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RESEARCH ARTICLE

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Maternal and offspring behavior in free-ranging Japanese and moor macaques: A comparative approach

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Abstract

Female primates represent the most important social partner for their developing offspring. However, mothers may strongly differ in the way they relate to their offspring (e.g., in terms of two different dimensions: protectiveness and rejection). In this study, we aimed to assess how dominance style predicts (i) changes in maternal behavior through offspring development, and (ii) the link between maternal behavior and offspring behavior. We conducted behavioral observations on 34 free-ranging immatures of two species of macaques with different dominance styles: less tolerant Japanese macaques (JM; *Macaca fuscata*) and more tolerant moor macaques (MM; *Macaca maura*). Our results showed that maternal behavior differed between JM and MM: maternal proximity and grooming decreased through offspring development more quickly in MM than in JM, whereas maternal rejection and aggression, which were generally more frequent in JM, decreased with offspring age similarly in both species. In contrast, maternal restraint of offspring decreased similarly with offspring age in both species. Furthermore, dominance style was differentially associated with the link between maternal and offspring behavior: in MM only, maternal grooming predicted an increase of the probability that offspring interacted with partners other than their mothers and engaged in solitary play, whereas maternal rejection predicted a decrease in the occurrence of solitary play. Overall, these results suggest interspecific variation in maternal behavior during offspring's first years of life, and point to the possibility that these differences may have an important role in shaping their behavioral development.

KEYWORDS

dominance style, interspecific differences, mother–offspring relationship, primate, social development

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Abbreviations: *CI*, confidence interval; *df*, degrees of freedom; E, east; GLMM, generalized linear mixed model; h, hour; ha, hectare; ID, identity; JM, Japanese macaques; *LRT*, likelihood ratio test; M, model; MM, moor macaques; N, north; *N*, population size; *n*, sample size; *p*, probability value; S, south; *SD*, standard deviation; *SE*, standard error; *S* index, stability index; χ^2, chi-square test.

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1 | INTRODUCTION

During infancy, primate mothers are the most important social partner for their developing offspring. They provide care, nourishment, and protection, and facilitate their interactions with their physical and social environment (Amici et al., 2019; Gomendio, 1995; Maestripieri, 2018; Nakamichi, 2008; Rilling & Young, 2014; Suomi, 2005). However, mothers can strongly vary in the way they relate to their offspring. Partly building on work by developmental psychologists, several studies have described maternal styles in primates (mostly in cercopithecine monkeys) as varying along two main dimensions: protectiveness and rejection (Fairbanks, 1996; Maestripieri, 2018). Protective mothers, for instance, often initiate and spend time in proximity and in grooming interactions with their offspring. Moreover, they are also likely to restrain their offspring, preventing them from breaking proximity (Bardi & Huffman, 2002; Fairbanks, 1996; Maestripieri, 1994c, 1999; Sekizawa & Kutsukake, 2019). Rejective mothers, in contrast, frequently avoid contact with their offspring, preventing them from coming into close proximity or often breaking physical contact, even aggressively so (Bardi & Huffman, 2002, 2006; Fairbanks, 1996; Maestripieri, 1994c, 2018; Sekizawa & Kutsukake, 2019). These two dimensions can vary independently of each other (Fairbanks, 1996; Maestripieri, 2018), and their combination may result in four possible maternal styles: (i) “protective,” high in protectiveness and low in rejection; (ii) “controlling,” high in both protectiveness and rejection; (iii) “rejecting,” low in protectiveness and high in rejection; and (iv) “laissez-faire,” low in both protectiveness and rejection (Maestripieri, 1999, 2018).

Female primates appear to maintain their individual maternal styles consistently across different offspring, and may also transmit their styles across generations through a mixture of genetic factors, direct experience, and social learning (Fairbanks, 1996; Maestripieri, 2018; Nakamichi, 2008). However, mothers adjust their distribution of protective and rejective behaviors according to the offspring's developmental stage. For instance, primate mothers usually show more protectiveness toward younger offspring (e.g., Hernández-Lloreda & Colmenares, 2005; Negayama, 1981; Schino et al., 1993). Also, among macaques, rejection of offspring often peaks between 4–6 months (Maestripieri, 2002; Negayama, 1981) and 1–2 years of age (Kulik et al., 2016)—when mothers are more likely to resume their mating activities (Berman et al., 1993; Gomendio, 1991; Worlein et al., 1988)— and slowly decreases thereafter.

