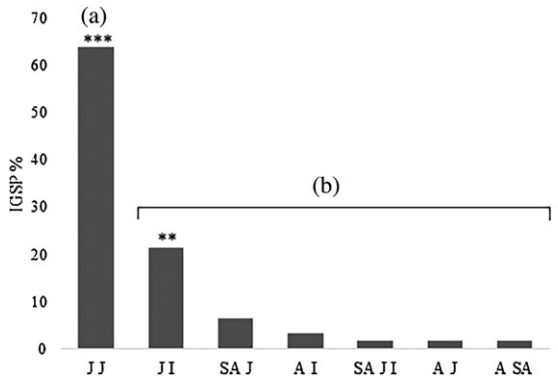

FIGURE 2 Percentages of IGSP for each age combination. a and b correspond to the subgrouping given by multiple comparison level from Bonferroni- type multiple-testing procedure (adjusted method: FDR) Signif. codes: 0.001 "***," 0.01 "**" correspond to GLMM results

3.2 | Seasonality

Season also turned out to be an important predictor in the GLMM model (Figure 4; Table 3); 56% ($N = 34$) of the events occurred in summer, 29% ($N = 18$) in spring, 15% ($N = 9$) in autumn, and there were no events in winter. Post hoc analyses found differences in the occurrence of IGSP between summer and autumn (Table 5), and winter differed from the rest of the seasons in that no IGSP events were observed during this season (Figure 4, Table 5).

4 | DISCUSSION

We studied social play among *A. caraya* immatures in the context of group encounters in twelve groups inhabiting two nearby sites in northern Argentina. We found sex differences in animals' participation in IGSP events. We also found that the occurrence of IGSP was related to the age category of the play participants as well as to the season of the year.

TABLE 5 Post hoc comparison test results: Bonferroni-type multiple-testing procedure (adjusted method: FDR), for the fixed effects that resulted significate in the occurrence of intergroup social play in *Alouatta caraya*

	Estimate	Std-error	Z value	*P*-value
Sex				
Mixed-sex—females	4.38	1.09	4.01	<0.001***
Males—females	3.06	1.1	2.78	<0.05*
Males—mixed-sex	−1.32	0.38	−3.49	<0.01**
Age				
J.J—A.I	3.55	0.8	4.4	<0.001***
J.J—A.J	4.31	1.1	3.91	<0.01**
J.J—A. SA	4.3	1.1	3.91	<0.01**
SA. J—J.J	−2.91	0.62	−4.7	<0.001***
SA.J.I—J.J	−4.31	1.1	−3.91	<0.01**
Season				
Summer vs. autumn	1.63	0.47	3.47	<0.01**

Only significate differences are considered, all the comparisons missing were not statistically significant.

4.1 | Sex differences

Our findings of greater mixed-sex and male-only IGSP events and fewer female-only IGSP events suggest sex differences in IGSP among *A. caraya* individuals. This result is comparable with the findings on social play of other primates, where males engage in social play more frequently than females (*M. mulatta*: Maestripieri & Hoffman, 2012; *P. anubis*: Owens, 1975; *P. hamadryas*: Leresche, 1976; *R. roxellana*: Li et al., 2011; *P. troglodytes*: Hayaki, 1985; Lonsdorf et al., 2014; *G. gorilla*: Maestripieri & Ross, 2004; *S. sciureus*: Baldwin, 1971; *C. apella*: Paukner & Suomi, 2008). Although studies of intragroup social play by *A. caraya* infants suggests that play participation is not related to participant sex (Pavé et al., 2016), is important to point out that most of IGSP events found in this study were among juveniles rather than infants, suggesting that sex differences may begin later in development. As in other primates (*Colobus polykomos polykomos*; Korstjens et al., 2005 and *Colobus guereza*; Fashing, 2001), both male and female *A. caraya* adults participate in group encounters; however, *A. caraya* adult males lead encounters more often (69%) and display a more active role in group encounters and fights than females. In contrast, females lead more movements to feeding sites (61%) and resting sites (53%) than do males (Fernández, Kowalewski, & Zunino, 2013; Kowalewski, 2007). Additionally, juvenile *A. caraya* males tend to migrate more often in solitary or in pairs toward neighboring groups than do juvenile females (Pavé et al., 2012). This suggests that male IGSP may help males to develop social and motor skills necessary for adult life, a time when males have higher participation than females in group encounters and are active in expelling solitary male intruders (Fagen, 1993; Garber & Kowalewski, 2011; Lonsdorf et al., 2014; Maestripieri & Ross, 2004). Our results suggest that, through IGSP, males may be developing skills relevant for the near and far

