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RESEARCH ARTICLE

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Play behavior in immature moor macaques (*Macaca maura*) and Japanese macaques (*Macaca fuscata*)

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Abstract

Play is widespread across mammalian taxa, but species strongly vary in the ways they play. In less despotic primate species (i.e., with less steep dominance hierarchies, less severe conflicts, and more reconciliation), play has been described as being more frequent, cooperative, and freely expressed. To study the link between social play and dominance style, we compared play behavior in free-ranging infants, juveniles and subadults of more despotic Japanese macaques (*Macaca fuscata*, $N = 24$) and less despotic moor macaques (*Macaca maura*, $N = 17$). We found interspecific differences in play behavior that corresponded with the contrasting dominance styles of the study species, largely confirming our predictions. In particular, moor macaques spent a larger proportion of time in solitary and social play than Japanese macaques, while Japanese macaques spent a larger proportion of time in grooming interactions. In moor macaques, play sessions included more players, a larger variety of play behaviors, greater play face rates, a greater proportion of time in contact play, and a higher rate of reciprocal play-biting than in Japanese macaques. Aggressive escalations were not common, but more frequent in Japanese macaques. Finally, a higher frequency of play faces during play sessions predicted the occurrence of more reciprocal play-bites, but not the proportion of time spent in contact play behaviors. Additional studies on other groups and species will allow a better understanding of the link between dominance style and social play.

KEYWORDS

cooperative play style, despotism, dominance style, play behavior, play face

1 | INTRODUCTION

Play has been defined as an exaggerated, spontaneous, and self-rewarding behavior that serves no immediate function and often occurs in non-stressful situations (Burghardt, 2005; Nathan, Pellegrini, & Burghardt, 2012). Play is a risky, energy- and time-consuming activity (de Almeida Rocha, Dos Reis, & de Carvalho Oliveira, 2014; Palagi, 2007, 2018), and its adaptive function has long been unclear (Bekoff & Allen, 1998; Marks, Vizconde, Gibson, Rodriguez, & Nunes, 2017; Martin & Caro, 1985). Nowadays, play is known to have a crucial function (Palagi, 2018; S. M. Pellis & Pellis, 2017). Social play (i.e., play involving two or more animals), for instance, may facilitate the acquisition of social knowledge and abilities, act as a buffer during stressful situations, and allow individuals to strengthen their social relationships and enlarge their social networks, gradually becoming part of the social group (Baldwin, 1986; Bekoff & Byers, 1998; Burghardt, 2005; Fagen, 1981; Lutz & Judge, 2017; Palagi, 2018; Shimada & Sueur, 2018). In contrast, solitary play (i.e., intense or sustained locomotion and exploratory behaviors in the absence of social partners; Berghänel, Schülke, & Ostner, 2015; Burghardt, 2005; S. M. Pellis & Burghardt, 2017; Petrů, Špinka, Lhota, & Šípek, 2008) may facilitate the acquisition of novel behavioral patterns. In Burmese long-tailed macaques (*Macaca fascicularis aurea*), for instance, juveniles increase their foraging skills through solitary object play (Pelletier et al., 2017). Therefore, depending on the socio-ecological challenges faced by different species, patterns of social and solitary play may vary across species to facilitate the selective acquisition of specific skills and behavioral patterns (Berghänel et al., 2015; Norscia & Palagi, 2015; Palagi, Cordoni, & Borgognini Tarli, 2004; Palagi, Paoli, & Tarli, 2006; Shimada, 2006).

Among primates, macaques constitute an ideal taxon to study inter-specific variation in play behavior. Macaques are a monophyletic group with similar kinship and demographic structures across species (e.g., female philopatry, matrilineal dominance hierarchies, multi-male multi-female social organization; Flack, Jeannotte, & de Waal, 2004; Thierry, 2000, 2007). Nonetheless, macaque species vary markedly in their dominance style and have been clustered into four grades, from more to less despotic (Thierry, 2000, 2007; Thierry, Singh, & Kaumanns, 2004). In less despotic species, aggressive conflicts are less intense and characterized by higher counter-aggression rates, more undecided outcomes, higher reconciliation rates, and shallower dominance hierarchies, as compared with more despotic species (e.g., de Waal & Luttrell, 1989; Demaria & Thierry, 2001; Petit, Abegg, & Thierry, 1997, 1985). In less despotic species, dominance also imposes fewer constraints on social choices, and individuals have more opportunities to interact with a larger variety of social partners, independently of rank and kinship (Butovskaya, 2004; Cooper & Bernstein, 2008; Duboscq et al., 2013; Matsumura & Okamoto, 1997; Thierry, Anderson, Demaria, Desportes, & Petit, 1994).

Clearly, these differences in dominance style might also affect individuals' play behavior. If social play facilitates the selective acquisition of skills and social partners, for instance, it should be more frequent in less despotic species, for two main reasons. First, social play is generally considered a risky behavior for the physical contact usually implied, the inclusion of uncertain modules in play sessions, and the risk of escalation into serious fighting (Palagi, 2007, 2018). Therefore, it may be more common in less despotic species, where aggressive conflicts are usually less intense and the risks of injury lower (e.g., de Waal & Luttrell, 1989; Thierry, 2000, 2007). Second, less despotic species usually have more extended social networks (Ciani, Dall'Olio, Stanyon, & Palagi, 2012; Petit, Bertrand, & Thierry, 2008; for similar results within the *Pan* genus, see Hare, Wobber, & Wrangham, 2012; Palagi, 2006; Palagi & Cordoni, 2012). Therefore, social play may be especially important in less despotic species, as bonding with many social partners from early on may allow individuals to lay the foundations of the large social networks they will have as adults (e.g., Adams et al., 2015; Amici, Kulik, Langos, & Widdig, 2019; Shimada & Sueur, 2018). In contrast, immatures in more despotic species may preferentially rely on grooming to form and maintain social bonds, as grooming is not as risky as play, and may be an alternative to social play in the formation and maintenance of social bonds (Shimada & Sueur, 2018). Furthermore, patterns of solitary play may also vary among species depending on their dominance style. In more despotic species, females largely inherit their maternal rank (Berman, 2017), while individuals in less despotic species have a higher chance of rising through the dominance hierarchy, as ranks are nor strictly inherited (Thierry, 2007). Therefore, individuals in less despotic species may especially benefit from exploratory behaviors (as in solitary play) that might facilitate the attainment of higher rank, by for instance fostering the acquisition of better ecological knowledge, reducing neophobia (Lockman, 2000; Parker & Gibson, 1977), or facilitating the emergence of novel functional behaviors (e.g., Fagen, 1981; Huffman & Quiatt, 1986).

Differences in dominance style might also affect the way in which individuals play. In less despotic species, individuals have a larger variety of partners with whom they can play (e.g., Ciani et al., 2012; Palagi & Paoli, 2007, 2008), and may engage in polyadic interactions more often than despotic species (Ciani et al., 2012; Palagi & Paoli, 2007, 2008; Petit et al., 2008), as in the latter the presence of many players may dramatically enhance the risk of aggressive behavior (Palagi, 2018; Petit et al., 2008; Reinhart et al., 2010). Similarly, social play in less despotic species may include a larger variety of behaviors than more despotic species: behavioral variation during play sessions increases the level of unpredictability and the risk of aggressive escalations (Palagi, 2018; Petit et al., 2008; Reinhart et al., 2010), which may be especially risky in more despotic species. Less despotic species may also show more cooperative play styles, with frequent variation in the players' roles (e.g., reciprocal bites; Petit et al., 2008; Reinhart et al., 2010) and more physical contact (e.g., sparring, wrestling; Ciani et al., 2012; Petit et al., 2008), as the risk of severe aggression is lower than in despotic species (Palagi, 2018; Petit et al., 2008; Reinhart et al., 2010).

Finally, less despotic species rely less on formal displays to manage their interactions (Thierry, 2000, 2007), and may hence have larger and more complex communicative repertoires than despotic species (Dobson, 2012; Flack et al., 2004; Maestripieri, 1995, 2005; Scopa & Palagi, 2016; Whiten & Schaik, 2007; Zannella, Stanyon, & Palagi, 2017). Play face (i.e., a relaxed open mouth facial expression), for instance, is considered a crucial communicative tool to express emotions and intentions during play sessions and may serve to prevent aggression between players and increase social play duration (de Waal, 2003; Demuru, Ferrari, & Palagi, 2015; Flack et al., 2004; Mancini, Ferrari, & Palagi, 2013; Palagi & Mancini, 2011; S. Pellis & Pellis, 2009; Scopa & Palagi, 2016; Špinka, Palečková, & Řeháková, 2016; Yanagi & Berman, 2014). Therefore, play faces may be more frequent in less despotic species, decrease the risk of aggressive escalations, and increase the proportion of potentially riskier play behaviors (e.g., contact behavior, reciprocal bites; see e.g., Demuru et al., 2015).

In this study, we aimed to assess inter-specific variation in play behavior linked to differences in their dominance styles, including highly despotic Japanese macaques (*Macaca fuscata*, hereafter JM) and less despotic moor macaques (*Macaca maura*, MM; Thierry, 2007). We added to previous research in three main ways. First, we included a species, MM, whose play behavior had not been previously studied. The inclusion of MM is important to assess whether differences in play styles really depend on the species' dominance styles, as MM add another data point for non-despotic species. Secondly, the large size of our study groups (*M. maura*: $N = 42$; *M. fuscata*: $N = 52$) allowed us to better take into account intraspecific variation in play, including possible rank, age, and sex differences. Third, the study groups we tested were both free-ranging. To date, all the studies comparing play in species with different dominance styles have been conducted in captivity (Ciani et al., 2012; Diamond, Daryl, Clio, & Bond, 2006; Palagi, 2006; Palagi & Cordoni, 2012; S. M. Pellis & Pellis, 1997; Petit et al., 2008; Scopa & Palagi, 2016), with one exception (Reinhart et al., 2010). Extending the study of interspecific differences in play behavior to the wild is especially important when it comes to the study of social behaviors which might have an adaptive function only in the wild (e.g., to build social relationships that may be important during male migration, see Amici et al., 2019).

We predicted that, if dominance style affects the relative proportion of play behavior, MM should spend a higher proportion of time in solitary play (Prediction 1) and in social play (Prediction 2), as compared with JM. In contrast, JM should spend a higher proportion of time grooming than MM (Prediction 3), as grooming is a less risky alternative to the formation and maintenance of social bonds (Shimada & Sueur, 2018). Moreover, if dominance style also affects the style of social play, play sessions in MM should include more players (Prediction 4), a larger variety of behaviors (Prediction 5), a higher rate of play faces (Prediction 6), a higher proportion of contact behaviors (Prediction 7), a higher occurrence of reciprocal bites (Prediction 8), and fewer aggressive escalations (Prediction 9) as compared to JM. Finally, we assessed the communicative role of play faces and, in particular, whether they facilitate the occurrence of riskier play behaviors in both JM and MM. We predicted that higher rates of play faces would predict a higher proportion of time spent in contact behaviors (Prediction 7b) and a higher occurrence of reciprocal bites (Prediction 8b), while decreasing the probability of aggressive escalations (Prediction 9b).

2 | METHODS

2.1 | Ethics statement

The study was purely observational, and the procedures approved by the Indonesian Foreign Research Permit Division, Ministry of Research and Technology/National Research and Innovation Agency, which allowed us access to the MM) and by the Primate Research Institute at the Kyoto University in Japan, which allowed us access to the JM. We strictly adhered to the legal requirements of the countries in which the research was conducted, and to the ASP Principles for the Ethical Treatment of Nonhuman Primates.

2.2 | Study populations and subject

We observed one group of free-ranging MM and one group of free-ranging JM. The MM were studied in the Karaenta forest area (5°02′59.4″ S, 119°44′13.2″ E), an approximately 10,282 ha primary forest sector of the 43,000 ha total area of Bantimurung-Bulusaraung National Park, in South Sulawesi, Indonesia. The group was well habituated, having been studied for more than 30 years (Matsumura, 1993, 1996; Okamoto & Matsumura, 2001). At the onset of our study, the group comprised 42 individuals, including 11 male (≥5 years) and 14 female adults (≥4 years), 2 male (4 years), and 3 female subadults (3 years), 2 male (3years) and 1 female juveniles (2 years), and 5 male and 4 female infants (up to 1 year). The first author collected data on all individuals in Karaenta from September 2018 to March 2019. During this period, two infants migrated out of the group, while another one was killed in a car accident (so that one had to be excluded from the analyses, because we were able to collect only a limited amount of data). All nine infants were still suckling when the study started (October 2018). Their age was estimated by the first and last authors (and Dr. Bonaventura Majolo) based on their size (Grand, 1981) and motor patterns (Thierry et al., 2000), as displayed by each infant in three videos. All three raters have been working with different species of macaques for more than 3 years, and always agreed on classifying the nine individuals as infants ($ICC = 1$, $p = 0$).

The JM were studied on Koshima Islet, Miyazaki prefecture, Japan (31°27′N, 131°22′E), an area of approximately 30 ha covered with evergreen broadleaf forest (Duboscq, Romano, Sueur, & MacIntosh, 2016). Our study group (i.e., main group) was well habituated and has been well studied since 1948, through collection of demographic, ecological, behavioral, and life-history data (Duboscq et al., 2016; Kawai, 1963; Rigaill et al., 2017; Watanabe, 1989, 2008; Yamagiwa, 2010). When the study started, the group consisted of 55 individuals, including 12 male and 24 female adults, 4 female and

3 male subadults, 5 male and 5 female juveniles, and 2 infants, 1 male and 1 female. Sex, age, and kin-relationships were already known (Duboscq et al., 2016; Kurita, Suzumura, Kanchi, & Hamada, 2012; Rigaill et al., 2017; Watanabe, 2008; Yamagiwa, 2010). Although the group lives on an island, this becomes occasionally connected to the mainland, allowing some exchange of individuals between groups. Moreover, animals on Koshima are fed twice a week, but individuals have to forage to retrieve most of their food. The second author collected on all individuals on Koshima from November 2016 to July 2017. Observations and video-recording took place from 06:00 to 18:00 in Sulawesi, and from 08:00 to 18:00 in Koshima. For a list of the study subjects (i.e., including only the infants, juveniles, and subadults of the group), see Table 1.

