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ORIGINAL ARTICLE

Does behavioral flexibility contribute to successful play among juvenile rhesus macaques?

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Abstract
Animal play often resembles aggressive interactions, making it difficult for players and third parties to distinguish between the two types of behavior or to concur on aspects of play. In this sense, social play involves some degree of social risk, and players may benefit by behaving flexibly particularly when playing with unmatched partners. Here, we ask (1) whether social play among free-ranging juvenile rhesus monkeys (*Macaca mulatta*) is more likely to fail when partners are unmatched by sex, age, rank/kinship, or when their mothers are nearby and (2) whether juveniles behave flexibly to overcome these social risks. We first identify the factors contributing to play failure, by describing social attributes that are associated with negative outcomes of play. We then compare behavior for matched vs. unmatched partners by examining tendencies to (1) refrain from play, (2) engage in short play durations, and (3) use enhanced play signaling. Males were responsive to several play failure factors; they disproportionately used enhanced play signaling and played for short durations with unmatched partners, suggesting that they have social knowledge that supports attempts to cope flexibly with diverse play partners/situations. Females were less actively responsive to these factors. Although they refrained from playing with many unmatched partners, they did not adjust play tactics to the same degree. These sex differences may be related to differences in life histories; males preparing to disperse eventually may benefit from expanding their social networks through play, while philopatric females may have less need to do so.

Significance statement
While social play provides many benefits for animals, play attempts may also involve risks of failure, from refusal by partners to escalation into aggression, particularly when players are mismatched physically or socially. Growing juveniles in despotic societies may be especially vulnerable to such risk. We ask whether juvenile rhesus monkeys behave flexibly when playing with mismatched partners in a way that may help them overcome such risks. We demonstrate that males, who typically emigrate from their natal groups, are indeed sensitive to mismatches in social characteristics or situations; they play in short durations and enhance their play signaling during play sessions involving mismatches. Females, who permanently remain in their maternal groups are less responsive. These sex differences suggest that juvenile males may hone social skills via playful interaction in preparation for emigration, while females have less need to do so.

Keywords Animal social play · Play signals · Juvenile primates · Despotic primates · Sex differences

Introduction

Social play is common in many mammal species and is also observed in some birds and a few reptiles (reviews in Fagen 1981; Burghardt 2005). Although there is no consensus about

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its precise function(s), most researchers agree that the widespread occurrence of social play in many lineages of mammals and other animals suggests that it is likely to have fitness benefits (e.g., development of motor and cognitive skills: Martin and Caro 1985; Dolhinow 1999; opportunities to assess one's own and others' abilities or social relationships: Thompson 1998; Pellis and Iwaniuk 1999, 2000; training for the unexpected: Špinka et al. 2001; a mechanism to ameliorate socially tense situations: Palagi et al. 2004). Researchers also generally agree that play is likely to have multiple functions and may provide different types of benefits (Dolhinow 1999) to different species or at different life stages of an individual (Palagi et al. 2004). As such, it is reasonable to examine the way animals play with the assumption that successful play experiences (e.g., having play invitations accepted or engaging in lasting play sessions with no disruption by the partner or third parties) should positively influence an individual's fitness, even before we achieve a full understanding of its precise benefits.

At the same time, it is widely accepted that play has costs, including energy, time lost from productive activities (e.g., Miller and Byers 1991), risk of injury and predation, as well as potential social costs (Fagen 1981). For example, when animals engage in vigorous play wrestling and chasing, their behavior often resembles functional behaviors in other contexts including aggression, predation, antipredation, or mating (Fagen 1981; Bekoff and Allen 1998; Pellegrini 2009; Pellis and Pellis 2009). This fact can make it difficult for both players and third parties to distinguish which actions are playful and which are serious (Meaney et al. 1985; Pellis and Pellis 1997, 1998). In fact, play sometimes becomes too rough for one partner and escalates into real aggression (Fedigan 1972; Symons 1978).

These potential costs may be particularly salient for species with despotic social styles such as rhesus macaques that live in strict, kin-based hierarchical societies where levels of social tolerance are low, intense aggression is relatively common, and reconciliation is infrequent (Aureli et al. 1997; Katsukake and Castles 2001; Thierry 2006). However, our understanding of how such costs influence play, particularly in despotic nonhuman primate species, is limited. Nevertheless, despotic macaques appear to adjust their play in ways that reduce potential costs relative to more relaxed macaque species (Petit et al. 2008). For instance, juvenile Japanese macaques (*Macaca fuscata*), another despotic species, are more likely to engage in wrestling in a sitting position, allowing for easier escape from partners, than relaxed crested macaques (*Macaca nigra*) that tend to wrestle laying down or in other vulnerable positions (Petit et al. 2008; Reinhart et al. 2010).

Here, we explore additional ways in which rhesus juveniles, a highly despotic species, may reduce potential costs of play and facilitate gaining successful play experiences by behaving flexibly (Montgomery 2014) in relation to player attributes or conditions. One possible way may be via partner choice; play partners may favor individuals with certain characteristics or avoid those with other characteristics (e.g., Hayaki 1983, 1985; Biben 1998). In many species, play solicitations typically occur among partners that are already familiar with each other or comparable in size and strength (e.g., Fagen 1981; Lewis 2005), age (e.g., baboons, *Papio anubis*: Owens 1975a; chimpanzees, *Pan trodglodytes*: Mendoza-Granados and Sommer 1995; red-necked wallabies, *Macropus rufogriseus*: Watson 1993; sable antelopes, *Hippotragus niger*: Thompson 1996), sex (e.g., Siberian ibex, *Capra ibex sibericus*: Byers 1980; Japanese macaques: Hayaki 1983; squirrel monkeys, *Saimiri sciureus*: Biben 1986), and rank (e.g., rhesus macaques: Caine and Mitchell 1979), or are close in kinship (e.g., vervet monkeys, *Cercopithecus aethiops*: Fedigan 1972; marmoset twins, *Callithrix jacchus*: Box 1975), when matched partners are available. This may be because matched players are more likely to concur about play aspects (e.g., types, intensities, or durations), and as such, play is less likely to end in failure (i.e., refusal of play invitations, aggressive responses, or premature play termination) (Altmann 1962; Baldwin and Baldwin 1972; Owens 1975a; Cheney 1978; Biben 1998). Matched play has also been hypothesized to maximize the physical and social benefits of social play (Owens 1975a; Symons 1978).

Another possible way that juveniles may reduce costs and facilitate successful play experiences would be to flexibly adjust the way they play with unmatched partners. For example, play with unmatched partners may be of shorter durations (Hayaki 1985; Flack et al. 2004) or involve self-handicapping (review in Špinka et al. 2001), in which animals restrain themselves and allow disadvantaged partners (e.g., younger partners) to freely attack them. In role reversals (Altmann 1962; Bekoff 1974; Aldis 1975), dominant animals outside the play context assume subordinate positions during play (Bauer and Smuts 2007) or animals switch their roles (Biben 1998).

Unmatched play also tends to attract protective third parties, particularly partners' mothers, who have an interest in how youngsters play (e.g., rhesus macaques: Gouzoules et al. 1984; chimpanzees: Hayaki 1985; Flack et al. 2004; golden lion tamarins, *Leontopithecus rosalia*: de Oliveira et al. 2003; domestic dogs, *Canis lupus familiaris*: Ward et al. 2009). Conversely, the presence of a protective third party may also encourage the disadvantaged player to play more roughly (Pereira and Preisser 1998). In any case, juveniles may reduce potential costs and enhance their play experiences by being sensitive to the presence of the partner's mother. For example, advantaged players may potentially avoid threats from the partner's mother, by playing for shorter durations in front of her.