Furthermore, it is relatively well established that mothers differentially treat their offspring depending on their own dominance rank and on the offspring's sex. Lower-ranking mothers, for instance, have been found to show more protectiveness toward their offspring, especially when there is higher risk of their young offspring to be mishandled, kidnaped, or attacked by other group members (Altmann, 2001; Gomendio, 1990; Onishi & Nakamichi, 2011; Tartabini et al., 1980; White & Hinde, 1975; but see Tanaka, 1989). In contrast, higher-ranking mothers may benefit from more “rejecting” maternal styles (i.e., low in protectiveness and high in rejection), being able to successfully raise their offspring with less maternal effort (Altmann, 2001; Berman, 1992; Fairbanks & McGuire, 1995; Nguyen et al., 2012). In relation to the offspring's sex, differences in maternal style usually increase as immatures approach sexual maturity (e.g., Kulik et al., 2016). In species with female philopatry, such as macaques and baboons, for example, mothers are usually more “rejecting” toward males, who are the dispersing sex (Kulik et al., 2016; Lonsdorf, 2017; Maestripieri, 2005; Sekizawa & Kutsukake, 2019).

Maternal behavior also differs between species and this difference could be linked to between-species differences in dominance style (Maestripieri, 1994c). In primates, dominance style varies from less tolerant to more tolerant depending on the steepness of the dominance hierarchy, and the intensity and frequency of aggressive conflicts, counter-aggression, and reconciliation rates (De Waal & Luttrell, 1989; Thierry, 2007, 2021). In less tolerant species, aggressive conflicts are usually more severe, and mothers may reduce the risk that their offspring suffer aggression during social interactions by showing more protectiveness (for a discussion, see e.g., Maestripieri, 1994c; Thierry, 2000, 2021). At the same time, whereas maternal proximity in the first months of offspring life is clearly essential for a healthy development of immatures (e.g., Caine et al., 1983; Capitanio & Reite, 1984; Lutz et al., 2003), maternal rejection has been found to promote offspring independence and the development of less anxious personalities in macaques (Fairbanks, 1996; Maestripieri et al., 2009; Schino et al., 2001). Therefore, maternal rejection might generally be higher in less tolerant species, as infants may especially benefit from developing skills to better cope with stressful situations (Maestripieri, 2018; Parker & Maestripieri, 2011). Although direct comparisons of species are rare, and have been limited to captive individuals, they suggest that mothers in less tolerant species (e.g., rhesus macaques, *Macaca mulatta*, Japanese macaques (JM), *M. fuscata*, pig-tailed macaques, *M. nemestrina*, long-tailed macaques, *M. fascicularis*) may indeed be more “controlling” (i.e., high in both protectiveness and rejection) toward their offspring, as compared to mothers in more tolerant species (e.g., stump-tailed macaques, *M. arctoides*, bonnet macaques, *M. radiata*, tonkean macaques, *M. tonkeana*; Bardi, Shimizu, Barrett, et al., 2003; Bardi, Shimizu & Borgognini-Tarli, 2003; Kaufman & Rosenblum, 1969; Maestripieri, 1994b, 1994b; Thierry, 1985).