2.3 | Data collection

To assess dominance relations of all group members, we used ad libitum observations of all dyadic agonistic interactions (i.e., aggression: threat, lunge, chase, bite; unidirectional agonistic and submissive behaviors: displacement, avoidance, bared-teeth, hindquarter presentation; Scopa & Palagi, 2016; Thierry et al., 2000) with clear winner–loser outcomes (i.e., the individual showing aggressive behavior to the other showed no submissive behavior during the interaction, and vice versa; Altmann, 1974).

To assess play behavior we conducted 20 min focal follows of all the females up to 4 years old and all the males up to 5 years old in the group. We spread focal samples through the day to balance observations over time of day, with at least one hour between two consecutive focals on the same individual, and followed a random order. During focal sampling (Altmann, 1974), we recorded on paper all instances of grooming, social play (i.e., play behavior involving at least another conspecific; Burghardt 2005) and solitary play (i.e., solitary intense or sustained locomotion movements, exploratory behaviors; Burghardt 2005; S. M. Pellis & Burghardt, 2017; Petrů et al., 2008) in which the focal individual was involved, including the identity of the individuals involved and the exact duration of the behavior (Scopa & Palagi, 2016; Shimada & Sueur, 2018; Thierry et al., 2000). We recorded a total of 397 focal samples, with a mean of 7.74 (range, 4.7–8) h per individual in MM and a total of 354 focal samples, with a mean of 4.9 (range, 4.7–5.7) h per individual in JM.

We further video-recorded all social play sessions involving at least one infant, juvenile, or subadult with a FinePix S8500 (Fujifilm, 2013). We recorded videos ad libitum whenever they occurred, including during focal follows. We considered a play session to start when an individual directed play behavior toward a partner and finished when both individuals did not show any play behavior for at least 10 s (Scopa & Palagi, 2016). For each session, we noted the identity of all the individuals involved in the play session and its duration. We further noted the exact duration of the following social play behaviors: object play (i.e., at least two individuals play with an object, without body contact), acrobatic play (i.e., more than one individual displays pirouettes, chasing and/or play faces, but without body contact), sparring (i.e., more than one individual makes body contact during play fighting, but using only two of the four limbs), and wrestling (i.e., like sparring, but at least one individual uses all four of its limbs; see Ciani et al., 2012; Petit et al., 2008). We also coded all instances of play faces (i.e., open mouth expression with the lower and—in JM occasionally—upper teeth exposed), play bites (i.e., an individual gently bites its partner's hair or skin while playing), and aggressive interactions (i.e., bite, chasing, threat, lunge) occurring within or ending the play session (Ciani et al., 2012; S. M. Pellis, Pellis, Reinhart, & Thierry, 2011; Petit et al., 2008; Reinhart et al., 2010; Scopa & Palagi, 2016). We recorded 453 play sessions for JM and 554 for MM.

Interobserver reliability between the first and second author was calculated posthoc on 10% of the video-recorded play sessions in both species (Spearman's correlation for session duration: $\rho = 0.84$, $p < .001$; number of behaviors: $\rho = 0.81$, $p < .001$; proportion of non-contact play behaviors: $\rho = 0.51$, $p = .005$; proportion of contact-play behaviors: $\rho = 0.72$, $p < .001$; number of play faces: $\rho = 1.00$, $p < .001$). Data will be made available to the readers upon request to the corresponding author.

2.4 | Data analysis

We determined the dominance hierarchy with the Elo method (EloRating package, version 0.43), based on all occurrence sampling of dyadic agonistic interactions with a clear winner-loser outcome (Neumann et al., 2011). We used an R function written by Lars Kulik and set the individual start values at 1000, and the k factor (a weighted constant based on the probability of winning) at 100. The values obtained were averaged throughout the study periods, standardized to range from 0 to 1 (with 0 indicating lowest and 1 highest rank), and hereafter simply referred to as Elo-ranks. Mother's rank was attributed to all the individuals younger than 1 year (Kerhoas et al., 2016; Paukner, Slonecker, Murphy, Wooddell, & Dettmer, 2018). Analyses of MM play included a data set of 346 interactions including 322 of the 528 possible dyads in the group. For JM, analyses included 2116 interactions of 706 of the 1378 possible dyads. For Elo-rating, we included no burn in periods, as Elo-ranks were highly stable throughout the study period, as assessed through visual inspection of the Elo-ranks and with the stab_elo function (which calculates the S index as metric for the overall stability of a hierarchy during the study period, with 0 meaning that the ordering reverses every other day, and 1 that no rank changes occur; see Neumann & Kulik, 2020). In particular, the Elo-ranks were highly stable over the study period, being 0.985 in MM and 0.988 in JM.

Furthermore, to confirm that the study groups really differed in terms of dominance style, we used two different measures: the steepness of the dominance hierarchy (de Vries, Stevens, & Vervaecke, 2006) and the percentage of reversals against the hierarchy (Young & Isbell, 2002). First, we used the package steepness (version 0.2–2; Leiva, & de Vries, 2014) in R to directly assess the steepness of the hierarchy in both species, which is

TABLE 1 Species, sex, age, rank and study subjects, and time (in minutes) spent in solitary play, social play, and grooming interactions during focal sampling

Species	Sex	Age	Rank	Subject	Solitary play	Social play	Grooming
JM	Female	1	0.643	Takana	20.15	28.15	43.17
JM	Male	1	0.484	Hirame	10.68	6.70	43.22
JM	Female	3	0.461	Tabu	5.48	9.43	77.03
JM	Male	4	0.416	Shiira	3.50	27.15	63.10
JM	Male	5	0.415	Yuu	0.95	8.13	90.55
JM	Male	4	0.392	Kote	2.40	18.03	100.90
JM	Male	2	0.375	Shida	0.00	4.28	68.50
JM	Male	4	0.332	Yomogi	0.75	5.45	88.12
JM	Female	4	0.327	Tsutsuji	6.43	6.27	82.28
JM	Male	2	0.321	Haku	0.25	0.05	86.85
JM	Male	2	0.319	Noko	1.47	6.70	15.62
JM	Female	2	0.287	Komatsu	10.60	13.87	84.22
JM	Female	4	0.286	Hado	2.75	3.47	138.12
JM	Female	3	0.263	Hiba	0.80	0.52	99.47
JM	Male	4	0.262	Bon	3.55	1.05	96.87
JM	Female	2	0.242	Pan	1.63	14.00	58.38
JM	Female	2	0.237	Yotsuba	0.00	0.20	112.68
JM	Female	2	0.217	Botan	0.83	5.40	72.17
JM	Female	2	0.209	Mochi	0.33	0.93	83.87
JM	Male	2	0.203	Mekki	0.08	2.73	69.65
JM	Male	2	0.189	Yumin	2.72	5.72	48.73
JM	Female	3	0.185	Pichi	1.50	0.00	22.15
JM	Female	3	0.159	Betei	0.33	0.52	77.58
JM	Female	4	0.111	Binega	1,17	0,22	97.90
MM	Male	3	0.512	Afwan	11.38	5.30	62.35
MM	Male	5	0.449	Kopi	2.63	0.40	40.65
MM	Female	0	0.429	Lida	174.97	33.93	29.05
MM	Male	4	0.428	Alif	0.72	5.83	62.70
MM	Male	4	0.422	Tara	16.35	4.40	53.60
MM	Male	1	0.389	Suco	243.67	67.23	22.78
MM	Female	1	0.378	Taro	287.53	36.95	30.35
MM	Male	2	0.339	Singa	53.93	50.15	48.62
MM	Male	1	0.326	Coko	201.60	73.80	24.62
MM	Female	3	0.319	Rissa	45.77	38.07	41.52
MM	Female	1	0.268	Bira	139.15	19.40	18.03
MM	Female	2	0.208	Ciro	12.87	26.63	19.72
MM	Male	1	0.203	Foc	256.60	84.35	53.00
MM	Female	3	0.169	Lucia	16.92	34.08	53.45
MM	Female	3	0.168	Sahril	23.70	30.83	43.95
MM	Female	1	0.132	Bolet	259.33	66.93	39.20
MM	Male	1	0.127	Crow	268.12	63.92	15.07

Abbreviations: JM, Japanese macaques; MM, moor macaques.

one core measure of macaque dominance styles (Balasubramaniam et al., 2012; Thierry, 2000). We calculated the steepness as the absolute value of the slope of a straight line fitted to the normalized David's scores, obtained on the basis of proportions of wins of dyadic agonistic interactions (de Vries et al., 2006). The steepness of the hierarchy was higher in more despotic JM (0.280) than in less despotic MM (0.163). However, steepness is known to decrease with the number of unknown relationships in a group (Klass & Cords, 2011). As the number of number of unknown relationships was higher in MM, we randomly removed dyads with known relationship from the JM dominance matrix (i.e., obtained by ordering the individuals in the matrix so that their Elo-ranks gradually increased from the left to the right, and from the top to the bottom of the matrix) to reach the same proportion of unknown relationships in both species, and averaged the values obtained over 1000 iterations to calculate the adjusted steepness for JM (0.255). Second, we calculated the percentage of reversals in the hierarchy, as the percentage of observations below the matrix diagonal out of the total number of observations (Young & Isbell, 2002). As expected, this percentage was higher in MM (68/346 = 20%) than in JM (193/2116 = 9%).

During focal sampling, we observed a total of 1.6 h (JM) and 33.6 h (MM) of solitary play, 2.8 h (JM) and 10.7 h (MM) of social play, and 30.4 h (JM) and 11.0 h (MM) of grooming interactions (for a distribution of these behaviors across individuals, see Table 1).

For statistical analyses of play behavior, we prepared two data sets. Firstly, we used the data collected during focal samples to assess differences in the proportion of time spent in solitary play, social play, and grooming between the species. Each line of data represented one focal sample and included information on the focal individual's identity, species, sex, age, and rank. We further included the proportion of time that the focal individual spent in solitary play, social play, or grooming interactions (i.e., out of the total observation time during the focal). Second, we used the data collected from the videos to assess inter-specific differences in play styles. Play sessions were analyzed with SONY Vegas PRO 12 (Sony Creative Software, 2012). For each dyad involved in the play session, we included one record in the data set that included the session number, the identity of players, their species, sex combination, absolute age difference, and absolute rank difference. We further included the exact duration of the play session, the total number of players involved in the session, the number of behavior types displayed during the session (i.e., wrestling, sparring, acrobatic, and object play), the number of play faces displayed by the two players during the play session, the proportion of time spent in noncontact play behavior (i.e., acrobatic and object play; out of the total time spent in noncontact and contact behavior, i.e., wrestling, sparring), whether reciprocal bites occurred during the session (i.e., whether both players performed at least one play bite), and whether the play session escalated into aggression.

We conducted analyses using generalized linear mixed models (hereafter, GLMM: Baayen, Davidson, & Bates, 2008) with the glmmTMB package (version 1.0.1; Brooks et al., 2017) in R (R Core Team, version 3.5.0). To assess inter-specific differences in the proportion of time spent in solitary play, social play and grooming, we used our first data set with focal data and modeled (1) the proportion of time spent in solitary play (Prediction 1), (2) social play (Prediction 2), and (3) grooming interactions (Prediction 3) with three GLMMs (family: β regression; Ferrari & Cribari-Neto, 2004). In the three models, we included species as test predictor, individual's sex, age, and rank as controls and focal subject identity as a random effect (Table 2).

To assess interspecific differences in play styles, we used our second data set with video data and three GLMMs (family: Poisson) to model (4) whether the number of players (Prediction 4), (5) the number of play behavior types (Prediction 5) and (6) the number of play faces displayed in a session (Prediction 6) were predicted by species, when controlling for players' sex combination, age and rank differences, including session duration as offset term, and session and players' identities as random effects (Table 2). To assess whether the proportion of contact play behavior was predicted by species and rate of play faces in the session, we modeled (7) the proportion of time spent in noncontact play behavior (out of the total time spent in noncontact and contact play behavior) with a GLMM (family: β regression). We used species and rate of play faces in the session as test predictors, players' sex combination, age and rank differences as controls, and session and players' identities as random effects (Prediction 7; Table 2). To investigate whether the occurrence of reciprocal bites was affected by species and rate of play faces in the session, we modeled (8) the occurrence of reciprocal bites with a GLMM (family: binomial), using species and rate of play faces in the session as test predictors, players' sex combination, age and rank differences as controls, session duration as offset term, and session and players' identities as random effects (Prediction 8; Table 2). Finally, we could not model whether the probability of aggressive escalations was affected by species and frequency of play faces (Predictions 9–9b), because only 13 play sessions escalated into an aggressive conflict.

For all models, age and age differences were *z*-transformed to facilitate model convergence and interpretation of model coefficients (Roger Mundry, personal communication). To accommodate 0 and 1 s in models with a β regression distribution, we added 1E−09 to 0 values and removed it from 1 values. We used likelihood ratio tests (Dobson, Zidek, & Lindsey, 2001) to compare full models containing all predictors with null models containing only control predictors, offset terms, and random factors. When full models differed significantly from null models, likelihood ratio tests were conducted to obtain the *p* values for each test predictor via single-term deletion using the R function drop1 (Barr, Levy, Scheepers, & Tily, 2013). No overdispersion was detected in Poisson models. To rule out collinearity, we determined the variance inflation factors (VIFs) (Field, 2005), which were minimal (maximum VIFs across all models = 1.16).