Finally, juveniles may adjust the use of metacommunicative signals (Altmann 1962, 1967; Bateson 1972; Bekoff 1972; van Hooff 1972) in a manner that enhances communication of a playful intent, by varying the intensity and frequency of their signals. In general, intense play, and hence more potentially risky play, is hypothesized to be associated with higher frequencies of signaling (e.g., Bekoff 1974, 1995; Hayaki 1985; Watson and Croft 1996; Todt 1997; Biben 1998; de Oliveira et al. 2003; Flack et al. 2004), particularly in despotic societies with high levels of intense aggression (Burghardt 2005; Palagi 2006, 2009). Flack et al. (2004) reported that captive chimpanzees give more play signals and more intense signals when the potential for escalation to aggression is high, for example, when an older player solicits play with a younger partner (but see Cordoni and Palagi 2011) or when the younger partner's mother is present. In captive bonobos (*Pan panisucus*), repeated play signaling occurs in the context of more risky play, such as play fighting, polyadic play, or more aggressive play (Palagi 2008), as well as when space available for play is limited (Palagi et al. 2004; Palagi et al. 2007; Tacconi and Palagi 2009). Similarly, captive male gorillas (*Gorilla gorilla gorilla*) that generally play roughly with one another display more play signals than other sex combinations that engage in more gentle play (Palagi et al. 2007), suggesting that signal use is associated with the prevalence of aggressive elements in social play. Captive bonobos who share good relationships also use signals less frequently (Palagi 2008), likely because they are familiar with each other. Conversely, captive adult ringtail lemurs (*Lemur catta*) that groom each other at lower rates (thus are less familiar with each other) signal more frequently with each other during play (Palagi 2009). Captive adult bonobos (Palagi and Paoli 2007), captive chimpanzees (Cordoni and Palagi 2011), and semi free-ranging Barbary macaques (*Macaca sylvanus*) (Preuschoft 1992) display play faces more frequently in contact play than in solitary play. Male ring-tailed lemurs direct *tail play* to transmit playful mood, when playing with female partners, who can be aggressive to them (Palagi et al. 2016). So far, most evidence on the use of play signals has come from captive or adult animals and has primarily concerned with the use of the play face. What types of behavioral strategies free-ranging or wild juvenile primates, particularly monkeys, adopt during play is still unclear (but see Fröhlich et al. 2016 for flexible gestural use during play in wild chimpanzees).

While there is ample evidence that adult primates have a great deal of social knowledge that they can apply flexibly to a variety of situations, we have little comparable data on juveniles as they navigate their play relationships or on the way that play patterns may be shaped by behavioral flexibility. Such potential flexibility in juveniles should be of particular interest, given that juveniles are more vulnerable to injury and mortality than adults and are in the process of developing skills needed to thrive as adults. Individuals with abilities to respond flexibly to social characteristics related to variations in play costs should be at an advantage over those without such abilities.

Here, we examine the hypothesis that free-ranging juvenile rhesus macaques on Cayo Santiago, Puerto Rico, are sensitive to factors that lead to play failure and behave flexibly in a manner that avoids potential costs and enhances probabilities of successful play experiences. We describe the types of social attributes that are associated with (1) positive and negative outcomes of play attempts, (2) tendencies to engage in vs. refrain from play, (3) short play durations, and (4) enhanced play signaling. In so doing, we tested the following non-mutually exclusive predictions:

P1. Social play is more likely to fail (i.e., to result in a play refusal, aggression by a partner, or intervention by a mother) when partners have unmatched social attributes or when partners' mothers are nearby. Unmatched partner conditions include opposite sex partners, older or younger partners, and distantly ranked mothers (thus distantly related partners).

P2. Juveniles are more likely to refrain altogether from playing with unmatched partners than matched partners. Since we were unable to determine whether individuals actively refrained from playing with unmatched partners or were simply less likely to be near these partners, our designation of *refraining from play* necessarily includes both possibilities.

P3. Successful play with unmatched partners is more likely to result in short duration bouts than play with matched partners. Similarly, successful play bouts with partners whose mothers are nearby are likely to be shorter than those without her presence.

P4. Juveniles are more likely to use or enhance play signals when playing with unmatched than matched partners or when the partners' mothers are nearby. We separately examine the presence vs. absence of at least one signal from the use of repeated signals, given that these aspects of signaling are viewed as conceptually distinct; the use of signals per se suggests a communicative function that may be general or specific, whereas repetition is associated specifically with decreasing ambiguity or the goal of maintaining an ongoing interaction (Bradury and Vehrencamp 1998; Cao et al. 2009).

   a. Juveniles are more likely to signal at least once when playing with unmatched than matched partners or when the partners' mothers are nearby.
   b. Juveniles are more likely to signal repeatedly (more than once) when playing with unmatched than matched partners or when the partners' mothers are nearby.
   c. Juveniles are more likely to use high-intensity play signals when playing with unmatched than matched partners or when the partners' mothers are nearby.

We examined males and females separately, as juveniles in many primate taxa exhibit marked sex differences in their patterns of social play. Typically, juvenile males play more frequently than females (macaques: Symons 1978; Eaton et al. 1986; Glick et al. 1986; Bardi and Borgognini-Tarli 2006; squirrel monkeys: Baldwin and Baldwin 1977; Biben 1986, 1998: baboon spp.: Aldis 1975; Owens 1975a; Pereira 1984; chimpanzees: Hayaki 1985; Nadler et al. 1987; Mendoza-Granados and Sommer 1995; Spijkerman et al. 1996; gorillas: Maestripieri and Ross 2004; orangutans, *Pongo pygmaeus*: Rijksen 1978; Rodman and Mitani 1987). Males also tend to play more roughly than females (e.g., squirrel monkeys: Baldwin 1969; Japanese macaques: Eaton et al. 1986), and females tend to avoid play fights with the intensity of male play (Meaney et al. 1985). These differences partly explain why play groups in many primate species gradually become more male biased in composition as infants develop into juveniles and adolescents (DeVore 1963; Kummer 1968; Owens 1975a). Preferred forms of play also often exhibit typical sex differences. For example, females typically engage in more chasing play (e.g., rhesus and other macaques: Chamove et al. 1967; Harlow 1969; Lancaster 1971; Symons 1978; Levy 1979; Ehardt and Bernstein 1987; Lovejoy and Wallen 1988; olive baboons: Owens 1975a), play mothering, and solitary play (Meaney et al. 1985) than males. Differences in form are hypothesized to correspond to later sex differences in adult roles (e.g., Kahlenberg and Wrangham 2010; Hassett et al. 2010), suggesting that male and female play reflect and perhaps contribute to differential developmental trajectories for each sex (Meaney et al. 1985). As such, play by each sex is likely to be shaped by different developmental needs.

Methods

The site and study group

The study was conducted between October 2006 and August 2007 in the free-ranging population of rhesus monkeys on Cayo Santiago, a 37-ha island off the east coast of Puerto Rico. The population consists of descendants of 409 rhesus monkeys that were brought from India by C. R. Carpenter and released in 1939 (Levy 1979). Since 1956, these monkeys have been marked and censused so that individuals are well habituated, easily observed, and easily identified (Berman 1980). Census takers have also recorded all births within 2 days of parturition. Hence, the maternal genealogical relationships of all individuals are known. The population is predator-free and provisioned with commercial monkey chow daily. Human intervention is limited to non-invasive tests and measurements during an annual trapping season (see Hernandez-Pacheco et al. 2016 for details of the population and management). Social groups on Cayo Santiago, although large, are organized in a species typical manner. Females remain in their natal groups for life and continue to associate closely with their female kin, whereas males disperse around puberty. In this way, the permanent core of the group is organized around maternal kinship lineages (Sade 1972). Formal linear dominance hierarchies can be constructed from the directions of agonistic interactions among dyads. Immature individuals take on ranks vis a vis one another that correlate with those of their mothers; females socially inherit ranks among the adult female hierarchy immediately below their mothers, and sisters rank in reverse order of age. As such, the dominance structure of the group is tightly linked to the kinship structure.

We collected data in one social group (R), the second highest-ranking group on the island, consisting of approximately 250 individuals. There were 11 sublineages, composed of living mothers and their descendants, in group R with 28 adult males, 62 adult females, 80 juveniles (2 to 4 years old), 28 yearlings, and 42 infants, as of March 2007. It was not possible to record data blind because our study involved focal animals in the field.

Subjects and data collection

We observed a total of 20 subjects (10 male and 10 female youngsters) from the 2005 birth cohort (approximately 2 years old at the time of the study) using focal animal sampling. Each subject was sampled a mean ± SE of 17.2 ± 0.12 (male: 17.2 ± 0.21; female: 17.2 ± 0.15) h. A total of 344 h of focal animal samples were collected. We selected 2-year olds as our focal subjects because they were expected to play at high rates with a variety of age groups. In addition, 2-year-old males were unlikely to disperse from the group during the course of the study. Two-year olds were also capable of exhibiting more complex and highly coordinated play behavior than younger counterparts. We chose one male and one female from each maternal sublineage in order to include subjects evenly from all maternal ranks, except for the lowest ranking sublineage that contained only two adult females and their offspring. Each subject had a living mother at the beginning of the study. As such, we compensated for a necessarily moderate sample size by insuring that it represented the entire age class well and by collecting a large amount of data on each subject.

AY collected focal data with a mini-DV camcorder in sessions of at least 30 min each. If the subject was engaged in a play bout at 30 min, observations were extended until 15 s after the end of the bout in order to record the final outcome of the bout. From March to July 2007, two field assistants also collected focal data. We collected data 6 to 7 days per week, whenever possible, from 700 to 1400 h during the weekdays and from 700 to 1300 h during the weekends (the maximum number of hours permitted by the boat schedule). These hours included peak play periods, as well as feeding, foraging, and rest.