Even though social behavior has a strong genetic component (see Ebstein et al., 2010), it is also linked to the socio-ecological conditions that individuals experience throughout their lives. Mothers, in particular, can contribute to the social development of their offspring through their own behavior, fostering their growth into the species-specific social roles that they will have as adults (Amici et al., 2019; Fairbanks, 1996; Lonsdorf, 2017; Maestripieri, 2018; Suomi, 2005). By forming strong social bonds with the offspring of the philopatric sex and with other group members, for instance, mothers may promote their offspring's social integration (e.g., Kulik et al., 2016; Murray et al., 2014) and contribute to their future roles in the group (Amici et al., 2019; Lonsdorf, 2017). Therefore, when mothers show more protective behaviors (e.g., spending more time in proximity and grooming interactions with their offspring), their offspring may more likely to interact with their mothers' partners and their offspring (Maestripieri, 2018). This effect may be stronger or limited to more tolerant species, where individuals have fewer constraints with regard to the social partners they can interact with (e.g., having fewer kin- and dominance-biases: Beltrán Francés et al., 2020; Maestripieri, 1994a; Thierry, 1985, 1990). However, mothers that show more protective behaviors are also more likely to restrain their offspring, protecting them from potential dangers but, at the same time, limiting their opportunities to socialize and increasing their stress and vigilance (Maestripieri et al., 2009; Mandalaywala et al., 2014) and thus decreasing their probability of interacting with other group members (Bardi & Huffman, 2006; Clarke & Schneider, 1993; Clarke & Schneider, 1997; Clarke et al., 1996). Furthermore, when mothers show more protective behaviors, the offspring may be less motivated to interact with the surrounding environment, and have less time to engage in exploration and solitary play, regardless of which species they belong to (Bardi & Huffman, 2002, 2006; Fairbanks & McGuire, 1988, 1993).

Finally, the frequency of maternal rejection and aggression during the first years of life may also predict offspring behavior, although the results of previous studies are not consistent. By fostering independence, for instance, maternal rejection seems to increase exploration and solitary play in the offspring (Bardi & Huffman, 2006; Maestripieri et al., 2006; Simpson et al., 1989; Simpson & Datta, 1991). However, the link between maternal rejection and the probability of interacting with other social partners is not clear. On the one hand, it has been found that maternal rejection promotes offspring independence, decreasing their fear of interacting with unrelated group members (Schino et al., 2001) and increasing their interactions with others (Bardi & Huffman, 2002, 2006). On the other hand, other studies have found that more maternal rejection-aggression increases stress and depression in their offspring (Birnie et al., 2013; Maestripieri et al., 2009; Maestripieri, 2002; Simpson, 1985), which in turn may decrease the likelihood that they will engage in social interactions with others (Bardi & Huffman, 2006; Clarke & Schneider, 1993, 1997; Clarke et al., 1996).

In this study, we aimed to assess how dominance style relates to (i) differences in maternal behavior according to offspring age, and (ii) the link between maternal and offspring behavior. For this purpose, we conducted behavioral observations on two species of macaques with different dominance styles: less tolerant JM (*Macaca fuscata*; grade 1 of social tolerance: Thierry, 2007) and more tolerant moor macaques (MM; *Macaca maura*; grade 4 of social tolerance: Thierry, 2007). The genus *Macaca* is ideal to study the link between dominance style and behavioral patterns, as it includes more than 20 species with similar kinship and demographic structures (e.g., matrilineal dominance hierarchies, multi-male multi-female social organization, female philopatry; Gouzoules & Gouzoules, 1987; Thierry, 2000, 2007), but high variation in their dominance style (Thierry, 2000, 2007, 2021). With the present study, we add to previous work in three main ways. First, we included a species, MM, whose maternal behavior has not been previously studied. The inclusion of this species is therefore especially important, as it may provide further evidence that the interspecific differences in maternal behavior found in previous studies are really linked to each species' dominance style rather than to the specific contingencies of the study groups. Second, we included two large groups (JM, *N* = 52; MM, *N* = 42), which allowed us to reliably account for other factors that may be linked to intraspecific variation in maternal behavior (e.g., offspring's age and sex, maternal rank). Third, both our study groups were free-ranging groups. As far as we know, all the studies directly comparing maternal behavior in species with different dominance styles have been conducted in captivity. Including free-ranging groups is therefore valuable, as there might be important intraspecific variation in maternal styles depending on the living conditions experienced by mother–offspring pairs (e.g., Berman, 1980; Fairbanks & McGuire, 1988).