TABLE 2 Predictions, model used for the statistical analysis, test predictors and control predictors included in the models, and whether the predictions were supported by the model (yes, no, or partially)

Predictions	Model	Test and *control predictors*
P1. MM spend a higher proportion of time in solitary play than JM	M1	species + *focal sex* + *focal age* + *focal rank*
P2. MM spend a higher proportion of time in social play than JM	M2	
P3. JM spend a higher proportion of time in grooming interactions than MM	M3	
P4. Play sessions include more players in MM than JM	M4	species + *sex combination* + *age difference* + *rank difference* + *session duration (offset)*
P5. Play sessions include more play behavior types in MM than JM	M5	
P6. Play sessions have a higher rate of play faces in MM than JM	M6	
P7. MM spend a higher proportion of play time in contact behavior than JM		
P7b. High play face rate predicts higher proportion of time in play contact behavior	M7	species + play face rate + *sex combination* + *age difference* + *rank difference*
P8. The occurrence of reciprocal bites is higher in MM than JM in play sessions		
P8b. High play face rate predicts higher occurrence of reciprocal bites in play sessions	M8	species + play face rate + *sex combination* + *age difference* + *rank difference* + *session duration (offset)*
P9. The occurrence of aggression is higher in JM than MM in play sessions		
P9b. High play face rate predicts lower occurrence of aggression in play sessions	–	–

Note: Significant test predictors are underlined ($p < .05$), control predictors in italics. Focal subject's identity was included as random effect in Models 1–3, and session and players' identities in Models 4–8. Predictions supported by our data are in bold. In Models 1–3, proportion of time refers to the time spent in solitary play, social play, or grooming interactions, out of the total observation time. In Model 6, rate of play faces refers to the number of play faces out of the time spent playing. In Model 8, the occurrence of reciprocal bites was entered as a binomial response (i.e., whether reciprocal bites occurred in the play session).

Abbreviations: JM, Japanese macaques; MM, moor macaques.

3 | RESULTS

For all models, the full model differed significantly from the corresponding null model (Table 3). The proportion of time spent in solitary play was higher for MM than JM, supporting prediction 1 (Tables 2 and 3, M1). The proportion of time spent in social play was also higher in MM than JM, whereas JM spent a higher proportion of time in grooming interactions than MM, supporting predictions 2 and 3, respectively (Tables 2 and 3, M2 and M3).

In line with prediction 4, the number of players in a session was higher for MM than JM (Figure 1a and Tables 2 and 3, M4). Similarly, both the number of play behavior types and the rate of play faces displayed in a session were higher in MM than JM, supporting predictions 5 and 6, respectively (Figure 1b,c; Tables 2 and 3, M5 and M6). In line with prediction 7a, the proportion of noncontact behavior was higher in JM than MM (Figure 1f), but the rate of play faces had no significant effect on this proportion, in contrast with our prediction 7b (Tables 2 and 3, M7). Moreover, the probability of reciprocal bites was higher in MM than in JM, and increased with a higher rate of play faces in the session, supporting predictions 8a and 8b (Figure 1c,d and Tables 2 and 3, M8). In Models M4–M8, rank difference between players was included as a control predictor. As infants were assigned their mother's rank, however, this measure might not have been precise (especially when infants played with non-infants, as the latter might have been likely to dominate infants), thus affecting our results. To check whether our conclusions were robust, we, therefore, re-ran the models above, after removing from the data-set all the interactions between infants and non-infants. Our analyses confirmed the results above, showing the same effect of species (in Models M4–M8) and rate of play faces (in M8) on our dependent variables.

Finally, aggressive escalations were uncommon in both species, with only 1.8% play sessions ending with aggression in JM, and 0.9% in MM, in line with our prediction 9 (=8/453 sessions in JM, and

TABLE 3 Results of Models 1–8, including estimates, standard errors (*SE*), confidence intervals (CIs), likelihood ratio tests (LRT), degrees of freedom (*df*), and *p* values

	Estimate	***SE***	**CIs: 2.5/97.5%**	**LRT**	***df***	***p***
M1: Proportion of time spent in solitary play (β regression distribution)						
Full-null comparison: LRT = 21.38, *df* = 1, *p* < .001						
Intercept	−2.39	0.36	−3.10/−1.67	–	–	–
Species (MM)	1.38	0.27	0.86/1.91	21.38	1	**<.001**
Sex (male)	0.11	0.27	−0.41/0.64	0.19	1	.667
Age	−0.64	0.13	−0.90/−0.38	18.39	1	<.001
Rank	−0.92	1.11	−3.10/1.26	0.68	1	.409
M2: Proportion of time spent in social play (β regression distribution)						
Full-null comparison: LRT = 27.80, *df* = 1, *p* < .001						
Intercept	−2.96	0.18	−3.32/−2.61	–	–	–
Species (MM)	0.74	0.12	0.51/0.98	27.80	1	**<.001**
Sex (male)	0.02	0.12	−0.23/0.26	0.21	1	.884
Age	−0.32	0.06	−0.44/−0.20	20.69	1	<.001
Rank	−0.50	1.52	−1.51/0.52	0.89	1	.345
M3: Proportion of time spent in grooming interactions (β regression distribution)						
Full-null comparison: LRT = 16.09, *df* = 1, *p* < .001						
Intercept	−2.15	0.15	−2.44/−1.86	–	–	–
Species (MM)	−0.40	0.09	−0.58/−0.23	16.09	1	**<.001**
Sex (male)	−0.23	0.09	−0.42/−0.05	5.81	1	.012
Age	−0.03	0.05	−0.12/0.06	0.51	1	.470
Rank	0.37	0.39	−0.39/0.41	0.89	1	.338
M4: Number of players (offset term = play session duration, Poisson distribution)						
Full-null comparison: LRT = 29.41, *df* = 1, *p* < .001						
Intercept	−1.90	0.10	−2.09/−1.71	–	–	–
Species (MM)	0.40	0.07	0.26/0.55	29.41	1	**<.001**
Sex combination (female–male)	−0.12	0.08	−0.29/0.04	4.47	2	.107
Sex combination (male–male)	−0.19	0.10	−0.37/−0.01			
Age difference	0.00	0.03	−0.06/0.06	0.01	1	.934
Rank difference	0.13	0.27	−0.39/0.66	0.24	1	.624
M5: number of types of play behavior (offset term = play session duration, Poisson distribution)						
Full-null comparison: LRT = 27.89, *df* = 1, *p* < .001						
Intercept	−2.46	0.09	−2.64/−2.28	–	–	–
Species (MM)	0.41	0.07	0.30/0.56	27.89	1	**<.001**
Sex combination (female–male)	−0.16	0.08	−0.32/0.01	9.01	2	.011
Sex combination (male–male)	−0.28	0.09	−0.45/−0.10			
Age difference	−0.01	0.03	−0.07/0.05	0.05	1	.808
Rank difference	0.09	0.27	−0.44/0.62	0.11	1	.740
M6: number of play faces (offset term = play session duration, Poisson distribution)						
Full-null comparison: LRT = 46.21, *df* = 1, *p* < .001						

TABLE 3 (Continued)

	Estimate	*SE*	CIs: 2.5/97.5%	LRT	*df*	*p*
Intercept	−3.95	0.21	−4.36/−3.54	–	–	–
Species (MM)	1.41	0.19	1.04/1.78	46.21	1	**<.001**
Sex combination (female–male)	0.32	0.16	0.01/0.64	32.31	2	<.001
Sex combination (male–male)	0.99	0.21	0.58/1.41			
Age difference	0.08	0.04	0.00/0.16	4.06	1	.044
Rank difference	0.30	0.45	−0.59/1.19	0.44	1	.507
M7: Proportion of time spent in noncontact play behavior (β regression distribution)						
Full-null comparison: LRT = 25.88, *df* = 2, *p* < .001						
Intercept	−0.28	0.12	−0.52/−0.05	–	–	–
Species (MM)	−0.56	0.08	−0.72/−0.40	25.81	1	**<.001**
Play face frequency	0.17	0.17	−0.17/0.51	0.92		.337
Sex combination (female-male)	0.01	0.12	−0.21/0.24	4.02	2	.134
Sex combination (male-male)	−0.14	0.12	−0.38/0.08			
Age difference	−0.01	0.04	−0.10/0.07	0.10	1	.750
Rank difference	1.25	0.36	0.54/1.95	10.64	1	.001
M8: Occurrence of reciprocal bites (offset term = play session duration, binomial distribution)						
Full-null comparison: LRT = 37.64, *df* = 2, *p* < .001						
Intercept	−7.18	0.60	−8.36/−6.00	–	–	–
Species (MM)	2.02	0.41	1.23/2.82	22.47	1	**<.001**
Play face frequency	1.81	0.44	0.94/2.67	12.67	1	**<.001**
Sex combination (female–male)	−0.05	0.48	−0.98/0.89	10.06	2	.007
Sex combination (male–male)	0.85	0.51	−0.15/1.85			
Age difference	−0.86	0.28	−1.40/−0.32	13.72	1	<.001
Rank difference	−1.37	1.50	−4.30/1.57	0.83	1	.361

Note: Significant test predictors are in bold, control predictors in italics. Age and age difference were *z*-transformed before analysis. We included subject identity as random effect in Models 1–3, session and players' identities in Models 4–8.
Abbreviation: MM, moor macaques.

5/554 in MM; Figure 1e and Table 2). The mean rate of play faces was similar in play sessions that escalated into aggressive conflicts (0.128), and those which did not (0.135).

4 | DISCUSSION

Our results revealed inter-specific differences in play behavior, that are in line with the different dominance styles of the study species, and largely confirmed our predictions (Table 2). In particular, MM spent a larger proportion of time in solitary play and social play than JM, while JM spent a higher proportion of time in grooming interactions than MM (in line with Predictions 1–3). In line with our predictions, play sessions in MM included more players (Prediction 4), more play behavior types (Prediction 5), a higher rate of play faces (Prediction 6), a higher proportion of contact play behavior (Prediction 7) and a higher occurrence of reciprocal bites than in JM (Prediction 8). Aggressive escalations were rare, but twice as frequent in JM than in MM (Prediction 9). Finally, a higher rate of play faces predicted the occurrence of reciprocal bites (in line with Prediction 8b), but had no significant effect on the proportion of contact play behaviors (in contrast with Prediction 7b).

As predicted, the proportion of both solitary and social play was higher in less despotic MM, in line with previous literature (Antonacci, Norscia, & Palagi, 2010; Ciani et al., 2012; Hare et al., 2012; Palagi, 2006; Palagi & Cordoni, 2012; Palagi et al., 2016; Scopa & Palagi, 2016). On the one hand, less despotic species may engage more in play behavior, as their less despotic style reduces the risks of social play (Scopa & Palagi, 2016). On the other hand, play may be especially adaptive in less despotic species, to acquire both novel

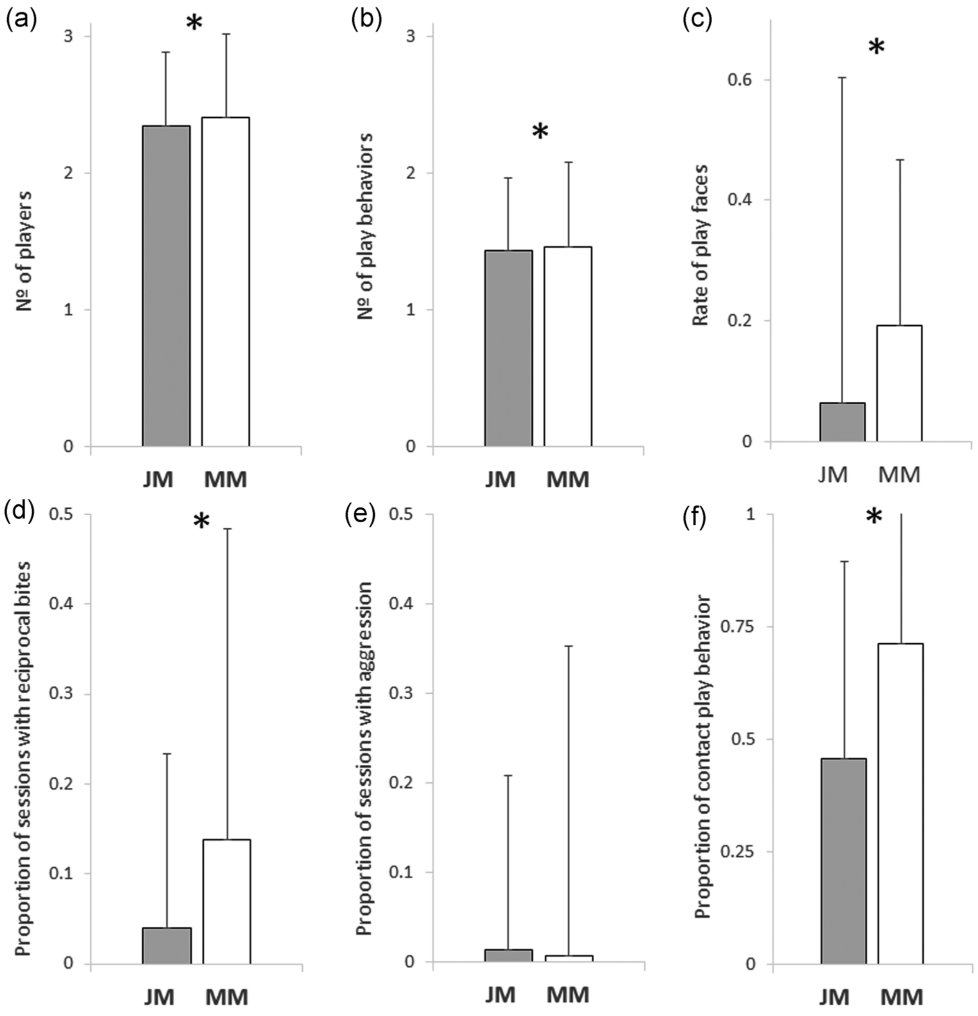

FIGURE 1 Species differences in play characteristics (Japanese macaques [JM], gray, $N = 559$ play sessions; moor macaques [MM], white, $N = 695$ play sessions). Panels show mean + *SD* for (a) number of players per session, (b) number of play behavior types per session (c) rate of play faces per session, (d) proportion of sessions in which reciprocal bites occurred, (e) proportion of sessions in which aggressive escalations occurred, and (f) proportion of play time spent in contact play. Asterisks indicate variables that differed by species in our models (Table 3). We did not run a model to test panel (e)

behavioral patterns and the necessary social skills to navigate the larger and more diversified social networks they will have as adults (Adams et al., 2015; Amici et al., 2019; Thierry, 2007). In contrast, the proportion of time spent in grooming interactions was higher in JM than MM, suggesting that social play and grooming may serve different alternative functions for the formation and maintenance of social bonds (e.g., Shimada & Sueur, 2018). In particular, grooming may be especially important in more despotic species, where aggressive interactions may become especially severe and riskier behaviors like social play are less common (e.g., Ciani et al., 2012; Palagi & Paoli, 2007, 2008). In the future, these findings should be confirmed by better controlling for variation in the number and characteristics of potential social partners in the study groups. For instance, it is possible that larger groups offer individuals a larger choice of potential social partners, thus positively affecting the occurrence of social play. However, it should be noted that the availability of potential social partners was overall larger in JM, which included 43 adults and subadults, and 12 immatures (in contrast to the 30 adults and subadults, and 12 immatures in MM).