Data transcription

AY transcribed the resulting videotapes by entering all playful behaviors and interacting individuals involved during each session. In order to avoid personal biases or expectations in data transcription, both authors conducted two inter-observer reliability tests using a sample of video clips ($N = 35$), one test on the type of play signal (kappa coefficient = 0.93) and the other on its intensity and speed of movement (kappa coefficient = 0.95).

The following was coded on spreadsheets when play occurred: the play partner's ID, its social attributes (sex, age cohort, rank, and kinship), the type of play signals given and other behaviors emitted during the focal session, the intensity of the play signals, the presence and distance of the mothers during play, types of play, and the duration and intensity of play (see the next section for descriptions).

Variables used in this study

Types of play were assigned to one of five simple observable categories: chasing, cuddling, play biting, slapping, and wrestling (Supplement 1: Table 1). Play signals were categorized into the following categories: no signal, play face only, crouch-and-stare, dangle-and-stare, gamboling, hide-and-peek, leg-peek, look-back, and roll-onto-back-and-stare (Supplement 1: Table 2). The eight signals are (1) used exclusively in playful contexts, (2) distinct in form from actual play, and (3) predictive of the imminent occurrence of play (Yanagi and Berman 2014a, b).

We considered a play encounter to be initiated when the first communicative behavior pattern was directed. These included the onset of mutual visual contact with an approach (Levy 1979) or an approach followed by physical contact to initiate one of the play types. The onset of an actual bout was determined when a play component, such as biting for play biting or running to/away for chasing, was first observed after the initial contact. Both play signal intensity and social play intensity were measured as low, medium, or high, based on the speed, frequency, or the extent of movement observed in performing the play signal or play behavior (Supplement 1: Tables 3 and 4). We considered a play bout to be terminated when two players stopped interacting with each other, ceased looking at each other, or started engaging in different activities, such as foraging, or began to interact with another individual for more than 5 s.

After the initial contact by a player, a play bout was considered to be successful when the first response (within 2–3 s) was (1) one or more of the play types described above or (2) a play signal that led to a play type and (3) the play did not end with aggression or interruption by a third party. Otherwise, the bout was considered unsuccessful. In such unsuccessful bouts, the receiver of the signal/contact may respond with aggression, by ignoring the signaler (paying no attention to the signaler, continuing to/moving on to engage in other activities, while staying in the scene), leaving the scene, refusing (staying in the scene but responding unfavorably or showing resistance to the contact/signal), or may be interrupted by the mother or other third parties. There were also cases in which the receiver engaged in signal exchanges with the signaler, but no actual play was initiated. If these signal exchanges did not lead to an aforementioned play type, they were also considered unsuccessful.

Partners' social attributes were recorded based on similarities and differences between players in sex (same vs. opposite), age cohort (peer/same age (cohort 2005), older than focal (cohorts 2003–2004), yearling (cohort 2006), infant (cohort 2007)), and mothers' ranks (similar rank/sibling, one or two ranks apart, at least three ranks apart) and maternal kinship (siblings [$r = 0.25$], other close kin [$0.25 > r \geq 0.125$], distant kin [$0.125 > r > 0$], and unrelated group members [$r = 0$]). For simplicity's sake, we did not specify the directions of rank differences (i.e., whether focal ranks were higher or lower than its partner's), because preliminary analyses found no asymmetries in the results based on direction. The distance of the focal's and partner's mother was analyzed in four categories: ≤ 1, > 1 but ≤ 3, > 3 m, and out of sight. Potential partners to focals included all individuals that were under 4 years old and were members of group R for five or more months of the study, except three 3-year-old females that already had offspring. One 5-year-old male was included because he consistently stayed in the group and was an active player with a few focal subjects.

Data analysis

All analyses were conducted using SPSS 24 (IBM SPSS Statistics, Armonk, NY, USA) and were two-tailed. We used generalized linear mixed models (GLMMs) to assess the effects of various social attributes on tendencies for play to be unsuccessful (P1), tendencies for focals to play with particular partners at all vs. refraining from play (P2), play durations (P3), and patterns of signaling behavior (P4). For P1 (play failure), the target variable was dichotomous: successful vs. unsuccessful play bouts. For P2 (tendencies to refrain from play), we examined whether or not focals engaged in playful communication with a particular partner at least once during the study. For P4a–c (signal occurrence, frequency, and intensity), we examined the following targeted outcomes: frequency (P4a: no signal vs. at least one signal; P4b: one signal vs. repeated signaling) and intensity (P4c: low vs. high). These dichotomous categories were used due to an excess number of zeros (i.e., when there was no signal used to initiate or maintain play). In the analysis for P4, all play signals from the initial play encounter to the end of the bout were considered in the analyses in order to maximize our sample sizes. We transformed values for play durations into a dichotomous variable (< 16 vs. ≥ 16 s) based on the mean value for each sex (see Table 1). We tested successful and unsuccessful bouts separately for all the tests of P4 (signal use), while P3 only involved successful bouts (as unsuccessful bouts would not involve any play durations), in order to examine the factors that led to the success of play negotiation. For all the GLMMs performed on successful bouts, we controlled for play intensity, as it is likely to influence juveniles' signaling behavior (see Flack et al. 2004).

Given our dichotomous target variables, we performed GLMMs with a binominal error distribution with logit link function. The following variables were fitted in GLMMs as fixed effects in all analyses: sex, age cohort, rank, partners' mothers' distances, and play intensity (for successful bouts). Individual focal IDs and focal sessions were set as random effects. We ran separate tests for male and female subjects not only because of sex differences in the qualities of play (see above) but also because the inclusion of an interaction factor with sex drastically reduced the power of our analyses. We also originally included kinship as a fixed effect; however, a strong correlation between kinship and rank distance ($r > 0.9$; VIF = 6.6–6.8) made it necessary to remove one of these variables to avoid collinearity (Supplement 2: Table 1). The choice was arbitrary; when we substituted kinship for rank distance, the results were virtually identical. Thus, the results we found for rank distance most likely should be interpreted as applying to rank distance and/or kinship. Similarly, it was necessary to drop the focal's mother's location from the analysis because we found that it was strongly correlated with the partner's mother's location ($r > 0.8$; VIF = 2.1–2.9; Supplement 2: Table 1) and that only the partner's mother's location showed strong associations with the variables of our interest.

We initially constructed two models for each hypothesis, one with all main effects and the other with main effects and

Table 1 Comparison of play attributes for females vs. males

Play attribute	Level	Female[a]	Male[a]	Significance[b]
Play characteristics	Total number of play bouts	919	*1754*	$U = 9$, $P = 0.002$
	Successful bouts (%)	40.7	*53.1*	$U = 14$, $P = 0.007$
	Mean duration of play bouts	15.9	16.2	NS
	Mean frequency of play signals	0.8	*1.4*	$U = 3$, $P \leq 0.0005$
	Mean proportion of play initiation	0.7	0.6	NS
	Mean number of play partners	19	*28*	$U = 15$, $P = 0.007$
Partner sex (%)	Same sex	58.3	*81.5*	$U = 11$, $P = 0.003$
	Opposite sex	*41.7*	18.5	$U = 11$, $P = 0.003$
Partner age cohort (%)	Peer	14.9	*29.9*	$U = 14$, $P = 0.007$
	Older	12.7	*22.5*	$U = 22$, $P = 0.034$
	Younger	29.5	32.5	NS
	Infant	*42.9*	15.2	$U = 13$, $P = 0.005$
Partner kinship (%)	Sibling	36.1	24.5	NS
	Other close relative	19.5	18.7	NS
	Distant relative	20	19.4	NS
	Unrelated	24.4	37.5	NS
Partner maternal rank (%)	Same rank	36.1	24.5	NS
	1–2 Ranks apart	28.9	25.5	NS
	3+ Ranks apart	34.9	50.1	NS
Focal mother distance (%)	≤ 1 m	*16.8*	7.3	$U = 20$, $P = 0.023$
	> 1–≤ 3 m	*12*	4.6	$U = 23$, $P = 0.041$
	> 3 m	*24.7*	11.1	$U = 20$, $P = 0.023$
	Out of sight	46.6	*77*	$U = 15$, $P = 0.008$
Partner mother distance (%)	≤ 1 m	*16.5*	7	$U = 15$, $P = 0.008$
	> 1–≤ 3 m	*10.9*	3.8	$U = 13$, $P = 0.005$
	> 3 m	*20.8*	7.2	$U = 0$, $P \leq 0.0005$
	Out of sight	51.9	*82.1*	$U = 2$, $P \leq 0.0005$

[a] Ital numbers represent significantly higher values

[b] Mann-Whitney U tests

all possible two-way interactions between main effects, and chose the model that produced the lower value of Akaike information criterion (AIC), indicating a better fit. All models except for two had lower AIC values for models with the main effects only. One of these models, however, did not actually include any significant interaction terms, and the other was ill fit as indicated by unusually large values of upper confidence intervals. Consequently, we report the results of the models with main effects only as our final models.