Based on previous literature, we hypothesized that groups with different dominance styles would differ in the way maternal behavior varies with offspring's age (Table 1). In particular, we predicted that the likelihood of maternal proximity (Prediction 1), grooming (Prediction 2), and restraint (Prediction 3)—three measures that we use as proxies of protective maternal style—, would be higher in younger and lower in older offspring in both species, but would more quickly decrease with age in MM. That is because more tolerant species likely have fewer social constraints in terms of partners they can interact with (Beltrán Francés et al., 2020; Maestripieri, 1994a; Thierry, 1985, 1990) and less risky social interactions, making maternal protection less relevant (Maestripieri, 1994c; Thierry, 2000, 2021). Similarly, we predicted that the likelihood of maternal rejection and aggression (Prediction 4) would decrease with offspring age after the first year of life in both species (Kulik et al., 2016; Maestripieri, 2002; Negayama, 1981), but more quickly in MM because promoting independence through rejection may be less needed in more tolerant species (Maestripieri, 2018; Parker & Maestripieri, 2011). Furthermore, we hypothesized that dominance style would partly predict the link between maternal and offspring behavior (Table 1). In particular, we predicted that mothers that are more likely to groom their offspring and less likely to restrain them would have offspring more likely to interact with others, especially in more tolerant MM (Prediction 5). That is, individuals have fewer constraints with regard to the social partners they can interact with (Beltrán Francés et al., 2020; Maestripieri, 1994a; Thierry, 1985, 1990). In both species, we predicted that mothers showing more protective behaviors (i.e., more grooming and restraint) would have offspring that are less likely to engage in solitary play (Prediction 6), because the offspring may be less motivated and/or have less time to engage in exploring the surrounding environment (e.g., Bardi & Huffman, 2002, 2006; Fairbanks & McGuire, 1988, 1993). Furthermore, because of the mixed results in the literature, we refrained from making directional predictions, but we expected that, in both species, maternal rejection and aggression could predict the probability that offspring interacted with others (Prediction 7; Bardi & Huffman, 2002, 2006). Finally, we predicted that mothers showing more rejective–aggressive behaviors would have more independent offspring, that are more likely to engage in solitary play, in both species (Prediction 8; Bardi & Huffman, 2006; Maestripieri et al., 2006; Simpson et al., 1989; Simpson & Datta, 1991). Since we expected both maternal rank (Fairbanks, 1996) and offspring sex (Kulik et al., 2016) to be linked to maternal and offspring behavior

TABLE 1 Predictions, whether they were supported by the results in the current study, models used for the statistical analysis, and test predictors, controls (in italics) and random factors (between parentheses) included in the models (main effects are also included in case of interactions)

Predictions	Support	Model	Predictors & controls
The probability that mothers…			
P1. Are in proximity to their offspring decreases with offspring age, especially in MM	**Yes**	M1	~age*species, *focal sex, maternal rank, observational effort (focal and mother ID)*
P2. Groom their offspring decreases with offspring age, especially in MM	**Yes**	M2	
P3. Restrain their offspring decreases with offspring age, especially in MM	**Partial** (similar decrease in both species)	M3	
P4. Are rejective-aggressive toward their offspring decreases with offspring age, especially in MM	**Partial** (similar decrease in both species, overall higher in JM)	M4	
When mothers groom their offspring more, and restrain them less…			~maternal grooming*species, maternal restraint*species, maternal rejection-aggression*species, *focal age, focal sex, maternal rank, observational effort (focal ID)*
P5. Offspring are more likely to groom/play with partners other than their mothers, especially in MM	**Partial** (only in MM, no effect of restraint)	M5/M6	
When mothers groom and restrain their offspring more…			
P6. Offspring are less likely to engage in solitary play, in both species	**Partial** (only in JM, only maternal grooming)	M7	
When mothers are more rejective-aggressive…			
P7. Offspring's likelihood of grooming/playing with partners other than mothers changes, in both species (no directional prediction)	**No** (no effect)	M5/M6	
P8. Offspring are more likely to engage in solitary play, in both species	**No** (in MM more rejection, less solitary play)	M7	

Note: JM stands for Japanese macaques; MM stands for moor macaques.

similarly in both species, these variables were included as controls in all our models (see Section 2.3).