Our study also showed inter-specific differences in play styles. As predicted, play sessions in less despotic MM included more players, a larger variety of play behavior types, a higher proportion of contact play behaviors (i.e., wrestling and sparring) and a higher occurrence of reciprocal bites than in JM (Figure 1), in line with previous studies on other species with different dominance styles (Ciani et al., 2012; Palagi & Paoli, 2007, 2008; Petit et al., 2008). In more despotic species, aggressive interactions are usually more severe (e.g., de Waal & Luttrell, 1989; Thierry, 2000, 2007). Therefore, individuals of more despotic species may avoid behaviors that might increase the risk of conflicts, like play sessions involving many individuals and/or including a rapid alternation of many different behaviors, which increase the unpredictability of the interactions and thus the risks involved (Palagi, 2018). Reciprocal bites, for instance, more likely occur in less despotic species, possibly because offensive and defensive roles may be better balanced during play sessions than in species with steeper dominance hierarchies (Palagi, 2006; Reinhart et al., 2010). Similarly, because physical contact may increase the risk that play escalates into overt aggression (Cordoni, Demuru, Ceccarelli, & Palagi, 2016), as, for example, when one individual uses disproportionate force (but see wolves, Cordoni, 2009; Smuts, 2014), less despotic species may more likely engage in physical contact when playing (Petit et al., 2008). Therefore, despotic species may be more cautious and preferentially engage in noncontact social play (Kraus, Pellis, & Pellis, 2019). Accordingly, the percentage of bouts ending with aggression were higher when players engaged in sparring and wrestling (in JM: 1.6%; in MM: 0.8%), as compared to when they avoided physical contact (in JM: 1.1%; in MM: 0%; Figure 1e).

As predicted, the rate of play faces during play sessions was higher in MM than in JM (Figure 1c). Play faces are generally considered spontaneous emotional expressions, rather than intentional communicative acts (Scopa & Palagi, 2016), and a higher rate of play faces (i.e., per unit of play time) in less despotic species may be explained by the fact that these species are more free to express their emotions (Mancini et al., 2013; Palagi & Mancini, 2011; Palagi et al., 2016; S. M. Pellis et al., 2011; Scopa & Palagi, 2016). Therefore, a higher rate of play faces in MM is not surprising, although previous studies have failed to find differences in the rate of play faces between more and less despotic species (Mancini et al., 2013; Palagi, Marchi, Cavicchio, & Bandoli, 2019; Palagi, Norscia, Pressi, & Cordoni, 2018; Scopa & Palagi, 2016). A higher rate of play faces was also linked to a higher occurrence of reciprocal bites, but had no significant effect on the proportion of time spent in noncontact play behavior. Similarly, the frequency of play faces was similar in play sessions that escalated to aggression and those that did not. Therefore, although play faces were clearly more frequent in less despotic species (MM), this difference alone cannot explain the variation in the play styles of the two study species.

Overall, our results provide support for the hypothesis that interspecific variation in play behavior is linked to differences in dominance style, with less despotic species (MM) playing more, with more players, more behavioral variation, more contact play behavior, more reciprocal bites and more play faces. Importantly, the study groups really differed in their dominance styles, as confirmed by the assessment of the steepness of their dominance hierarchies and of the percentage of reversals against the hierarchy. As play behavior had so far never been studied in MM, these results are important to add another data point for nondespotic species and confirm that these behavioral differences in play really reflect differences in the species dominance styles. Indeed, our study largely confirmed previous research comparing play styles in macaques with different dominance styles, which appear to be rather consistent across species with similar dominance styles (e.g., less despotic species play more: Ciani et al., 2012; Petit et al., 2008; less despotic species play more cooperatively: Reinhart et al., 2010). Interestingly, these differences appear to be consistent also across individuals with different rearing conditions: the few direct comparisons between captive and free-ranging individuals, for instance, have found no major differences in play behavior between groups (Reinhart et al. 2010; Pellis, Pellis, & Himmler, 2014). Taken together, these studies suggest that differences in play behavior linked to dominance styles may be relatively hard-wired, despite previous cross-fostering studies reporting an important effect of experience on macaque dominance styles (e.g., de Waal & Johanowicz, 1993).

Finally, several control predictors were significant in our models (see Table 3). In particular, the proportion of both solitary (M1) and social play (M2) was higher in younger individuals than older ones, in line with abundant literature (e.g., Amici et al., 2019; Kulik, Amici, Langos, & Widdig, 2015). Moreover, females spent a higher proportion of time in grooming interactions than males (M3), also in line with literature (e.g., Cords, Sheehan, & Ekernas, 2010; Kulik et al., 2015; Nakamichi, 1989; Rowell & Chism, 1986; van Noordwijk, Hemelrijk, Herremans, & Sterck, 1993). The number of play behavior types shown in a session was higher in female-female dyads, than in female–male dyads and male–male dyads (M5). In contrast, the rate of play faces was higher in male–male dyads than in female–male and female–female dyads, and when the difference between the players' age was higher (M6). Finally, the proportion of time spent in play contact behavior was higher when players' rank difference was low (M7), while the probability to reciprocate bites was higher in male–male dyads than in female-male and female-female dyads, and when players' age difference was low (M8).

In the future, studies on interspecific differences in play behavior will need to include more conspecific groups and more species with different dominance styles, as well as genera other than *Pan* and *Macaca*, which are the ones that have been most thoroughly studied. In this way, we will be able to confirm that differences in play behavior are consistent within species and so linked to differences in dominance style rather than to other socio-ecological factors, such as food availability or climatic conditions, or rearing conditions. Future studies should also observe individuals longitudinally, to examine the development of play behavior and its long-term effects on primate sociality (e.g., play partners in the early years form close social bonds also as adults; larger networks of play partners predict survival and fitness in the adulthood). Finally, more detailed studies on the functions of play face are needed, including research on rapid facial mimicry and the role it plays across different species (Mancini et al., 2013; Palagi et al., 2019; Scopa & Palagi, 2016).

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DATA AVAILABILITY STATEMENT

Data will be made available to the readers upon request to the corresponding author.

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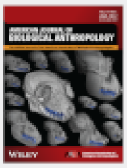

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RESEARCH ARTICLES

Relationship tenure differentially influences pair-bond behavior in male and female socially monogamous titi monkeys (*Callicebus cupreus*)

Emily S. Rothwell, Sarah B. Carp, Logan E. Savidge, Sally P. Mendoza, Karen L. Bales

First Published: 04 August 2020

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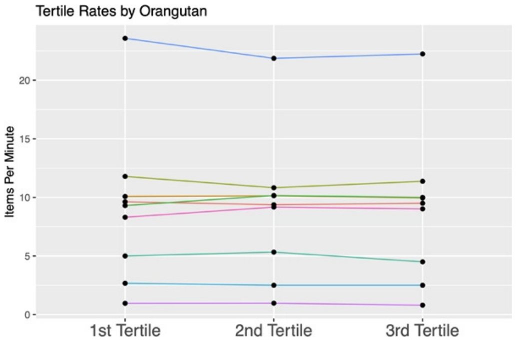
Wild Bornean orangutan (*Pongo pygmaeus wurmbii*) feeding rates and the Marginal Value Theorem

Andrea L. DiGiorgio, Elizabeth M. Upton, Tri Wahyu Susanto, Cheryl D. Knott

First Published: 05 August 2020



Feeding rates of wild Bornean orangutans do not decrease during a feeding bout, as measured by the average feeding rate in each third (tertile) of the bout. Average feeding rates (items per minute) of nine orangutans are presented over the first, second, and third tertiles of a feeding bout. This finding is contrary to the critical assumption of Marginal Value Theorem (MVT), that feeding rates decrease over patch residence, and suggests that MVT is not sufficient to explain all patch departure choices in wild Bornean orangutans.

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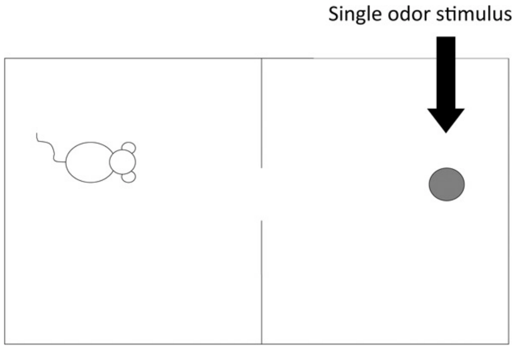
Olfactory predator recognition in the brown mouse lemur (*Microcebus rufus*) in Ranomafana National Park, Madagascar

Anja M. Deppe, Geoff Kushnick

First Published: 08 August 2020



Set-up of the laboratory experiment. Trials were four minutes during which behavioral reactions were recorded and categorized.

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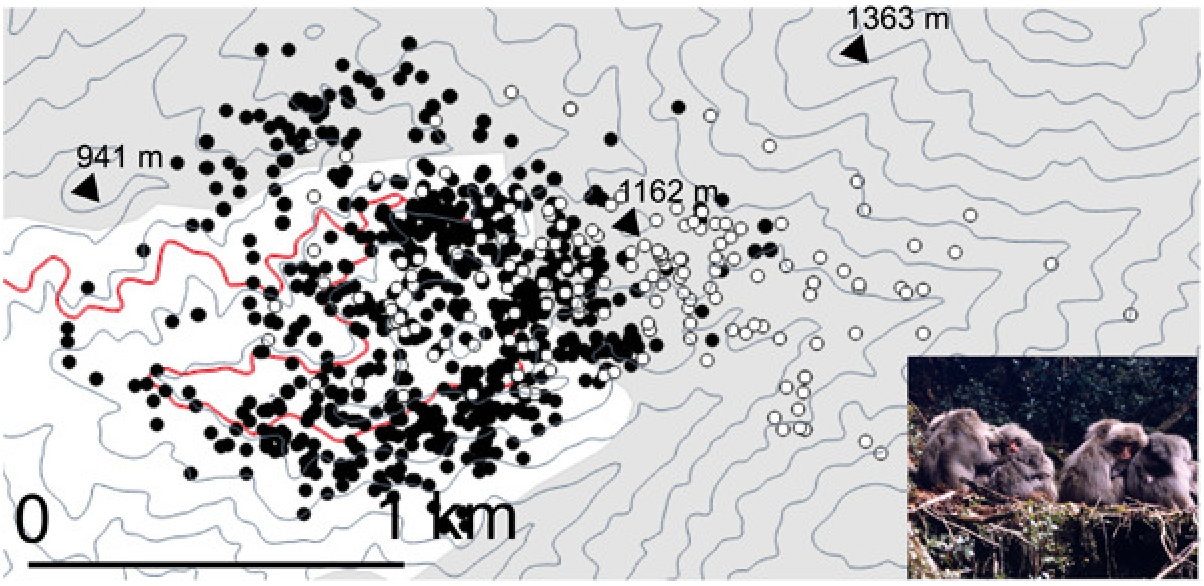
Ranging patterns of Japanese macaques in the coniferous forest of Yakushima: Home range shift and travel rate

Goro Hanya, Shin-ichi Yoshihiro, Shuhei Hayaishi, Yukio Takahata

First Published: 13 August 2020



A group of Japanese macaques shifted their home range eastward (open circles) in summer and westward (closed circles) in other months.

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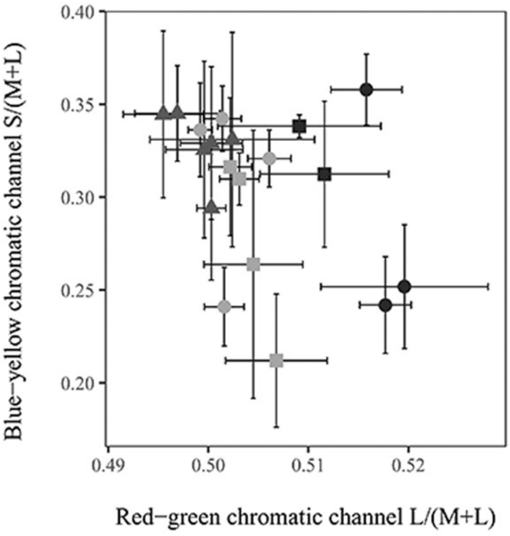
Visual detection and fruit selection by the mantled howler monkey (*Alouatta palliata*)

Karem G. Sánchez-Solano, Jorge É. Morales-Mávil, Matthias Laska, Amanda Melin, Laura T. Hernández-Salazar

First Published: 19 August 2020



Visual detection of howler monkeys for ripe and unripe fruits over leaves. The values are the mean reflectance spectra along the visible spectrum (400–700 nm).