Finally, as we used the same dataset to test eight predictions (P1: factors contributing to unsuccessful play; P3: play durations; P4: (a) presence, (b) repetition, and (c) intensity during successful vs. unsuccessful play), we adjusted our critical values for all overall model effects (i.e., the significance of the full models against their corresponding null models) to overcome possible multiple comparison effects. We used the false discovery rate (FDR) (Benjamini and Hochberg 1995), because it is a more equitable compromise between type I and type II errors than a Bonferroni correction, retaining more statistical power. We set the FDR at 0.05, and the resulting critical values were used: male play: $P \leq 0.0438$; female play: $P \leq 0.0063$. The hypothesis assessing the effects of social attributes on tendencies to refrain from play used a separate dataset; thus, the alpha level remained as $P \leq 0.05$. $P < 0.1$ was considered as a non-significant tendency for all individual variables provided that the overall model was significant after the FDR adjustment.

Results

We summarize the descriptive statistics for male and female play under Table 1, confirming widespread sex differences in play attributes. Below, we describe the results of GLMMs for predictions 1–3 in Table 2 for male play and in Table 3 for female play. The results for the use of play signals (predictions 4a–c) during successful bouts are described in Tables 4 (males) and 5 (females), while those during unsuccessful bouts are described in Tables 6 (males) and 7 (females).

We first identified factors that are likely to lead to play failure by testing the prediction that play attempts with unmatched partners or near mothers were disproportionately likely to be unsuccessful (prediction 1). The percentages of unsuccessful play bouts represented by different forms of negative outcomes are broken down in Fig. 1. As predicted, male play with opposite sex (Fig. 2), infant, and distantly ranked partners by at least three ranks were disproportionately more likely to lead to unsuccessful play (Table 2). Similarly, female play was disproportionately likely to be unsuccessful with infants and partners that differed by at least three ranks (Table 3).

We also examined whether juveniles reduced the risk of play failure by refraining from play (prediction 2) and playing for short durations (prediction 3) with unmatched or otherwise risky partners or near partners' mothers. In both males and females, as predicted, juveniles were disproportionately likely to refrain from playing with partners who were of the opposite sex, distant in age cohort, and of different rank (Tables 2 and 3). However, unlike males, females were disproportionately more likely to play with infants vs. peers (Table 3, Fig. 3). Play with infants was particularly gentle; odds ratios based on chi-squared testing (χ^2 = 27.7, df = 1, $P < 0.0005$) revealed that the females were 37.5 times more likely to engage in gentle forms of play (e.g., cuddle play) than other types of play with infants. The intensity of female play with infants also tended to be low (χ^2 = 5.7, df = 1, $P = 0.01$); females were 2.2 times more likely to play at low intensities with infants than with other types of partners. None of the variables we tested was significantly associated with durations of female play (Table 3). As predicted, males were disproportionately more likely to play for longer durations when the partner's mother was at any distance beyond an arm's reach (Table 2, Fig. 4a). Although the fixed effect for play intensity was significant for male play, none of its fixed coefficients reached significance.

We then examined whether juveniles reduced the risk of play failure by adjusting the presence, repetition, and intensity of play signaling (predictions 4a–c) both during successful and unsuccessful bouts. Males showed a variety of results in this regard. During successful play, as predicted, males were disproportionately more likely to signal at least once to partners that differed in rank by at least three ranks (Table 4, Fig. 4b). Males also tended to signal repeatedly more and were disproportionately likely to signal intensely when the partner's mother was within an arm's reach vs. when she was in the distance of more than 3 m (Table 4). Contrary to our prediction, males were disproportionately likely to forgo signaling to infants (Table 4) once, repeatedly (Fig. 4c), and intensely during successful bouts (Table 4). During unsuccessful bouts (Table 6), males were disproportionately less likely to signal once or repeatedly toward opposite sex partners. They were also disproportionately less likely to signal repeatedly to infants and tended to signal repeatedly less when the mother was out of sight vs. within arm's reach. They were disproportionately likely to signal to moderately closely ranked partners vs. partners of the same rank. We found no significant associations between partner attributes or the partner's mother's distance and intensity during unsuccessful male bouts.

In contrast, none of the models for female play reached significance after applying the FDR adjustment, suggesting that females did not differentiate among partner attributes or conditions (near partners' mothers) with regard to play signaling (Tables 5 and 7). This was in spite of the

Table 2 The results of GLMMs for play failure, refraining from play and play duration in male play

Prediction	Fixed effect[a]	*F*	DF1	DF2	*P* value	Fixed coefficient	*T*	Estimate	SE	*P* value	OR[b]
P1	Play failure overall***	6.6	9	1744	*0.000*						
	Sex***	42.2	1		*0.000*	Opposite sex***	6.50	0.97	0.15	*0.000*	2.6
						Same sex				Reference	
	Age cohort(*)	2.2	1		*0.081*	Infant*	2.24	0.51	0.23	*0.025*	1.7
						Yearling	0.05	0.01	0.15	0.964	
						Older partner	1.06	0.16	0.16	0.291	
						Peer				Reference	
	Rank**	6.3	2		*0.002*	3+ Ranks apart*	2.82	0.48	0.17	*0.005*	1.6
						1–2 Ranks apart	0.09	0.02	0.17	0.931	
						Same rank				Reference	
	Partner mother distance	1.9	3		0.127						
P2	Refrain from play overall***	34.3	6	1433	*0.000*						
	Sex***	111.1	1		*0.000*	Opposite sex***	10.54	2.08	0.20	*0.000*	8.0
						Same sex				Reference	
	Age cohort***	32.0	3		*0.000*	Infant***	9.04	2.40	0.27	*0.000*	11.0
						Yearling***	4.93	1.07	0.22	*0.000*	2.9
						Older Partner***	7.10	1.42	0.20	*0.000*	4.1
						Peer				Reference	
	Rank***	51.2	2		*0.000*	3+ Ranks apart***	5.97	5.06	0.85	*0.000*	157.7
						1–2 Ranks apart*	2.47	2.18	0.89	*0.014*	8.9
						Same rank				Reference	
P3	Play duration overall*	2.1	11	920	*0.031*						
	Sex	0.2	1		0.657						
	Age cohort	0.7	3		0.669						
	Rank	1.2	2		0.559						
	Partner mother distance*	2.6	2		*0.019*	Out of sight*	2.24	0.88	0.39	*0.025*	2.4
						> 3 m*	2.20	0.98	0.44	*0.028*	2.7
						1–3 m**	3.10	1.64	0.53	*0.002*	5.1
						Within arm's reach				Reference	
	Play intensity**	6.0	2		*0.004*	Low	1.38	0.73	0.53	0.169	
						Medium	0.13	0.07	0.55	0.895	
						High				Reference	

[a] Overall model indicates the *P* value of the full model against the null model

[b] Odds ratios were obtained from exp (coefficient) of the result

Significant values are shown in italic

*$P \le 0.05$ (FDR adjustment for overall male models: $P \le 0.044$); **$P \le 0.01$; ***$P \le 0.001$; (*) non-significant tendency ($P < 0.1$)

fact that both males (chi-squared test: $\chi^2 = 130.52$, $df = 1$, $P \leq 0.0005$) and females (chi-squared test: $\chi^2 = 70.59$, $df = 1$, $P \leq 0.0005$) were more likely to signal at least once to their partners during successful bouts.