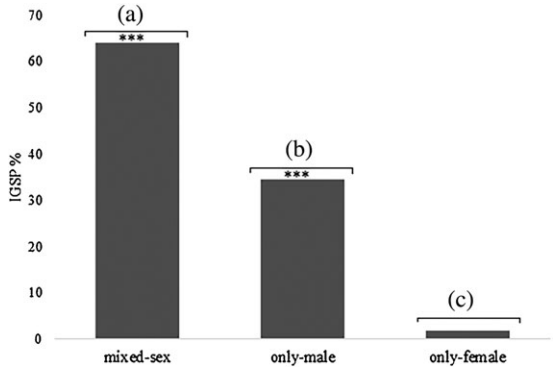

FIGURE 3 Percentages of IGSP for each sex combination a, b, and c correspond to the subgrouping given by multiple comparison level from Bonferroni- type multiple-testing procedure (adjusted method: FDR). Signif. code: 0.001 "***" correspond to GLMM results

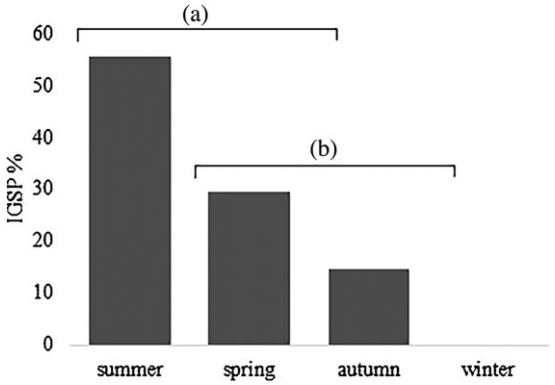

FIGURE 4 IGSP (%) across seasons. a and b correspond to the subgrouping given by multiple comparison level from Bonferroni-type multiple-testing procedure (adjusted method: FDR), note that winter is not included in any group because no IGSP were registered in this season

future (Baldwin & Baldwin, 1978; Pellis & Iwaniuk, 2000a; Pellis et al., 2010). Still, we encourage more detailed studies on social play and social activities in general in wild *Alouatta caraya* immatures to clarify the issue of distinguishing sex behaviors.

4.2 | Age of participants

Like previous studies in *P. anubis* (Owens, 1975), *Alouatta palliata* (Baldwin & Baldwin, 1978; Zucker & Clarke, 1992), and *Cercopithecus aethiops sabaeus* (Govindarajulu et al., 1993), young *A. caraya* individuals appeared to prefer similar age class play partners during IGSP. Just as a kindergarten constitutes a place where children interact and form social bonds with unknown children (Delval, 1994), group encounters constitute a particular context, which provides several advantages to the development of social aptitudes during the juvenile period. We suggest that play with individuals of similar ages from other groups results in more effective social interactions by experiencing "horizontal interactions," which is when individuals of similar ages have similar developments of social and motor skills (Delval, 1994; Govindarajulu et al., 1993; Owens, 1975), size, and strength (Fairbanks, 1993). Though in infrequent, we did observe three events of IGSP that involved the participation of adults and subadults. Infants and juveniles were involved in two of these cases, while the remaining case involved only an adult and a subadult. The occurrence of social play by adults suggests that this behavior might also provide immediate benefits (Palagi, Cordoni, & Borgognini Tarli, 2004; Pellis & Iwaniuk, 2000b). For example, in many primates, play among mature individuals appears to be used in promoting and maintaining social bonds (O'Meara et al., 2015; Pellis & Iwaniuk, 2000b). In other species, IGSP, especially among adults, appears to have a role in managing new social situations and reducing xenophobia (Antonacci et al., 2010). The low frequencies observed for these events in our study, however, do not allow us to adequately assess the social function of such behavior among adult individuals.