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REVIEW ARTICLE

Words matter: Reflections on language projects with chimpanzees and their implications

Mark A. Krause, Michael J. Beran

First Published: 24 August 2020

Correction(s) for this article ›

Volume 82, Issue 12, American Journal of Primatology | First Published online: October 11, 2020

The chimpanzee named Panzee with her lexigram keyboard.

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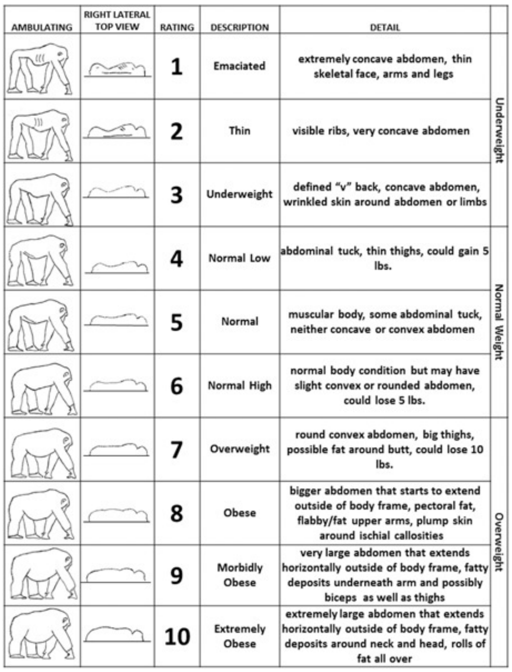
RESEARCH ARTICLES

Validation and utility of a body condition scoring system for chimpanzees (*Pan troglodytes*)

Lisa A. Reamer, Sarah J. Neal Webb, Rebekah Jones, Erica Thiele, Rachel L. Haller, Steven J. Schapiro, Susan P. Lambeth, Patrick W. Hanley

First Published: 27 August 2020



AMBULATING	RIGHT LATERAL TOP VIEW	RATING	DESCRIPTION	DETAIL	
		1	Emaciated	extremely concave abdomen, thin skeletal face, arms and legs	Underweight
		2	Thin	visible ribs, very concave abdomen	
		3	Underweight	defined "v" back, concave abdomen, wrinkled skin around abdomen or limbs	
		4	Normal Low	abdominal tuck, thin thighs, could gain 5 lbs.	Normal Weight
		5	Normal	muscular body, some abdominal tuck, neither concave or convex abdomen	
		6	Normal High	normal body condition but may have slight convex or rounded abdomen, could lose 5 lbs.	
		7	Overweight	round convex abdomen, big thighs, possible fat around butt, could lose 10 lbs.	Overweight
		8	Obese	bigger abdomen that starts to extend outside of body frame, pectoral fat, flabby/fat upper arms, plump skin around ischial callosities	
		9	Morbidly Obese	very large abdomen that extends horizontally outside of body frame, fatty deposits underneath arm and possibly biceps as well as thighs	
		10	Extremely Obese	extremely large abdomen that extends horizontally outside of body frame, fatty deposits around neck and head, rolls of fat all over	

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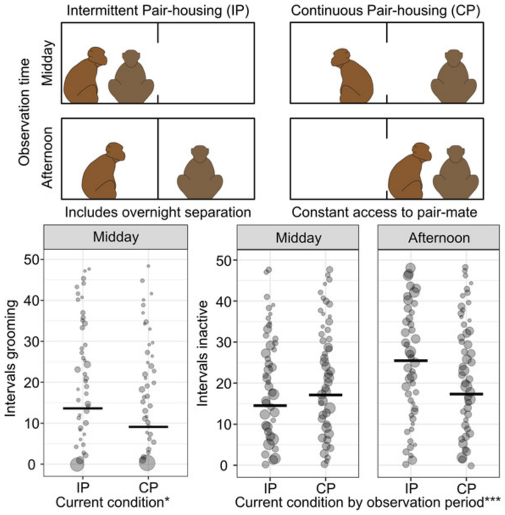
Improved behavioral indices of welfare in continuous compared to intermittent pair-housing in adult female rhesus macaques (*Macaca mulatta*)

Lauren C. Cassidy, Darcy L. Hannibal, Stuart Semple, Brenda McCowan

First Published: 05 September 2020



Female rhesus exhibit improved behavioral indices of welfare in continuous pair-housing.

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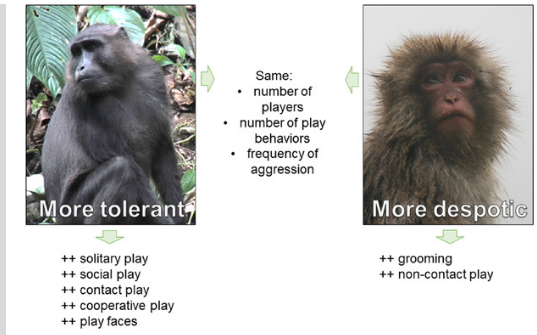
Play behavior in immature moor macaques (*Macaca maura*) and Japanese macaques (*Macaca fuscata*)

Víctor Beltrán Francés, Alba Castellano-Navarro, Risma Illa Maulany, Putu O. Ngakan, Andrew J. J. MacIntosh, Miquel Llorente, Federica Amici

First Published: 03 September 2020



More tolerant moor macaques showed more solitary and social play and a more cooperative style during social play than more despotic Japanese macaques.

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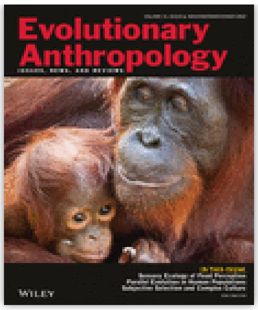

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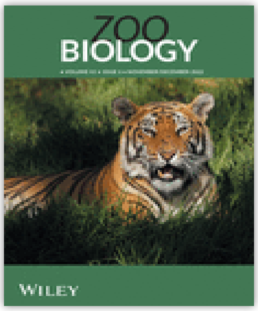

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DOI: 10.1002/ajp.23192

RESEARCH ARTICLE

Play behavior in immature moor macaques (*Macaca maura*) and Japanese macaques (*Macaca fuscata*)

Víctor Beltrán Francés[1] | **Alba Castellano-Navarro**[2] | **Risma Illa Maulany**[3] | **Putu O. Ngakan**[3] | **Andrew J. J. MacIntosh**[4] | **Miquel Llorente**[5,6,7] | **Federica Amici**[8,9]

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Abstract

Play is widespread across mammalian taxa, but species strongly vary in the ways they play. In less despotic primate species (i.e., with less steep dominance hierarchies, less severe conflicts, and more reconciliation), play has been described as being more frequent, cooperative, and freely expressed. To study the link between social play and dominance style, we compared play behavior in free-ranging infants, juveniles and subadults of more despotic Japanese macaques (*Macaca fuscata*, $N = 24$) and less despotic moor macaques (*Macaca maura*, $N = 17$). We found interspecific differences in play behavior that corresponded with the contrasting dominance styles of the study species, largely confirming our predictions. In particular, moor macaques spent a larger proportion of time in solitary and social play than Japanese macaques, while Japanese macaques spent a larger proportion of time in grooming interactions. In moor macaques, play sessions included more players, a larger variety of play behaviors, greater play face rates, a greater proportion of time in contact play, and a higher rate of reciprocal play-biting than in Japanese macaques. Aggressive escalations were not common, but more frequent in Japanese macaques. Finally, a higher frequency of play faces during play sessions predicted the occurrence of more reciprocal play-bites, but not the proportion of time spent in contact play behaviors. Additional studies on other groups and species will allow a better understanding of the link between dominance style and social play.

KEYWORDS
cooperative play style, despotism, dominance style, play behavior, play face

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1 | INTRODUCTION

Play has been defined as an exaggerated, spontaneous, and self-rewarding behavior that serves no immediate function and often occurs in non-stressful situations (Burghardt, 2005; Nathan, Pellegrini, & Burghardt, 2012). Play is a risky, energy- and time-consuming activity (de Almeida Rocha, Dos Reis, & de Carvalho Oliveira, 2014; Palagi, 2007, 2018), and its adaptive function has long been unclear (Bekoff & Allen, 1998; Marks, Vizconde, Gibson, Rodriguez, & Nunes, 2017; Martin & Caro, 1985). Nowadays, play is known to have a crucial function (Palagi, 2018; S. M. Pellis & Pellis, 2017). Social play (i.e., play involving two or more animals), for instance, may facilitate the acquisition of social knowledge and abilities, act as a buffer during stressful situations, and allow individuals to strengthen their social relationships and enlarge their social networks, gradually becoming part of the social group (Baldwin, 1986; Bekoff & Byers, 1998; Burghardt, 2005; Fagen, 1981; Lutz & Judge, 2017; Palagi, 2018; Shimada & Sueur, 2018). In contrast, solitary play (i.e., intense or sustained locomotion and exploratory behaviors in the absence of social partners; Berghänel, Schülke, & Ostner, 2015; Burghardt, 2005; S. M. Pellis & Burghardt, 2017; Petrů, Špinka, Lhota, & Šípek, 2008) may facilitate the acquisition of novel behavioral patterns. In Burmese long-tailed macaques (*Macaca fascicularis aurea*), for instance, juveniles increase their foraging skills through solitary object play (Pelletier et al., 2017). Therefore, depending on the socio-ecological challenges faced by different species, patterns of social and solitary play may vary across species to facilitate the selective acquisition of specific skills and behavioral patterns (Berghänel et al., 2015; Norscia & Palagi, 2015; Palagi, Cordoni, & Borgognini Tarli, 2004; Palagi, Paoli, & Tarli, 2006; Shimada, 2006).

Among primates, macaques constitute an ideal taxon to study inter-specific variation in play behavior. Macaques are a monophyletic group with similar kinship and demographic structures across species (e.g., female philopatry, matrilineal dominance hierarchies, multi-male multi-female social organization; Flack, Jeannotte, & de Waal, 2004; Thierry, 2000, 2007). Nonetheless, macaque species vary markedly in their dominance style and have been clustered into four grades, from more to less despotic (Thierry, 2000, 2007; Thierry, Singh, & Kaumanns, 2004). In less despotic species, aggressive conflicts are less intense and characterized by higher counter-aggression rates, more undecided outcomes, higher reconciliation rates, and shallower dominance hierarchies, as compared with more despotic species (e.g., de Waal & Luttrell, 1989; Demaria & Thierry, 2001; Petit, Abegg, & Thierry, 1997, 1985). In less despotic species, dominance also imposes fewer constraints on social choices, and individuals have more opportunities to interact with a larger variety of social partners, independently of rank and kinship (Butovskaya, 2004; Cooper & Bernstein, 2008; Duboscq et al., 2013; Matsumura & Okamoto, 1997; Thierry, Anderson, Demaria, Desportes, & Petit, 1994).

Clearly, these differences in dominance style might also affect individuals' play behavior. If social play facilitates the selective acquisition of skills and social partners, for instance, it should be more frequent in less despotic species, for two main reasons. First, social play is generally considered a risky behavior for the physical contact usually implied, the inclusion of uncertain modules in play sessions, and the risk of escalation into serious fighting (Palagi, 2007, 2018). Therefore, it may be more common in less despotic species, where aggressive conflicts are usually less intense and the risks of injury lower (e.g., de Waal & Luttrell, 1989; Thierry, 2000, 2007). Second, less despotic species usually have more extended social networks (Ciani, Dall'Olio, Stanyon, & Palagi, 2012; Petit, Bertrand, & Thierry, 2008; for similar results within the *Pan* genus, see Hare, Wobber, & Wrangham, 2012; Palagi, 2006; Palagi & Cordoni, 2012). Therefore, social play may be especially important in less despotic species, as bonding with many social partners from early on may allow individuals to lay the foundations of the large social networks they will have as adults (e.g., Adams et al., 2015; Amici, Kulik, Langos, & Widdig, 2019; Shimada & Sueur, 2018). In contrast, immatures in more despotic species may preferentially rely on grooming to form and maintain social bonds, as grooming is not as risky as play, and may be an alternative to social play in the formation and maintenance of social bonds (Shimada & Sueur, 2018). Furthermore, patterns of solitary play may also vary among species depending on their dominance style. In more despotic species, females largely inherit their maternal rank (Berman, 2017), while individuals in less despotic species have a higher chance of rising through the dominance hierarchy, as ranks are nor strictly inherited (Thierry, 2007). Therefore, individuals in less despotic species may especially benefit from exploratory behaviors (as in solitary play) that might facilitate the attainment of higher rank, by for instance fostering the acquisition of better ecological knowledge, reducing neophobia (Lockman, 2000; Parker & Gibson, 1977), or facilitating the emergence of novel functional behaviors (e.g., Fagen, 1981; Huffman & Quiatt, 1986).