Discussion

The aim of this study was to better understand the ways in which free-ranging juvenile rhesus macaques behave flexibly in social play and the ways in which those responses may shape play patterns. We identified several factors contributing to play failure for juvenile males and found that they were responsive to some of them. They flexibly used short play durations and enhanced play signaling toward certain types of unmatched partners or situations, suggesting that they may have social knowledge that allows them to cope to some degree with differential likelihoods of play failure. In contrast, while we identified similar factors that led to play failure for juvenile females, they appeared to be less responsive to them. Although they disproportionately refrained from playing with many unmatched partners, when they played with them, they

Table 3 The results of GLMMs for play failure, refraining from play and play duration in female play

Prediction	Fixed effect[a]	*F*	DF1	DF2	*P* value	Fixed coefficient	*T*	Estimate	SE	*P* value	OR[b]
P1	Play failure overall***	3.8	9	909	*0.000*						
	Sex	0.4	1		0.527						
	Age cohort***	8.5	1		*0.000*	Infant**	2.94	0.78	0.26	*0.003*	2.2
						Yearling	−0.77	−0.20	0.27	0.444	
						Older partner	0.16	0.05	0.32	0.872	
						Peer				Reference	
	Rank*	4.3	2		*0.014*	3+ Ranks apart*	2.56	0.59	0.23	*0.011*	1.8
						1–2 Ranks apart	0.24	0.05	0.22	0.815	
						Same rank				Reference	
	Partner mother distance	1.5	3		0.226						
P2	Refraining from play overall***	23.9	6	1433	*0.000*						
	Sex***	11.6	1		*0.001*	Opposite sex***	3.41	0.66	0.19	*0.001*	1.9
						Same sex				Reference	
	Age cohort***	17.0	3		*0.000*	Infant*	−2.19	−0.52	0.24	*0.028*	1.7
						Yearling	0.35	0.10	0.28	0.727	
						Older partner***	5.37	1.90	0.35	*0.000*	6.7
						Peer				Reference	
	Rank***	63.9	2		*0.000*	3+ Ranks apart***	7.00	4.64	0.66	*0.000*	102.3
						1–2 Ranks apart*	2.01	1.41	0.70	*0.045*	4.1
						Same rank				Reference	
P3	Play duration overall	0.9	11	362	0.494						
	Sex	0.8	1		0.359						
	Age cohort	0.3	3		0.794						
	Rank	0.9	2		0.794						
	Partner mother distance	1.2	2		0.298						
	Play intensity	1.0	2		0.381						

[a] Overall model indicates the *P* value of the full model against the null model

[b] Odds ratios were obtained from exp (coefficient) of the result

Significant values are shown in italic

*$P \leq 0.05$ (FDR adjustment for overall female models: $P \leq 0.006$); **$P \leq 0.01$; ***$P \leq 0.001$; (*) non-significant tendency ($P < 0.1$)

did not apparently adjust their play tactics to the same degree. We suggest that these sex differences may be related to differences in life histories. Below, we discuss each of our findings in more detail. Since our results differed markedly between males and females, we will discuss each sex separately.

Male play

Male play with several types of partners was clearly at risk of failure, including opposite sex partners and distantly ranked partners. Males largely refrained from playing with almost all types of unmatched partners. In general, juvenile males played longer when the partner's mother was at a distance. When males played with unmatched partners, they adjusted their signaling, but only when faced with particular kinds of partners or situations. During successful bouts, males were disproportionately more likely to signal at least once to distantly ranked partners than to those that were similarly ranked. Given the strong link between rank distance and kinship in this sample, as well as among rhesus in general (Sade 1972), our results for rank distance should be interpreted as applying to rank distance and/or kinship. Males also disproportionately signaled repeatedly and more intensely when the partner's mother was nearby than when she was at a distance. However, males did not apparently enhance their signals toward opposite sex partners, nor toward those in different age cohorts.

These findings indicate that males may be more likely to respond actively to mismatches involving rank distance/kinship and partners' mothers' location than other social attributes of their partners. Although both males and females were more likely to signal at least once to their partners during successful bouts vs. during unsuccessful bouts, the fact that only males directed signals specifically to particular mismatched partners suggests that only they flexibly attempted to reduce the risks of playing with

Table 4 The results of GLMMs for the use of play signals during successful male bouts

Prediction	Fixed effect[a]	*F*	DF1[b]	DF2[b]	*P* value	Fixed coefficient	*T*	Estimate	SE	*P* value	OR[c]
P4a	Presence of signals overall**	2.7	11	920	*0.002*						
	Sex	2.4	1		0.120						
	Age cohort*	2.8	3		*0.038*	Infant**	− 2.71	− 0.95	0.35	*0.007*	2.6
						Yearling	− 0.57	− 0.14	0.25	0.571	
						Older partner	− 0.84	− 0.22	0.27	0.403	
						Peer				Reference	
	Rank*	3.1	2		*0.044*	3+ Ranks apart*	2.41	0.64	0.27	*0.016*	1.9
						1–2 Ranks apart	0.92	0.24	0.26	0.359	
						Same rank				Reference	
	Partner mother distance	1.3	3		0.278						
	Play intensity	0.3	2		0.706						
P4b	Repeated signaling overall***	3.3			*0.000*						
	Sex$^{(*)}$	3.1			*0.079*	Opposite sex$^{(*)}$	− 1.76	− 0.41	0.23	*0.079*	1.5
						Same sex				Reference	
	Age cohort**	4.1			*0.006*	Infant***	− 3.24	− 1.02	0.32	*0.001*	2.8
						Yearling	− 0.71	− 0.14	0.20	0.477	
						Older partner	0.06	0.01	0.21	0.956	
						Peer				Reference	
	Rank	1.5			0.217						
	Partner mother distance*	2.8			*0.040*	Out of sight	− 1.12	− 0.39	0.35	0.263	
						> 3 m$^{(*)}$	− 1.75	− 0.73	0.42	*0.081*	2.1
						1–3 m	1.24	0.62	0.50	0.216	
						Within arm's reach				Reference	
	Play intensity	2.3			0.099						
P4c	Intense signaling overall***	3.8			*0.000*						
	Sex	2.6			0.109						
	Age cohort**	4.9			*0.002*	Infant***	− 3.69	− 1.24	0.34	*0.000*	3.5
						Yearling	− 0.95	− 0.20	0.21	0.342	
						Older partner	− 1.45	− 0.31	0.22	0.147	
						Peer				Reference	
	Rank	1.7			0.187						
	Partner mother distance$^{(*)}$	2.5			*0.059*	Out of sight	− 1.44	− 0.51	0.35	0.150	
						> 3 m**	− 2.66	− 1.13	0.42	*0.008*	3.1
						1–3 m	− 1.40	− 0.53	0.51	0.298	
						Within arm's reach				Reference	
	Play intensity	1.3			0.264						

[a] Overall model indicates the *P* value of the full model against the null model

[b] DF1 and DF2 are the same for all predictions

[c] Odds ratios were obtained from exp (coefficient) of the result

Significant values are shown in italic

$^{*}P \le 0.05$ (FDR adjustment for overall male models: $P \le 0.044$); $^{**}P \le 0.01$; $^{***}P \le 0.001$; $^{(*)}$ non-significant tendency ($P < 0.1$)

them. Indeed, males were more likely than females to exchange signals even when play resulted in failure (Fig. 1, data for *initiator* and *receiver no follow-up*), suggesting that they generally utilize play signals more than females to invite their partners to play. Some evidence suggests that signaling may have had a degree of success. For example, successful play bouts near partners' mothers were more likely to be associated with enhanced signaling (i.e., repeated and high-intensity signaling) than were unsuccessful bouts (Tables 4 and 6). Successful play bouts near the partner's mother were also associated with short duration play. It is possible that males were responding to the mere presence of the partner's mother during play. If so, this raises the

Table 5 The results of GLMMs for the use of play signals during successful female bouts

Prediction	Fixed effect[a]	*F*	DF1[b]	DF2[b]	*P* value
P4a	Presence of signals overall	1.8	11	362	0.054
	Sex	3.0	1		0.084
	Age cohort	2.4	3		0.071
	Rank	0.2	2		0.810
	Partner mother distance	1.7	3		0.169
	Play intensity	0.4	2		0.667
P4b	Repeated signaling overall	1.7			0.062
	Sex	1.4			0.245
	Age cohort	4.6			0.004
	Rank	0.6			0.572
	Partner mother distance	0.3			0.812
	Play intensity	0.7			0.496
P4c	Intense signaling overall	1.8			0.049
	Sex	1.5			0.228
	Age cohort	3.6			0.014
	Rank	0.0			0.995
	Partner mother distance	0.8			0.513
	Play intensity	1.5			0.218

Fixed coefficients are not shown because none of the fixed effects was significant

[a] Overall model indicates the *P* value of the full model against the null model (FDR adjustment for overall female models: $P \leq 0.006$)

[b] DF1 and DF2 are the same for all predictions

possibility that they understood that this situation was potentially risky and that they adjusted their play and signaling strategically to reduce that risk. However, it is also possible that males or their partners may have responded to subtle threats from the partner's mother (i.e., threats that did not reach the level of overt interventions), which ended play prematurely (personal observations).

Contrary to our prediction, males did not disproportionately signal to females in either successful or unsuccessful bouts, even though play with opposite sex partners was disproportionately likely to fail. This may have been because males were simply not highly motivated to play with females (i.e., refraining from play), perhaps due to females' less vigorous play style (e.g., vervet monkeys: Fedigan 1972; Japanese macaques: Eaton et al. 1986). Conversely, females may not have shown interest at the onset of a play encounter, perhaps due to an aversion and/or the reduced need for rough play, leading to an early refusal of their play solicitation. In many primate species, males prefer to play with other males over females, building closer bonds with the same sex peers (e.g., Cheney and Seyfarth 1977; Cheney 1978). Additionally, since females were more likely than males to play nearby their own (or partners') mothers (Table 1), such play attempts may have ended prematurely due to subtle threats by their mothers (personal observations).