4.3 | Seasonality

Most group encounters and IGSP events occurred during spring (29%) and summer (56%) seasons, both of which exhibit highest availability of fleshy fruits (Kowalewski & Zunino, 2004; Pavé et al., 2012; Raño et al., 2016; Zunino et al., 2017). Thus, we suggest that the availability of fruits rich in sugar (Behie & Pavelka, 2015; Garber, Righini, & Kowalewski, 2015) promotes the engagement in social play, especially when considering the energetic cost of IGSP (Coelho, 1974; Burghardt, 2005). Additionally, it is suggested that primate species that inhabit areas with high temperature seasonality (e.g., *R. roxellana*, *M. sylvanus*, *M. fuscata)* invest energy and time in thermoregulation at the expense of other behaviors such as social activities (Hanya, 2004; Hanya, Kiyono, & Hayaishi, 2007; Majolo, McFarland, Young, & Qarro, 2013). In our study sites, low temperatures during winter (average = 16 °C) could have a negative impact on the engagement of individuals in social activities due to the high energetic cost of thermoregulation (Hanya, 2004). Additionally, it is important to point out that the daily path length of *A. caraya* in the EBCo site has previously been recorded as longer during summer (Raño et al., 2016), which could explain why probabilities of group encounters (and IGSP) events are higher during this time of the year. However, more studies are needed to analyze the relationship among daily path length, thermoregulation, group encounters and IGSP.

Even though intragroup social play allows immatures to enhance social skills, we suggest that interactions with individuals from neighboring groups have an additional value in promoting behavioral flexibility (Fagen, 1981; Montgomery, 2014). This ability is considered important for the primate's survival to cope with their unpredictable ecological environment (Poirier, 1969), but it could also be considered as an adaptive quality in a changing social environment, when group composition is dynamic (male replacement, dispersion, and migrations of individuals) and when several interactions occur with neighboring groups. Group encounters could be suitable situations for immatures to interact with minimal injury risk. Nevertheless, intragroup social play seems to be a safer environment than IGSP and is frequently available (in this study all groups had more than one immature individual). We suggest, then, that IGSP in *A. caraya* promotes behavioral flexibility by placing juveniles in unfamiliar situations. Participating in IGSP could also lead to long term advantages such as knowing the characteristics and social aptitudes of neighboring individuals.

In summary, we found that IGSP is influenced by both sex and age of the participants as intrinsic factors and seasonality as an extrinsic factor. Specifically, mixed-sex and male-only IGSP tended to be more frequent than female-only IGSP. In particular, immatures, which are mostly juveniles, tended to play with similar age partners. Seasonality seems to influence play events, with higher IGSP in summer.

ACKNOWLEDGMENTS

We are grateful to all the field assistants who helped us with data collection, as well as to the collaborators and local people at Isla del Cerrito and San Cayetano, and technicians from Estación Biológica Corrientes (MACN-CONICET). We thank Tobias Welp, Sahana Kuthyar and Lotte Skovmand for helping with the English revision of this manuscript. We thank Giselle Mangini, Ignacio Alcántara and Micaela Medina for advising in statistics. We thank K. Bales, P. Garber, A. Di Fiore, P. Dias and two anonymous reviewers for their comments and discussion on earlier versions of this manuscript. RP thanks M. Amparo Perez Rueda for helping in the field. MK and MR thank Bruno K for teaching them different types of play. MB thanks Lorenzo and Ariel for their love and support. This study was financed by the American Society of Mammalogists (SG), Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina (SG, MB, RP, MR, MK), Zoo of Barcelona (RP), Idea Wild (RP), International Primatological Society (MR) and Animal Behavior Society (MB). This research complied with the current laws and permits of Argentina and also adhered to the American Society of Primatologists Principles for the Ethical Treatment of Primates.

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How to cite this article: Gennuso MS, Brividoro M, Pavé R, Raño M, Kowalewski M. Social play among black and gold howler monkey (*Alouatta caraya*) immatures during intergroup encounters. *Am J Primatol*. 2018;e22909. https://doi.org/10.1002/ajp.22909