Differences in dominance style might also affect the way in which individuals play. In less despotic species, individuals have a larger variety of partners with whom they can play (e.g., Ciani et al., 2012; Palagi & Paoli, 2007, 2008), and may engage in polyadic interactions more often than despotic species (Ciani et al., 2012; Palagi & Paoli, 2007, 2008; Petit et al., 2008), as in the latter the presence of many players may dramatically enhance the risk of aggressive behavior (Palagi, 2018; Petit et al., 2008; Reinhart et al., 2010). Similarly, social play in less despotic species may include a larger variety of behaviors than more despotic species: behavioral variation during play sessions increases the level of unpredictability and the risk of aggressive escalations (Palagi, 2018; Petit et al., 2008; Reinhart et al., 2010), which may be especially risky in more despotic species. Less despotic species may also show more cooperative play styles, with frequent variation in the players' roles (e.g., reciprocal bites; Petit et al., 2008; Reinhart et al., 2010) and more physical contact (e.g., sparring, wrestling; Ciani et al., 2012; Petit et al., 2008), as the risk of severe aggression is lower than in despotic species (Palagi, 2018; Petit et al., 2008; Reinhart et al., 2010).

Finally, less despotic species rely less on formal displays to manage their interactions (Thierry, 2000, 2007), and may hence have larger and more complex communicative repertoires than despotic species (Dobson, 2012; Flack et al., 2004; Maestripieri, 1995, 2005; Scopa & Palagi, 2016; Whiten & Schaik, 2007; Zannella, Stanyon, & Palagi, 2017). Play face (i.e., a relaxed open mouth facial expression), for instance, is considered a crucial communicative tool to express emotions and intentions during play sessions and may serve to prevent aggression between players and increase social play duration (de Waal, 2003; Demuru, Ferrari, & Palagi, 2015; Flack et al., 2004; Mancini, Ferrari, & Palagi, 2013; Palagi & Mancini, 2011; S. Pellis & Pellis, 2009; Scopa & Palagi, 2016; Špinka, Palečková, & Řeháková, 2016; Yanagi & Berman, 2014). Therefore, play faces may be more frequent in less despotic species, decrease the risk of aggressive escalations, and increase the proportion of potentially riskier play behaviors (e.g., contact behavior, reciprocal bites; see e.g., Demuru et al., 2015).

In this study, we aimed to assess inter-specific variation in play behavior linked to differences in their dominance styles, including highly despotic Japanese macaques (*Macaca fuscata*, hereafter JM) and less despotic moor macaques (*Macaca maura*, MM; Thierry, 2007). We added to previous research in three main ways. First, we included a species, MM, whose play behavior had not been previously studied. The inclusion of MM is important to assess whether differences in play styles really depend on the species' dominance styles, as MM add another data point for non-despotic species. Secondly, the large size of our study groups (*M. maura*: *N* = 42; *M. fuscata*: *N* = 52) allowed us to better take into account intraspecific variation in play, including possible rank, age, and sex differences. Third, the study groups we tested were both free-ranging. To date, all the studies comparing play in species with different dominance styles have been conducted in captivity (Ciani et al., 2012; Diamond, Daryl, Clio, & Bond, 2006; Palagi, 2006; Palagi & Cordoni, 2012; S. M. Pellis & Pellis, 1997; Petit et al., 2008; Scopa & Palagi, 2016), with one exception (Reinhart et al., 2010). Extending the study of interspecific differences in play behavior to the wild is especially important when it comes to the study of social behaviors which might have an adaptive function only in the wild (e.g., to build social relationships that may be important during male migration, see Amici et al., 2019).

We predicted that, if dominance style affects the relative proportion of play behavior, MM should spend a higher proportion of time in solitary play (Prediction 1) and in social play (Prediction 2), as compared with JM. In contrast, JM should spend a higher proportion of time grooming than MM (Prediction 3), as grooming is a less risky alternative to the formation and maintenance of social bonds (Shimada & Sueur, 2018). Moreover, if dominance style also affects the style of social play, play sessions in MM should include more players (Prediction 4), a larger variety of behaviors (Prediction 5), a higher rate of play faces (Prediction 6), a higher proportion of contact behaviors (Prediction 7), a higher occurrence of reciprocal bites (Prediction 8), and fewer aggressive escalations (Prediction 9) as compared to JM. Finally, we assessed the communicative role of play faces and, in particular, whether they facilitate the occurrence of riskier play behaviors in both JM and MM. We predicted that higher rates of play faces would predict a higher proportion of time spent in contact behaviors (Prediction 7b) and a higher occurrence of reciprocal bites (Prediction 8b), while decreasing the probability of aggressive escalations (Prediction 9b).

2 | METHODS

2.1 | Ethics statement

The study was purely observational, and the procedures approved by the Indonesian Foreign Research Permit Division, Ministry of Research and Technology/National Research and Innovation Agency, which allowed us access to the MM) and by the Primate Research Institute at the Kyoto University in Japan, which allowed us access to the JM. We strictly adhered to the legal requirements of the countries in which the research was conducted, and to the ASP Principles for the Ethical Treatment of Nonhuman Primates.

2.2 | Study populations and subject

We observed one group of free-ranging MM and one group of free-ranging JM. The MM were studied in the Karaenta forest area (5°02′ 59.4″ S, 119°44′13.2″ E), an approximately 10,282 ha primary forest sector of the 43,000 ha total area of Bantimurung-Bulusaraung National Park, in South Sulawesi, Indonesia. The group was well habituated, having been studied for more than 30 years (Matsumura, 1993, 1996; Okamoto & Matsumura, 2001). At the onset of our study, the group comprised 42 individuals, including 11 male (≥5 years) and 14 female adults (≥4 years), 2 male (4 years), and 3 female subadults (3 years), 2 male (3years) and 1 female juveniles (2 years), and 5 male and 4 female infants (up to 1 year). The first author collected data on all individuals in Karaenta from September 2018 to March 2019. During this period, two infants migrated out of the group, while another one was killed in a car accident (so that one had to be excluded from the analyses, because we were able to collect only a limited amount of data). All nine infants were still suckling when the study started (October 2018). Their age was estimated by the first and last authors (and Dr. Bonaventura Majolo) based on their size (Grand, 1981) and motor patterns (Thierry et al., 2000), as displayed by each infant in three videos. All three raters have been working with different species of macaques for more than 3 years, and always agreed on classifying the nine individuals as infants (ICC = 1, *p* = 0).

The JM were studied on Koshima Islet, Miyazaki prefecture, Japan (31°27′N, 131°22′E), an area of approximately 30 ha covered with evergreen broadleaf forest (Duboscq, Romano, Sueur, & MacIntosh, 2016). Our study group (i.e., main group) was well habituated and has been well studied since 1948, through collection of demographic, ecological, behavioral, and life-history data (Duboscq et al., 2016; Kawai, 1963; Rigaill et al., 2017; Watanabe, 1989, 2008; Yamagiwa, 2010). When the study started, the group consisted of 55 individuals, including 12 male and 24 female adults, 4 female and

3 male subadults, 5 male and 5 female juveniles, and 2 infants, 1 male and 1 female. Sex, age, and kin-relationships were already known (Duboscq et al., 2016; Kurita, Suzumura, Kanchi, & Hamada, 2012; Rigaill et al., 2017; Watanabe, 2008; Yamagiwa, 2010). Although the group lives on an island, this becomes occasionally connected to the mainland, allowing some exchange of individuals between groups. Moreover, animals on Koshima are fed twice a week, but individuals have to forage to retrieve most of their food. The second author collected on all individuals on Koshima from November 2016 to July 2017. Observations and video-recording took place from 06:00 to 18:00 in Sulawesi, and from 08:00 to 18:00 in Koshima. For a list of the study subjects (i.e., including only the infants, juveniles, and subadults of the group), see Table 1.

2.3 | Data collection

To assess dominance relations of all group members, we used ad libitum observations of all dyadic agonistic interactions (i.e., aggression: threat, lunge, chase, bite; unidirectional agonistic and submissive behaviors: displacement, avoidance, bared-teeth, hindquarter presentation; Scopa & Palagi, 2016; Thierry et al., 2000) with clear winner–loser outcomes (i.e., the individual showing aggressive behavior to the other showed no submissive behavior during the interaction, and vice versa; Altmann, 1974).

To assess play behavior we conducted 20 min focal follows of all the females up to 4 years old and all the males up to 5 years old in the group. We spread focal samples through the day to balance observations over time of day, with at least one hour between two consecutive focals on the same individual, and followed a random order. During focal sampling (Altmann, 1974), we recorded on paper all instances of grooming, social play (i.e., play behavior involving at least another conspecific; Burghardt 2005) and solitary play (i.e., solitary intense or sustained locomotion movements, exploratory behaviors; Burghardt 2005; S. M. Pellis & Burghardt, 2017; Petrů et al., 2008) in which the focal individual was involved, including the identity of the individuals involved and the exact duration of the behavior (Scopa & Palagi, 2016; Shimada & Sueur, 2018; Thierry et al., 2000). We recorded a total of 397 focal samples, with a mean of 7.74 (range, 4.7–8) h per individual in MM and a total of 354 focal samples, with a mean of 4.9 (range, 4.7–5.7) h per individual in JM.

We further video-recorded all social play sessions involving at least one infant, juvenile, or subadult with a FinePix S8500 (Fujifilm, 2013). We recorded videos ad libitum whenever they occurred, including during focal follows. We considered a play session to start when an individual directed play behavior toward a partner and finished when both individuals did not show any play behavior for at least 10 s (Scopa & Palagi, 2016). For each session, we noted the identity of all the individuals involved in the play session and its duration. We further noted the exact duration of the following social play behaviors: object play (i.e., at least two individuals play with an object, without body contact), acrobatic play (i.e., more than one individual displays pirouettes, chasing and/or play faces, but without body contact), sparring (i.e., more than one individual makes body contact during play fighting, but using only two of the four limbs), and wrestling (i.e., like sparring, but at least one individual uses all four of its limbs; see Ciani et al., 2012; Petit et al., 2008). We also coded all instances of play faces (i.e., open mouth expression with the lower and—in JM occasionally—upper teeth exposed), play bites (i.e., an individual gently bites its partner's hair or skin while playing), and aggressive interactions (i.e., bite, chasing, threat, lunge) occurring within or ending the play session (Ciani et al., 2012; S. M. Pellis, Pellis, Reinhart, & Thierry, 2011; Petit et al., 2008; Reinhart et al., 2010; Scopa & Palagi, 2016). We recorded 453 play sessions for JM and 554 for MM.

Interobserver reliability between the first and second author was calculated posthoc on 10% of the video-recorded play sessions in both species (Spearman's correlation for session duration: $\rho = 0.84$, $p < .001$; number of behaviors: $\rho = 0.81$, $p < .001$; proportion of non-contact play behaviors: $\rho = 0.51$, $p = .005$; proportion of contact-play behaviors: $\rho = 0.72$, $p < .001$; number of play faces: $\rho = 1.00$, $p < .001$). Data will be made available to the readers upon request to the corresponding author.

2.4 | Data analysis

We determined the dominance hierarchy with the Elo method (EloRating package, version 0.43), based on all occurrence sampling of dyadic agonistic interactions with a clear winner-loser outcome (Neumann et al., 2011). We used an R function written by Lars Kulik and set the individual start values at 1000, and the *k* factor (a weighted constant based on the probability of winning) at 100. The values obtained were averaged throughout the study periods, standardized to range from 0 to 1 (with 0 indicating lowest and 1 highest rank), and hereafter simply referred to as Elo-ranks. Mother's rank was attributed to all the individuals younger than 1 year (Kerhoas et al., 2016; Paukner, Slonecker, Murphy, Wooddell, & Dettmer, 2018). Analyses of MM play included a data set of 346 interactions including 322 of the 528 possible dyads in the group. For JM, analyses included 2116 interactions of 706 of the 1378 possible dyads. For Elo-rating, we included no burn in periods, as Elo-ranks were highly stable throughout the study period, as assessed through visual inspection of the Elo-ranks and with the stab_elo function (which calculates the S index as metric for the overall stability of a hierarchy during the study period, with 0 meaning that the ordering reverses every other day, and 1 that no rank changes occur; see Neumann & Kulik, 2020). In particular, the Elo-ranks were highly stable over the study period, being 0.985 in MM and 0.988 in JM.