Also contrary to our predictions and previous findings (e.g., Levy 1979; Flack et al. 2004), males did not signal disproportionally more to differentially aged partners, particularly infants. Indeed, they were less likely to direct enhanced play signals to infants than to peers, despite our finding that play with infants was less likely to be successful. Instead, males simply refrained from playing with infants, perhaps because they were risky, unappealing, or difficult to access due to the protectiveness of the partner's mother. On a more functional level, males had less need to interact with infants to prepare for their adult roles (e.g., Lancaster 1971; Fairbanks 1990). Refraining from play with infants, therefore, may incur less cost for males compared with other strategies (i.e., playing for shorter durations in front of the infant's mother).

Female play

Two factors were associated with negative outcomes for female play: infant partners and partners that differed by at least three ranks. Contrary to our predictions, females preferentially played with infants over peers. They disproportionately refrained from playing with opposite sex partners, older partners, and partners whose ranks differed by at least three places. However, unlike males, females showed no evidence of enhanced signaling in relation to our hypothesized play failure factors either during successful or unsuccessful bouts. A plausible interpretation of these results is that females may have experienced less social risk than males, and hence had less need to use enhanced signals or behave flexibly in relation to mismatches. This may have been due, in turn, to their lower play frequencies (e.g., Symons 1978; Eaton et al. 1986; Glick et al. 1986; Bardi and Borgognini-Tarli 2006), tendencies to play less roughly (e.g., Baldwin 1969; Eaton et al. 1986), engage in less rough forms of play (Meaney et al. 1985), refrain from playing with several types of potentially risky partners, and/or better integration into a protective kinship network (e.g., Kulik et al. 2016).

Unlike males, we found no evidence that female play was affected by the presence of the partner's mother. There was no apparent increased risk of play failure, and females did not refrain from playing near partners' mothers (Table 1) or adjust their play in any way when near them. Similarly, although there was evidence that females refrained from playing with distantly ranked partners, they did not adjust their play at all in relation to the partner's rank. The explanation for this finding is unclear. However, it may be related to the tendency for females to be highly motivated to play with females that rank higher than themselves as a way to establish and maintain tolerant and supportive relationships within their group and particularly within their matriline (Cheney 1977). In despotic species, avoiding conflict and gaining access to resources can be stressful, especially for low ranking juveniles, as the dominance hierarchy largely dictates the order of access to resources (Brennan and Anderson 1988; Deutsch and Lee

Table 6 The results of GLMMs for the use of play signals during unsuccessful male bouts

Prediction	Fixed effect[a]	*F*	DF1[b]	DF2[b]	*P* value	Fixed coefficient	*T*	Estimate	SE	*P* value	OR[c]
4a	Presence of signals overall**	2.3	9	812	*0.007*						
	Sex**	8.8	1		*0.003*	Opposite sex**	− 2.96	− 0.55	0.19	*0.003*	1.7
						Same sex				Reference	
	Age cohort	1.2	3		0.321						
	Rank(*)	2.4	2		*0.093*	3+ Ranks apart(*)	1.75	0.40	0.23	*0.080*	1.5
						1–2 Ranks apart*	2.11	0.51	0.24	*0.035*	1.7
						Same rank				Reference	
	Partner mother distance	0.9	3		0.424						
4b	Repeated signaling overall**	2.9			*0.002*						
	Sex**	7.8			*0.006*	Opposite sex**	− 2.75	− 0.852	0.31	*0.006*	3.1
						Same sex				Reference	
	Age cohort*	3.4			*0.018*	Infant**	− 2.72	− 1.50	0.55	*0.007*	4.5
						Yearling	− 0.86	− 0.24	0.28	0.392	
						Older partner	0.63	0.17	0.27	0.529	
						Peer				Reference	
	Rank	0.9			0.411						
	Partner mother distance(*)	2.4			*0.070*	Out of sight(*)	− 1.68	− 0.79	0.47	*0.093*	
						> 3 m	− 0.10	− 0.065	0.63	0.917	
						1–3 m	0.428	0.262	0.61	0.668	
						Within arm's reach				Reference	
4c	Intense signaling overall	1.3			0.244						
	Sex	7.4			0.007						
	Age cohort	0.7			0.564						
	Rank	0.0			0.971						
	Partner mother distance	0.1			0.954						

[a] Overall model indicates the *P* value of the full model against the null model

[b] DF1 and DF2 are the same for all predictions

[c] Odds ratios were obtained from exp (coefficient) of the result

Significant values are shown in italic

*$P \leq 0.05$ (FDR adjustment for overall male models: $P \leq 0.044$); **$P \leq 0.01$; ***$P \leq 0.001$; (*) non-significant tendency ($P < 0.1$)

1991). Engaging moderately higher ranking individuals (those that rank one or two ranks apart) through social play may lead to increased tolerance and a general reduction of social risk or stress (cf. Seyfarth 1977). However, soliciting play with partners who are more distantly ranked is likely to involve substantial risk. Partners that are moderately apart in rank would also tend to be more accessible (i.e., nearby) and more likely to be related than those that rank far above or below them.

Patterns of play bouts with infants also require an explanation. Although play with infants was disproportionately prone to fail for both male and female juveniles, unlike males, females appeared to be highly motivated to play with infants (e.g., baboons: Cheney 1978; Japanese macaques: Hayaki 1983). Yet neither sex made use of enhanced signaling when playing with infants. In addition, females were much less likely than males to play at a distance from mothers (Table 1), further increasing their potential risk of failure. We suggest that rhesus females attempted to reduce risk in other ways, for example, by engaging in a type of self-handicapping as evidenced by our findings that females were disproportionately likely to engage in particularly gentle, low-intensity forms of play with infants. The fact that both males and females rarely signaled to infants even during successful bouts also raises the possibility that infants may not yet be capable of responding or exchanging signals properly.

Sex differences in behavioral flexibility during play

Although we could not directly compare sex differences within our models, our findings shed light on sex differences in behavioral flexibility displayed during play among juvenile rhesus macaques. Sex differences in social play behavior have been well documented in a number of primate species with males typically playing more frequently and more roughly than females (Baldwin and Baldwin 1977; Symons 1978).

Table 7 The results of GLMMs for the use of play signals during unsuccessful female bouts

Prediction	Fixed effect[a]	*F*	DF1[b]	DF2[b]	*P* value
P4a	Presence of signals overall	1.7	9	535	0.097
	Sex	3.0	1		0.085
	Age cohort	3.8	3		0.329
	Rank	1.1	2		0.329
	Partner mother distance	0.5	3		0.675
P4b	Repeated signaling overall	0.7			0.738
	Sex	0.0			0.830
	Age cohort	1.3			0.286
	Rank	0.2			0.819
	Partner mother distance	0.3			0.850
P4c	Intense signaling overall	1.4			0.181
	Sex	0.0			0.927
	Age cohort	2.8			0.039
	Rank	2.6			0.077
	Partner mother distance	0.4			0.755

Fixed coefficients are not shown because none of the fixed effects was significant

[a] Overall model indicates the *P* value of the full model against the null model (FDR adjustment for overall female models: $P \leq 0.006$)

[b] DF1 and DF2 are the same for all predictions

This sex difference is attributed to the idea that fighting skills are more important for males than females (Symons 1978; Fagen 1981) at least partly because individual fighting ability has more influence on adult rank for males than females (e.g., Bekoff 1972; Fedigan 1972; Owens 1975b). In contrast to well-documented findings about sex differences in play itself, there have been only a few studies showing sex differences in the use of play signals, with male-male play involving more frequent use of the signals than male-female or female-female play (e.g., Palagi et al. 2007). It is possible that play behavioral flexibility is easier to detect in males, simply because they play more frequently, thus providing researchers with larger datasets. In this study, although we collected data on a total of 2673 bouts involving 20 juveniles, the number of male play bouts was almost twice that of female bouts (Table 1). Hence, it is possible that the relatively smaller dataset for females may have influenced our results.

However, it is also reasonable to hypothesize that male juvenile macaques are more exposed and responsive to social risk during play and that their apparent increased responsiveness is related to a greater need to behave flexibly during play. Whereas philopatric rhesus females continue to interact intensely with their maternal kin and become gradually more integrated into supportive matrilineal social networks as they mature, young males engage in fewer interactions with their matrilines over time (Kulik et al. 2016), focusing instead on relationships with adult and juvenile males within the group, before they disperse from their natal groups typically during their third and fourth years of life (Widdig et al. 2016). At this point, they typically attempt to join other social groups directly or form small temporary unisexual clusters of extra-group males before eventually attempting to join another group. In these clusters or new groups, males may encounter other familiar males that are also dispersing or that have emigrated from the same natal group. However, they are also likely to encounter less familiar males. It is in this context that they may benefit from prior experience with a variety of play partners and from the exercise of behavioral flexibility. For male juvenile macaques nearing the age of emigration, playful interaction is likely to play a pivotal role in learning how to establish or maintain positive social relationships with both familiar and unfamiliar conspecifics. The ability to efficiently communicate to solicit and maintain play with other familiar and unfamiliar males could help them (a) gain reliable emigration partners and (b) prepare to form new social bonds with strange individuals in non-natal groups.