Furthermore, to confirm that the study groups really differed in terms of dominance style, we used two different measures: the steepness of the dominance hierarchy (de Vries, Stevens, & Vervaecke, 2006) and the percentage of reversals against the hierarchy (Young & Isbell, 2002). First, we used the package steepness (version 0.2–2; Leiva, & de Vries, 2014) in R to directly assess the steepness of the hierarchy in both species, which is

TABLE 1 Species, sex, age, rank and study subjects, and time (in minutes) spent in solitary play, social play, and grooming interactions during focal sampling

Species	Sex	Age	Rank	Subject	Solitary play	Social play	Grooming
JM	Female	1	0.643	Takana	20.15	28.15	43.17
JM	Male	1	0.484	Hirame	10.68	6.70	43.22
JM	Female	3	0.461	Tabu	5.48	9.43	77.03
JM	Male	4	0.416	Shiira	3.50	27.15	63.10
JM	Male	5	0.415	Yuu	0.95	8.13	90.55
JM	Male	4	0.392	Kote	2.40	18.03	100.90
JM	Male	2	0.375	Shida	0.00	4.28	68.50
JM	Male	4	0.332	Yomogi	0.75	5.45	88.12
JM	Female	4	0.327	Tsutsuji	6.43	6.27	82.28
JM	Male	2	0.321	Haku	0.25	0.05	86.85
JM	Male	2	0.319	Noko	1.47	6.70	15.62
JM	Female	2	0.287	Komatsu	10.60	13.87	84.22
JM	Female	4	0.286	Hado	2.75	3.47	138.12
JM	Female	3	0.263	Hiba	0.80	0.52	99.47
JM	Male	4	0.262	Bon	3.55	1.05	96.87
JM	Female	2	0.242	Pan	1.63	14.00	58.38
JM	Female	2	0.237	Yotsuba	0.00	0.20	112.68
JM	Female	2	0.217	Botan	0.83	5.40	72.17
JM	Female	2	0.209	Mochi	0.33	0.93	83.87
JM	Male	2	0.203	Mekki	0.08	2.73	69.65
JM	Male	2	0.189	Yumin	2.72	5.72	48.73
JM	Female	3	0.185	Pichi	1.50	0.00	22.15
JM	Female	3	0.159	Betei	0.33	0.52	77.58
JM	Female	4	0.111	Binega	1,17	0,22	97.90
MM	Male	3	0.512	Afwan	11.38	5.30	62.35
MM	Male	5	0.449	Kopi	2.63	0.40	40.65
MM	Female	0	0.429	Lida	174.97	33.93	29.05
MM	Male	4	0.428	Alif	0.72	5.83	62.70
MM	Male	4	0.422	Tara	16.35	4.40	53.60
MM	Male	1	0.389	Suco	243.67	67.23	22.78
MM	Female	1	0.378	Taro	287.53	36.95	30.35
MM	Male	2	0.339	Singa	53.93	50.15	48.62
MM	Male	1	0.326	Coko	201.60	73.80	24.62
MM	Female	3	0.319	Rissa	45.77	38.07	41.52
MM	Female	1	0.268	Bira	139.15	19.40	18.03
MM	Female	2	0.208	Ciro	12.87	26.63	19.72
MM	Male	1	0.203	Foc	256.60	84.35	53.00
MM	Female	3	0.169	Lucia	16.92	34.08	53.45
MM	Female	3	0.168	Sahril	23.70	30.83	43.95
MM	Female	1	0.132	Bolet	259.33	66.93	39.20
MM	Male	1	0.127	Crow	268.12	63.92	15.07

Abbreviations: JM, Japanese macaques; MM, moor macaques.

one core measure of macaque dominance styles (Balasubramaniam et al., 2012; Thierry, 2000). We calculated the steepness as the absolute value of the slope of a straight line fitted to the normalized David's scores, obtained on the basis of proportions of wins of dyadic agonistic interactions (de Vries et al., 2006). The steepness of the hierarchy was higher in more despotic JM (0.280) than in less despotic MM (0.163). However, steepness is known to decrease with the number of unknown relationships in a group (Klass & Cords, 2011). As the number of number of unknown relationships was higher in MM, we randomly removed dyads with known relationship from the JM dominance matrix (i.e., obtained by ordering the individuals in the matrix so that their Elo-ranks gradually increased from the left to the right, and from the top to the bottom of the matrix) to reach the same proportion of unknown relationships in both species, and averaged the values obtained over 1000 iterations to calculate the adjusted steepness for JM (0.255). Second, we calculated the percentage of reversals in the hierarchy, as the percentage of observations below the matrix diagonal out of the total number of observations (Young & Isbell, 2002). As expected, this percentage was higher in MM (68/346 = 20%) than in JM (193/2116 = 9%).

During focal sampling, we observed a total of 1.6 h (JM) and 33.6 h (MM) of solitary play, 2.8 h (JM) and 10.7 h (MM) of social play, and 30.4 h (JM) and 11.0 h (MM) of grooming interactions (for a distribution of these behaviors across individuals, see Table 1).

For statistical analyses of play behavior, we prepared two data sets. Firstly, we used the data collected during focal samples to assess differences in the proportion of time spent in solitary play, social play, and grooming between the species. Each line of data represented one focal sample and included information on the focal individual's identity, species, sex, age, and rank. We further included the proportion of time that the focal individual spent in solitary play, social play, or grooming interactions (i.e., out of the total observation time during the focal). Second, we used the data collected from the videos to assess inter-specific differences in play styles. Play sessions were analyzed with SONY Vegas PRO 12 (Sony Creative Software, 2012). For each dyad involved in the play session, we included one record in the data set that included the session number, the identity of players, their species, sex combination, absolute age difference, and absolute rank difference. We further included the exact duration of the play session, the total number of players involved in the session, the number of behavior types displayed during the session (i.e., wrestling, sparring, acrobatic, and object play), the number of play faces displayed by the two players during the play session, the proportion of time spent in noncontact play behavior (i.e., acrobatic and object play; out of the total time spent in noncontact and contact behavior, i.e., wrestling, sparring), whether reciprocal bites occurred during the session (i.e., whether both players performed at least one play bite), and whether the play session escalated into aggression.

We conducted analyses using generalized linear mixed models (hereafter, GLMM: Baayen, Davidson, & Bates, 2008) with the glmmTMB package (version 1.0.1; Brooks et al., 2017) in R (R Core Team, version 3.5.0). To assess inter-specific differences in the proportion of time spent in solitary play, social play and grooming, we used our first data set with focal data and modeled (1) the proportion of time spent in solitary play (Prediction 1), (2) social play (Prediction 2), and (3) grooming interactions (Prediction 3) with three GLMMs (family: β regression; Ferrari & Cribari-Neto, 2004). In the three models, we included species as test predictor, individual's sex, age, and rank as controls and focal subject identity as a random effect (Table 2).

To assess interspecific differences in play styles, we used our second data set with video data and three GLMMs (family: Poisson) to model (4) whether the number of players (Prediction 4), (5) the number of play behavior types (Prediction 5) and (6) the number of play faces displayed in a session (Prediction 6) were predicted by species, when controlling for players' sex combination, age and rank differences, including session duration as offset term, and session and players' identities as random effects (Table 2). To assess whether the proportion of contact play behavior was predicted by species and rate of play faces in the session, we modeled (7) the proportion of time spent in noncontact play behavior (out of the total time spent in noncontact and contact play behavior) with a GLMM (family: β regression). We used species and rate of play faces in the session as test predictors, players' sex combination, age and rank differences as controls, and session and players' identities as random effects (Prediction 7; Table 2). To investigate whether the occurrence of reciprocal bites was affected by species and rate of play faces in the session, we modeled (8) the occurrence of reciprocal bites with a GLMM (family: binomial), using species and rate of play faces in the session as test predictors, players' sex combination, age and rank differences as controls, session duration as offset term, and session and players' identities as random effects (Prediction 8; Table 2). Finally, we could not model whether the probability of aggressive escalations was affected by species and frequency of play faces (Predictions 9–9b), because only 13 play sessions escalated into an aggressive conflict.

For all models, age and age differences were z-transformed to facilitate model convergence and interpretation of model coefficients (Roger Mundry, personal communication). To accommodate 0 and 1 s in models with a β regression distribution, we added 1E−09 to 0 values and removed it from 1 values. We used likelihood ratio tests (Dobson, Zidek, & Lindsey, 2001) to compare full models containing all predictors with null models containing only control predictors, offset terms, and random factors. When full models differed significantly from null models, likelihood ratio tests were conducted to obtain the *p* values for each test predictor via single-term deletion using the R function drop1 (Barr, Levy, Scheepers, & Tily, 2013). No overdispersion was detected in Poisson models. To rule out collinearity, we determined the variance inflation factors (VIFs) (Field, 2005), which were minimal (maximum VIFs across all models = 1.16).

TABLE 2 Predictions, model used for the statistical analysis, test predictors and control predictors included in the models, and whether the predictions were supported by the model (yes, no, or partially)

Predictions	Model	Test and *control predictors*
P1. MM spend a higher proportion of time in solitary play than JM	M1	species + *focal sex* + *focal age* + *focal rank*
P2. MM spend a higher proportion of time in social play than JM	M2	
P3. JM spend a higher proportion of time in grooming interactions than MM	M3	
P4. Play sessions include more players in MM than JM	M4	species + *sex combination* + *age difference* + *rank difference* + *session duration (offset)*
P5. Play sessions include more play behavior types in MM than JM	M5	
P6. Play sessions have a higher rate of play faces in MM than JM	M6	
P7. MM spend a higher proportion of play time in contact behavior than JM		
P7b. High play face rate predicts higher proportion of time in play contact behavior	M7	species + play face rate + *sex combination* + *age difference* + *rank difference*
P8. The occurrence of reciprocal bites is higher in MM than JM in play sessions		
P8b. High play face rate predicts higher occurrence of reciprocal bites in play sessions	M8	species + play face rate + *sex combination* + *age difference* + *rank difference* + *session duration (offset)*
P9. The occurrence of aggression is higher in JM than MM in play sessions		
P9b. High play face rate predicts lower occurrence of aggression in play sessions	–	–

Note: Significant test predictors are underlined ($p < .05$), control predictors in italics. Focal subject's identity was included as random effect in Models 1–3, and session and players' identities in Models 4–8. Predictions supported by our data are in bold. In Models 1–3, proportion of time refers to the time spent in solitary play, social play, or grooming interactions, out of the total observation time. In Model 6, rate of play faces refers to the number of play faces out of the time spent playing. In Model 8, the occurrence of reciprocal bites was entered as a binomial response (i.e., whether reciprocal bites occurred in the play session).

Abbreviations: JM, Japanese macaques; MM, moor macaques.

3 | RESULTS

For all models, the full model differed significantly from the corresponding null model (Table 3). The proportion of time spent in solitary play was higher for MM than JM, supporting prediction 1 (Tables 2 and 3, M1). The proportion of time spent in social play was also higher in MM than JM, whereas JM spent a higher proportion of time in grooming interactions than MM, supporting predictions 2 and 3, respectively (Tables 2 and 3, M2 and M3).

In line with prediction 4, the number of players in a session was higher for MM than JM (Figure 1a and Tables 2 and 3, M4). Similarly, both the number of play behavior types and the rate of play faces displayed in a session were higher in MM than JM, supporting predictions 5 and 6, respectively (Figure 1b,c; Tables 2 and 3, M5 and M6). In line with prediction 7a, the proportion of noncontact behavior was higher in JM than MM (Figure 1f), but the rate of play faces had no significant effect on this proportion, in contrast with our prediction 7b (Tables 2 and 3, M7). Moreover, the probability of reciprocal bites was higher in MM than in JM, and increased with a higher rate of play faces in the session, supporting predictions 8a and 8b (Figure 1c,d and Tables 2 and 3, M8). In Models M4–M8, rank difference between players was included as a control predictor. As infants were assigned their mother's rank, however, this measure might not have been precise (especially when infants played with non-infants, as the latter might have been likely to dominate infants), thus affecting our results. To check whether our conclusions were robust, we, therefore, re-ran the models above, after removing from the data-set all the interactions between infants and non-infants. Our analyses confirmed the results above, showing the same effect of species (in Models M4–M8) and rate of play faces (in M8) on our dependent variables.

Finally, aggressive escalations were uncommon in both species, with only 1.8% play sessions ending with aggression in JM, and 0.9% in MM, in line with our prediction 9 (=8/453 sessions in JM, and

TABLE 3 Results of Models 1–8, including estimates, standard errors (*SE*), confidence intervals (CIs), likelihood ratio tests (LRT), degrees of freedom (*df*), and *p* values

	Estimate	***SE***	**CIs: 2.5/97.5%**	**LRT**	***df***	***p***
M1: Proportion of time spent in solitary play (β regression distribution)						
Full-null comparison: LRT = 21.38, *df* = 1, *p* < .001						
Intercept	−2.39	0.36	−3.10/−1.67	–	–	–
Species (MM)	1.38	0.27	0.86/1.91	21.38	1	**<.001**
Sex (male)	0.11	0.27	−0.41/0.64	0.19	1	.667
Age	−0.64	0.13	−0.90/−0.38	18.39	1	<.001
Rank	−0.92	1.11	−3.10/1.26	0.68	1	.409
M2: Proportion of time spent in social play (β regression distribution)						
Full-null comparison: LRT = 27.80, *df* = 1, *p* < .001						
Intercept	−2.96	0.18	−3.32/−2.61	–	–	–
Species (MM)	0.74	0.12	0.51/0.98	27.80	1	**<.001**
Sex (male)	0.02	0.12	−0.23/0.26	0.21	1	.884
Age	−0.32	0.06	−0.44/−0.20	20.69	1	<.001
Rank	−0.50	1.52	−1.51/0.52	0.89	1	.345
M3: Proportion of time spent in grooming interactions (β regression distribution)						
Full-null comparison: LRT = 16.09, *df* = 1, *p* < .001						
Intercept	−2.15	0.15	−2.44/−1.86	–	–	–
Species (MM)	−0.40	0.09	−0.58/−0.23	16.09	1	**<.001**
Sex (male)	−0.23	0.09	−0.42/−0.05	5.81	1	.012
Age	−0.03	0.05	−0.12/0.06	0.51	1	.470
Rank	0.37	0.39	−0.39/0.41	0.89	1	.338
M4: Number of players (offset term = play session duration, Poisson distribution)						
Full-null comparison: LRT = 29.41, *df* = 1, *p* < .001						
Intercept	−1.90	0.10	−2.09/−1.71	–	–	–
Species (MM)	0.40	0.07	0.26/0.55	29.41	1	**<.001**
Sex combination (female–male)	−0.12	0.08	−0.29/0.04	4.47	2	.107
Sex combination (male–male)	−0.19	0.10	−0.37/−0.01			
Age difference	0.00	0.03	−0.06/0.06	0.01	1	.934
Rank difference	0.13	0.27	−0.39/0.66	0.24	1	.624
M5: number of types of play behavior (offset term = play session duration, Poisson distribution)						
Full-null comparison: LRT = 27.89, *df* = 1, *p* < .001						
Intercept	−2.46	0.09	−2.64/−2.28	–	–	–
Species (MM)	0.41	0.07	0.30/0.56	27.89	1	**<.001**
Sex combination (female–male)	−0.16	0.08	−0.32/0.01	9.01	2	.011
Sex combination (male–male)	−0.28	0.09	−0.45/−0.10			
Age difference	−0.01	0.03	−0.07/0.05	0.05	1	.808
Rank difference	0.09	0.27	−0.44/0.62	0.11	1	.740
M6: number of play faces (offset term = play session duration, Poisson distribution)						
Full-null comparison: LRT = 46.21, *df* = 1, *p* < .001						

TABLE 3 (Continued)