In many mammals, including humans, social play is hypothesized to provide youngsters a platform from which to assess others' behavior by gaining information about their strengths or weaknesses in play fights (e.g., humans: Smith and Boulton 1990; chimpanzees: Paquette 1994), their mutual willingness to play, and their styles of play (Palagi et al. 2016). Play is also hypothesized to facilitate an understanding of the consequences of one's own behavior on others and to adjust one's own behavior through interaction with others (Paquette 1994; Pellis and Pellis 2006; Pellegrini et al. 2007; Pellis et al. 2010). Ultimately, play can function to test the strength of social bonds and the level of cooperation among individuals (Palagi et al. 2004; Mancini and Palagi 2009) and to promote tolerance, cooperation, and reciprocity (Palagi et al. 2016) beyond the playful interaction (Clark 2011; Palagi and Cordoni 2012; Smith et al. 2013). As such, successful play interaction with both related and unrelated (more or less familiar) group members as well as occasional peers from other social groups is likely to help male juveniles prepare for dispersal by reducing *xenophobia* (Antonacci et al. 2010) and honing social skills needed during and after dispersal. Prior play relationships with members of other groups may be particularly effective in reducing aggression and easing an immigrant male's transition, if he migrates into those groups in the future. While we did not observe dispersals in detail in our study, we observed juvenile males, but not juvenile females, in our group solicit play with young adult males who were new to the group and with males that belonged to other groups (Hausfater 1972; AY personal observations), suggesting that males may be more likely than females to use playful interactions than females as a means to engage unfamiliar conspecifics and overcome xenophobic tendencies.

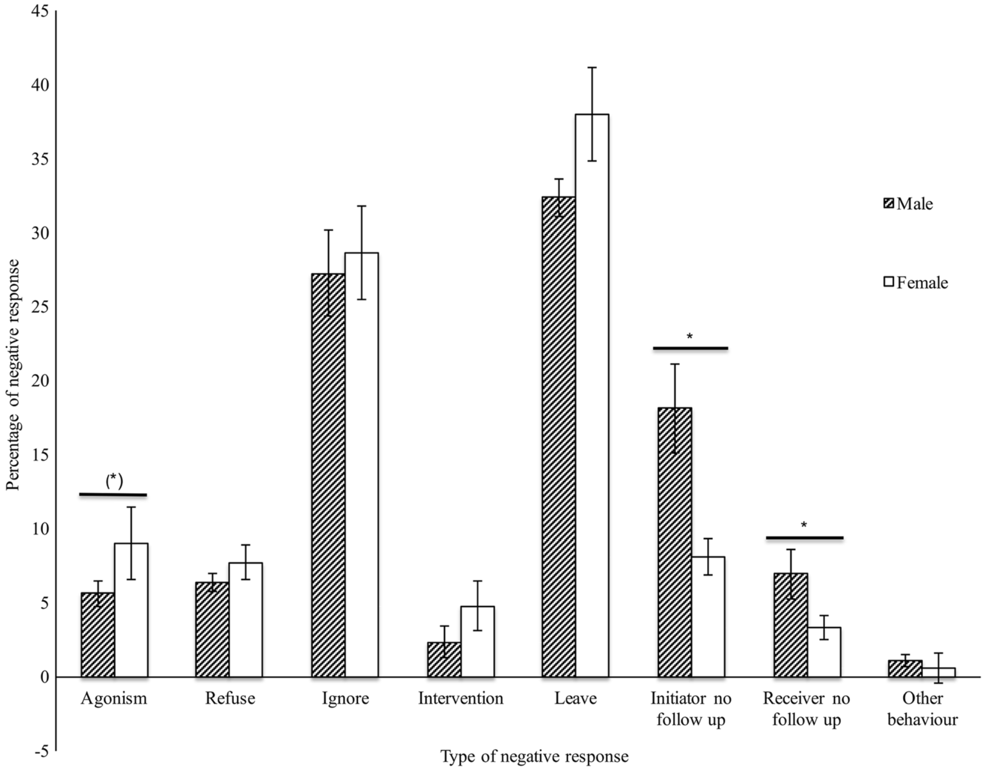

Fig. 1 Percentages of negative responses in male and female play. *Error bars* indicate the standard deviation of the mean (standard error). Male-male, male-female, and female-female play bouts are included. In an agonistic response, the receiver responded to a play solicitation with physical or non-physical aggression (e.g., lunging, open mouth threat). In ignoring, the receiver paid no attention to the play initiator, continued to or moved on to engage in other activities without leaving the scene. Intervention occurred when a play bout was interrupted by the mother or other third parties. Leaving was recorded when the receiver physically ran or walked away from the scene after a play solicitation. In refusing, the receiver stayed in the scene, but responded unfavorably or showed resistance to a play solicitation. A response was recorded as *initiator no follow-up* when two players exchanged signals but the play initiator did not proceed to play with the receiver after the signal exchange, while *receiver no follow-up* occurred when the receiver did not proceed to play after the signal exchange. Other behavior included responses other than play, such as grooming or mounting. $^{(*)}P < 0.1$, Mann-Whitney U test; $^{*}P < 0.05$, Mann-Whitney U tests

Implications of behavioral flexibility in rhesus juvenile play

Our findings suggest that (male) juvenile rhesus are able to flexibly adjust their play signaling and play behavior in order to increase their likelihoods of engaging in successful play experiences, and thereby effectively reducing social risk. However, the extent to which they use simple vs. high-level cognitive skills when engaging in play is unclear. On one hand, it is possible that the use of repeated or intense signals

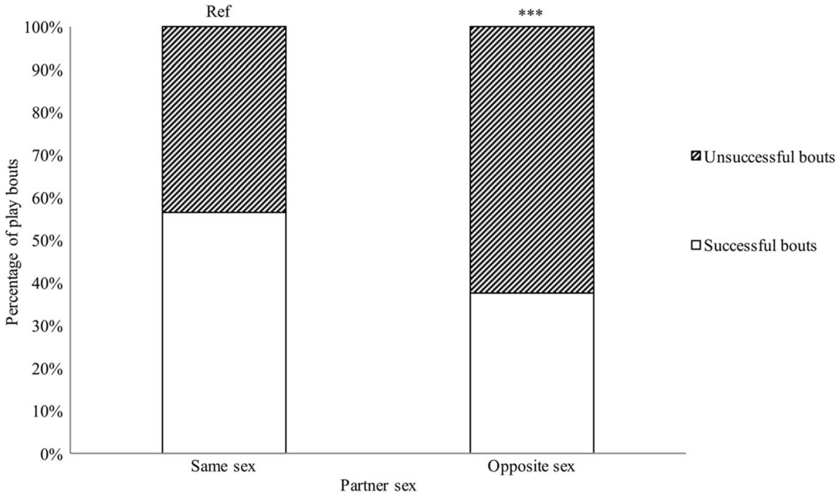

Fig. 2 Play failure according to the partner's sex. 100% stack column describing the percentage of total male play bouts (based on raw count data). Both male-male and male-female play bouts are included. Males had significantly higher percentages of unsuccessful play bouts with the opposite sex partners. $^{\mathrm{Ref}}$The reference category in the GLMM; $^{***}P \leq 0.0005$

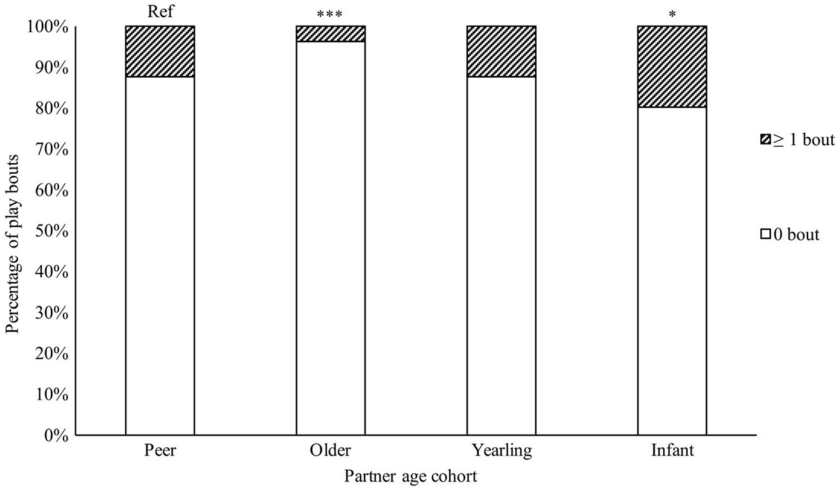

Fig. 3 Females' tendency to refrain from play with partners of different age cohorts. 100% stack column describing the percentage of total number of female interactions with potential play partners (based on raw count data). Both female-female and female-male play bouts are included. Females were disproportionately more likely to refrain from playing with older partners, but more likely to play with infants. RefThe reference category in the GLMM; ***$P \leq 0.001$; *$P \leq 0.05$

may be a simple outcome of increased arousal of players caused by a perception of potential risks. Longer durations of play bouts could conceivably lead to more frequent signaling, if animals signal at constant rates. Short play durations could also be simple by-products of play becoming unpleasant or frightening, rather than an intentional *strategy* to reduce risk. On the other hand, most primate researchers agree that nonhuman primates, including monkeys, are capable of predicting the behavior of others in a variety of situations (Tomasello and Call 1997) and of responding appropriately based on those predictions, raising the possibility that behavioral flexibility during social play involves cognitive processes beyond direct responses to arousal or fearful stimuli or even simple S-R associations with fearful stimuli.

While not definitive, the results of this study suggest that juvenile male rhesus are sensitive and actively responsive to a variety of social parameters governing the risk of play failure, and are able to behave flexibly. As such, they suggest that juvenile males possess knowledge about social attributes associated with social risk. This is not to imply that females do not possess such social knowledge; rather, we can only conclude that they do not respond to it in the same way or they

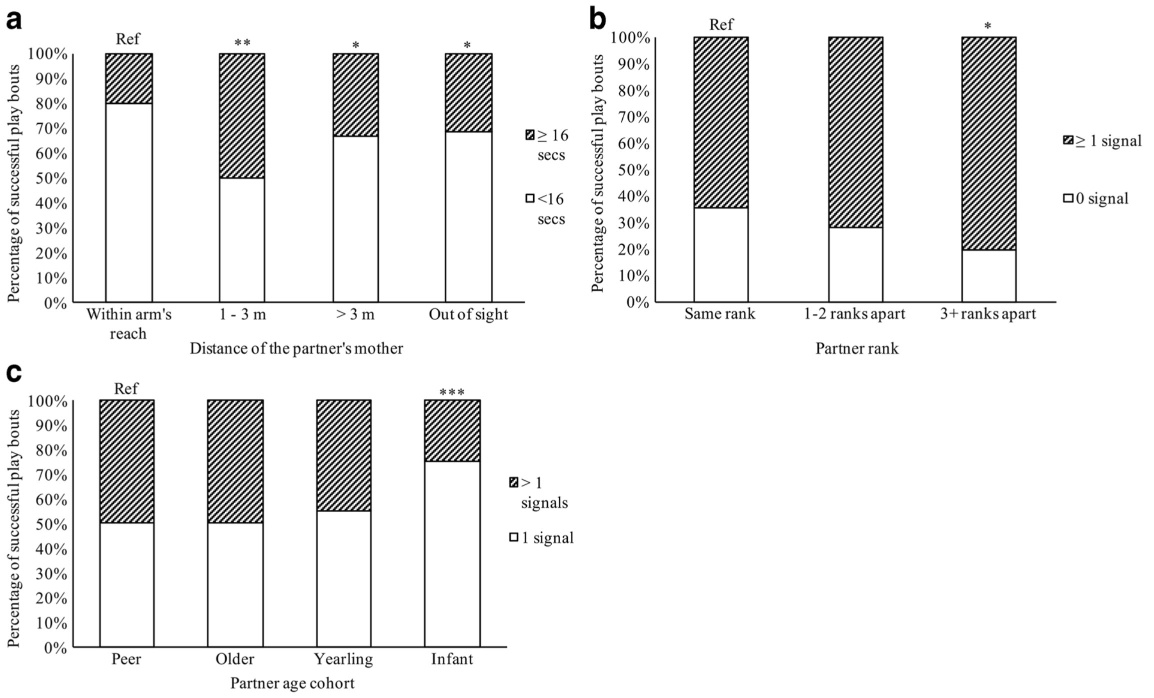

Fig. 4 Percentages of successful play bouts involving male focal subjects with both male and female partners. *Bars* represent 100% stack columns (based on raw count data): **a** durations of play bouts broken down by distance from the partner's mother, **b** presence vs. absence of a signal broken down by partner's rank distance, and **c** single vs. repeated signals broken down by partner age cohort. RefThe reference category in the GLMM; ***$P \leq 0.001$, **$P \leq 0.01$, *$P \leq 0.05$ represent significant differences from the reference category

may not encounter the same play situations as males. They may simply be less vulnerable than males in this matriarchal species, due to their tendencies to interact within tightly focused and supportive social networks and to refrain from playing with a wide range of potentially risky partners.

Although juveniles of both sexes disproportionately refrained from playing with many types of unmatched partners, it remains unclear whether refraining from play with them represented active avoidance, a lack of motivation to play (e.g., because play with certain partners could be uninteresting or unpleasant), or simply a lack of opportunity to play with particular kinds of partners. Lack of availability within the group is an unlikely explanation because unmatched potential partners within the group outnumbered matched ones (e.g., unrelated/distantly ranked partners vs. close kin/closely ranked individuals). On the other hand, in many cercopithecine species, partners that are unmatched by rank, sex, and kinship are less likely to be near one another (Berman 1978), making them less accessible as play partners. Thus, lack of accessibility may provide a plausible alternative explanation to active avoidance.

Limitations and recommendations for future studies

Given its dense population, large group sizes, provisioning, and predator-free status, some researchers have speculated that behavior on Cayo Santiago is not representative of wild rhesus (Maestripieri and Hoffman 2012). Although this may be true, no detailed study of play has been done on wild rhesus, and no detailed study of play signaling has been done on either wild or captive rhesus populations. Nevertheless, Cayo Santiago displays many parallels to conditions under which wild rhesus on the Indian subcontinent have lived for several thousands of years (e.g., Chauhan and Pitra 2010; Radhakrishna et al. 2013). Indeed, they live under a variety of conditions, in large and small groups, and in forests and cities. Many populations live closely with humans who provision them with large amounts of high-quality food distributed as clumped resources. Humans also discourage the presence of predators. Thus, we have no reason to expect Cayo Santiago rhesus to differ qualitatively from wild rhesus in their signaling behavior or behavioral flexibility during play. At the same time, Cayo Santiago provides more opportunities to closely examine responses of juveniles with a wide range of partners, both matched and unmatched than most wild settings. Although we acknowledge the need to validate our findings in wild populations, we suggest that such future studies are likely to benefit from our findings and interpretations.

Although we focused on several organizing principles of social relationships here that correlate closely with social bond strength, it may also be useful to look directly at the role of social bond strength by examining proximity patterns, grooming, or other affiliative interactions of player dyads outside play contexts. In this study, we looked only at immediate responses to play invitations. Future studies that look at responses with longer delays (e.g., 5–10 s) will enhance our understanding of play communication. The fact that directional differences in rank did not produce asymmetrical results also raises questions (see "Methods" section), suggesting that the magnitude of rank distance may convey clearer cues than the direction of such differences to juveniles when assessing who is unmatched vs. matched. Alternatively, it may suggest that avoiding play failure is in the interest of both higher and lower ranking play partners. Future studies may be able to distinguish these possibilities.

To further enhance our understanding of behavioral flexibility during play, we suggest investigating self-handicapping and role reversals in addition to the strategies examined here. We also suggest examining data on younger and older immatures in longitudinal analyses in order to both enhance our understanding of the development of behavioral flexibility and better place them within a life history framework. Such a study would particularly help shed light on the relative lack of signaling toward infants found in this study. Studying other species of macaques with varied social styles would also lead to insights about the factors that facilitate or inhibit the expression of behavioral flexibility in play. Limiting the analysis to a subset of signals that were given only prior to play initiations will allow to reveal the degree of foresight that these juveniles may have in these socially delicate situations. Unfortunately, our current dataset, although large, was not large enough to do this. Similarly, larger datasets, especially ones including larger numbers of focal subjects and signals, might allow direct statistical comparison between the two sexes to verify sex differences in behavioral flexibility during play. Finally, examining the relationship between play partners at the juvenile stage and their dispersal partners at a later life history stage would not only provide a clearer view of the relationship between play communication and life history patterns but also provide insights into the functions of play behavior itself as well as mechanisms involved in dispersal.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This study was approved by the Institutional Animal Care and Use Committees (IACUC) at the Caribbean Primate Research Center, University of Puerto Rico (Protocol No. A3460107), as well as the State University of New York at Buffalo (Protocol No. N/A).

Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

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