	Estimate	*SE*	CIs: 2.5/97.5%	LRT	*df*	*p*
Intercept	−3.95	0.21	−4.36/−3.54	–	–	–
Species (MM)	1.41	0.19	1.04/1.78	46.21	1	**<.001**
Sex combination (female-male)	0.32	0.16	0.01/0.64	32.31	2	<.001
Sex combination (male-male)	0.99	0.21	0.58/1.41			
Age difference	0.08	0.04	0.00/0.16	4.06	1	.044
Rank difference	0.30	0.45	−0.59/1.19	0.44	1	.507
M7: Proportion of time spent in noncontact play behavior (β regression distribution)						
Full-null comparison: LRT = 25.88, *df* = 2, *p* < .001						
Intercept	−0.28	0.12	−0.52/−0.05	–	–	–
Species (MM)	−0.56	0.08	−0.72/−0.40	25.81	1	**<.001**
Play face frequency	0.17	0.17	−0.17/0.51	0.92		.337
Sex combination (female-male)	0.01	0.12	−0.21/0.24	4.02	2	.134
Sex combination (male-male)	−0.14	0.12	−0.38/0.08			
Age difference	−0.01	0.04	−0.10/0.07	0.10	1	.750
Rank difference	1.25	0.36	0.54/1.95	10.64	1	.001
M8: Occurrence of reciprocal bites (offset term = play session duration, binomial distribution)						
Full-null comparison: LRT = 37.64, *df* = 2, *p* < .001						
Intercept	−7.18	0.60	−8.36/−6.00	–	–	–
Species (MM)	2.02	0.41	1.23/2.82	22.47	1	**<.001**
Play face frequency	1.81	0.44	0.94/2.67	12.67	1	**<.001**
Sex combination (female-male)	−0.05	0.48	−0.98/0.89	10.06	2	.007
Sex combination (male-male)	0.85	0.51	−0.15/1.85			
Age difference	−0.86	0.28	−1.40/−0.32	13.72	1	<.001
Rank difference	−1.37	1.50	−4.30/1.57	0.83	1	.361

Note: Significant test predictors are in bold, control predictors in italics. Age and age difference were *z*-transformed before analysis. We included subject identity as random effect in Models 1–3, session and players' identities in Models 4–8.

Abbreviation: MM, moor macaques.

5/554 in MM; Figure 1e and Table 2). The mean rate of play faces was similar in play sessions that escalated into aggressive conflicts (0.128), and those which did not (0.135).

4 | DISCUSSION

Our results revealed inter-specific differences in play behavior, that are in line with the different dominance styles of the study species, and largely confirmed our predictions (Table 2). In particular, MM spent a larger proportion of time in solitary play and social play than JM, while JM spent a higher proportion of time in grooming interactions than MM (in line with Predictions 1–3). In line with our predictions, play sessions in MM included more players (Prediction 4), more play behavior types (Prediction 5), a higher rate of play faces (Prediction 6), a higher proportion of contact play behavior (Prediction 7) and a higher occurrence of reciprocal bites than in JM (Prediction 8). Aggressive escalations were rare, but twice as frequent in JM than in MM (Prediction 9). Finally, a higher rate of play faces predicted the occurrence of reciprocal bites (in line with Prediction 8b), but had no significant effect on the proportion of contact play behaviors (in contrast with Prediction 7b).

As predicted, the proportion of both solitary and social play was higher in less despotic MM, in line with previous literature (Antonacci, Norscia, & Palagi, 2010; Ciani et al., 2012; Hare et al., 2012; Palagi, 2006; Palagi & Cordoni, 2012; Palagi et al., 2016; Scopa & Palagi, 2016). On the one hand, less despotic species may engage more in play behavior, as their less despotic style reduces the risks of social play (Scopa & Palagi, 2016). On the other hand, play may be especially adaptive in less despotic species, to acquire both novel

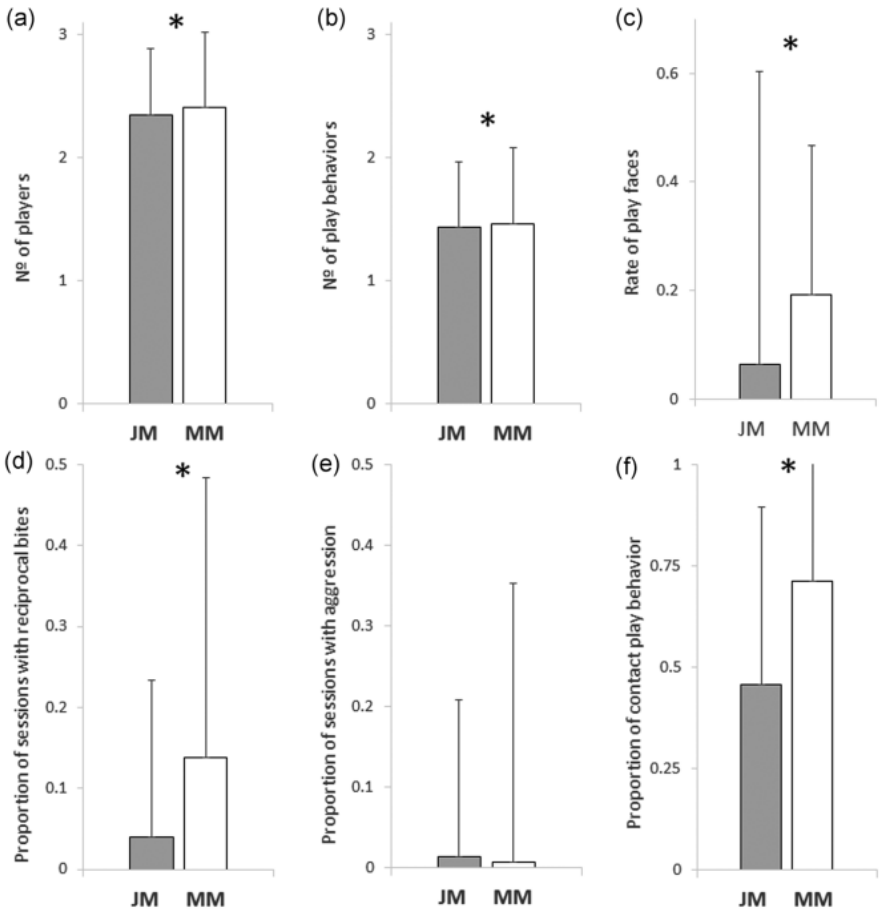

FIGURE 1 Species differences in play characteristics (Japanese macaques [JM], gray, $N = 559$ play sessions; moor macaques [MM], white, $N = 695$ play sessions). Panels show mean + *SD* for (a) number of players per session, (b) number of play behavior types per session (c) rate of play faces per session, (d) proportion of sessions in which reciprocal bites occurred, (e) proportion of sessions in which aggressive escalations occurred, and (f) proportion of play time spent in contact play. Asterisks indicate variables that differed by species in our models (Table 3). We did not run a model to test panel (e)

behavioral patterns and the necessary social skills to navigate the larger and more diversified social networks they will have as adults (Adams et al., 2015; Amici et al., 2019; Thierry, 2007). In contrast, the proportion of time spent in grooming interactions was higher in JM than MM, suggesting that social play and grooming may serve different alternative functions for the formation and maintenance of social bonds (e.g., Shimada & Sueur, 2018). In particular, grooming may be especially important in more despotic species, where aggressive interactions may become especially severe and riskier behaviors like social play are less common (e.g., Ciani et al., 2012; Palagi & Paoli, 2007, 2008). In the future, these findings should be confirmed by better controlling for variation in the number and characteristics of potential social partners in the study groups. For instance, it is possible that larger groups offer individuals a larger choice of potential social partners, thus positively affecting the occurrence of social play. However, it should be noted that the availability of potential social partners was overall larger in JM, which included 43 adults and subadults, and 12 immatures (in contrast to the 30 adults and subadults, and 12 immatures in MM).

Our study also showed inter-specific differences in play styles. As predicted, play sessions in less despotic MM included more players, a larger variety of play behavior types, a higher proportion of contact play behaviors (i.e., wrestling and sparring) and a higher occurrence of reciprocal bites than in JM (Figure 1), in line with previous studies on other species with different dominance styles (Ciani et al., 2012; Palagi & Paoli, 2007, 2008; Petit et al., 2008). In more despotic species, aggressive interactions are usually more severe (e.g., de Waal & Luttrell, 1989; Thierry, 2000, 2007). Therefore, individuals of more despotic species may avoid behaviors that might increase the risk of conflicts, like play sessions involving many individuals and/or including a rapid alternation of many different behaviors, which increase the unpredictability of the interactions and thus the risks involved (Palagi, 2018). Reciprocal bites, for instance, more likely occur in less despotic species, possibly because offensive and defensive roles may be better balanced during play sessions than in species with steeper dominance hierarchies (Palagi, 2006; Reinhart et al., 2010). Similarly, because physical contact may increase the risk that play escalates into overt aggression (Cordoni, Demuru, Ceccarelli, & Palagi, 2016), as, for example, when one individual uses disproportionate force (but see wolves, Cordoni, 2009; Smuts, 2014), less despotic species may more likely engage in physical contact when playing (Petit et al., 2008). Therefore, despotic species may be more cautious and preferentially engage in noncontact social play (Kraus, Pellis, & Pellis, 2019). Accordingly, the percentage of bouts ending with aggression were higher when players engaged in sparring and wrestling (in JM: 1.6%; in MM: 0.8%), as compared to when they avoided physical contact (in JM: 1.1%; in MM: 0%; Figure 1e).

As predicted, the rate of play faces during play sessions was higher in MM than in JM (Figure 1c). Play faces are generally considered spontaneous emotional expressions, rather than intentional communicative acts (Scopa & Palagi, 2016), and a higher rate of play faces (i.e., per unit of play time) in less despotic species may be explained by the fact that these species are more free to express their emotions (Mancini et al., 2013; Palagi & Mancini, 2011; Palagi et al., 2016; S. M. Pellis et al., 2011; Scopa & Palagi, 2016). Therefore, a higher rate of play faces in MM is not surprising, although previous studies have failed to find differences in the rate of play faces between more and less despotic species (Mancini et al., 2013; Palagi, Marchi, Cavicchio, & Bandoli, 2019; Palagi, Norscia, Pressi, & Cordoni, 2018; Scopa & Palagi, 2016). A higher rate of play faces was also linked to a higher occurrence of reciprocal bites, but had no significant effect on the proportion of time spent in noncontact play behavior. Similarly, the frequency of play faces was similar in play sessions that escalated to aggression and those that did not. Therefore, although play faces were clearly more frequent in less despotic species (MM), this difference alone cannot explain the variation in the play styles of the two study species.

Overall, our results provide support for the hypothesis that interspecific variation in play behavior is linked to differences in dominance style, with less despotic species (MM) playing more, with more players, more behavioral variation, more contact play behavior, more reciprocal bites and more play faces. Importantly, the study groups really differed in their dominance styles, as confirmed by the assessment of the steepness of their dominance hierarchies and of the percentage of reversals against the hierarchy. As play behavior had so far never been studied in MM, these results are important to add another data point for nondespotic species and confirm that these behavioral differences in play really reflect differences in the species dominance styles. Indeed, our study largely confirmed previous research comparing play styles in macaques with different dominance styles, which appear to be rather consistent across species with similar dominance styles (e.g., less despotic species play more: Ciani et al., 2012; Petit et al., 2008; less despotic species play more cooperatively: Reinhart et al., 2010). Interestingly, these differences appear to be consistent also across individuals with different rearing conditions: the few direct comparisons between captive and free-ranging individuals, for instance, have found no major differences in play behavior between groups (Reinhart et al. 2010; Pellis, Pellis, & Himmler, 2014). Taken together, these studies suggest that differences in play behavior linked to dominance styles may be relatively hard-wired, despite previous cross-fostering studies reporting an important effect of experience on macaque dominance styles (e.g., de Waal & Johanowicz, 1993).

Finally, several control predictors were significant in our models (see Table 3). In particular, the proportion of both solitary (M1) and social play (M2) was higher in younger individuals than older ones, in line with abundant literature (e.g., Amici et al., 2019; Kulik, Amici, Langos, & Widdig, 2015). Moreover, females spent a higher proportion of time in grooming interactions than males (M3), also in line with literature (e.g., Cords, Sheehan, & Ekernas, 2010; Kulik et al., 2015; Nakamichi, 1989; Rowell & Chism, 1986; van Noordwijk, Hemelrijk, Herremans, & Sterck, 1993). The number of play behavior types shown in a session was higher in female-female dyads, than in female–male dyads and male–male dyads (M5). In contrast, the rate of play faces was higher in male–male dyads than in female–male and female–female dyads, and when the difference between the players' age was higher (M6). Finally, the proportion of time spent in play contact behavior was higher when players' rank difference was low (M7), while the probability to reciprocate bites was higher in male–male dyads than in female-male and female-female dyads, and when players' age difference was low (M8).

In the future, studies on interspecific differences in play behavior will need to include more conspecific groups and more species with different dominance styles, as well as genera other than *Pan* and *Macaca*, which are the ones that have been most thoroughly studied. In this way, we will be able to confirm that differences in play behavior are consistent within species and so linked to differences in dominance style rather than to other socio-ecological factors, such as food availability or climatic conditions, or rearing conditions. Future studies should also observe individuals longitudinally, to examine the development of play behavior and its long-term effects on primate sociality (e.g., play partners in the early years form close social bonds also as adults; larger networks of play partners predict survival and fitness in the adulthood). Finally, more detailed studies on the functions of play face are needed, including research on rapid facial mimicry and the role it plays across different species (Mancini et al., 2013; Palagi et al., 2019; Scopa & Palagi, 2016).

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DATA AVAILABILITY STATEMENT

Data will be made available to the readers upon request to the corresponding author.

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