2 | METHODS

2.1 | Study populations

We studied a group of 52 free-ranging JM and a group of 42 free-ranging MM living in their natural habitats. We studied JM on Koshima islet (31°27′N, 131°22′E), Miyazaki prefecture, Japan, an area of approximately 30 ha covered with evergreen forest. Depending on the tides, the islet becomes periodically connected to the mainland, but there is little exchange of individuals with the mainland. The JM at Koshima have been studied since 1948. They are provided with wheat and/or sweet potatoes on a semi-daily basis since 1952 (Nakagawa et al., 2010), although individuals need to forage to obtain most of the food (Go, 2010). Therefore, the group is well habituated to human presence, and the age, sex, and maternal kin relationships are known for all individuals. During the study, the group included 28 adults (>5 years), 7 subadults (4–5 years), 15 juveniles (1–3 years), and 2 infants (up to 1 year).

We studied MM in the Karaenta forest (5°02′59.4″ S, 119°44′ 13.2″ E), a sector of approximately 10,282 ha of primary forest, belonging to the Bantimurung-Bulusaraung National Park, in South Sulawesi, Indonesia. This group has been studied intermittently for more than 30 years (Amici et al., 2020; Beltrán Francés et al., 2020; Gomez-Melara et al., 2021; Matsumura, 1993, 1996; Riley, 2010; Riley et al., 2014). The group is occasionally provided with food by visitors, so individuals are habituated to human presence. During the study, the group included 24 adults, 4 subadults, 5 juveniles, and 9 infants. The age of immatures was estimated by the second and last authors, and by Dr. Bonaventura Majolo, based on their size (Grand, 1981) and motor patterns (Thierry et al., 2000). Mother–offspring kinship was determined based on the occurrence of breastfeeding and the knowledge of local park guides, who had observed the group for more than 20 years. However, kinship with the other group members could not be established with certainty in this study group.

2.2 | Data collection and data coding

Two observers collected data on JM (from November 2016 until July 2017) and one on MM (from September 2018 until March 2019). All three observers underwent a prior training period and did not start the observations until adequate interobserver reliability was reached (Cohen's Kappa coefficient > 0.90).

To determine the dominance hierarchy and assess each individual's rank (see below), we used all-occurrences sampling to record all dyadic agonistic interactions with a clear winner-loser outcome (i.e., aggression, chase, threat, displacement, scream, hind-quarter presentation and, only for JM, bared-teeth display; Thierry, 2000). We recorded a total of 2116 interactions in JM (ranging from 18 to 419 interactions per dyad) and 381 in MM (ranging from 4 to 47 interactions per dyad).

Moreover, we collected 20-min focal animal samples of all immatures in each group (i.e., females up to 4 years and males up to 5 years). We excluded the individuals who were orphans (*n* = 2), those whose mother–offspring kinship could not be identified with certainty (*n* = 5), and one who disappeared from the group at the beginning of data collection (*n* = 1). Overall, we included a total of 22 immature JM and 12 immature MM (Table 2), which were observed for a total of 205.68 h, with a mean (±*SD*) of 5.05 (±0.30) h per subject in JM and 7.89 (±0.98) h per subject in MM. Focal samples were randomly distributed across individuals and time of day (from 08:00 to 18:00 for JM and from 06:00 to 18:00 for MM), with at least 1 h elapsing between two consecutive focal samples on the same individual.

Following previous studies (e.g., Bardi & Huffman, 2002; Maestripieri, 2001), during each focal sample we recorded the occurrence of the following maternal behaviors received by the focal subject: (i) maternal restraint (i.e., preventing the offspring from breaking body contact), (ii) maternal rejection (i.e., preventing the offspring from making body contact), and (iii) maternalaggressive behavior (i.e., bite, lunge, chase, and threat). We further recorded (iv) all instances of 2-m proximity to the mother, (v) all instances of allo-grooming given or received by the focal, including partner identity, (vi) all instances of social play (i.e., playful chasing, sparring, wrestling or mouthing directed to at least another individual: Bardi & Huffman, 2002; Burghardt, 2005) in which the focal was involved, including partner identity, and (vii) all instances of solitary play (i.e., solitary climbing, swinging, rolling or jumping on objects: Bardi & Huffman, 2002; Burghardt, 2005). Finally, as a measure of observation effort, we recorded the exact duration of each focal sample, removing the time in which the focal subject was not visible.

2.3 | Data analysis

All analyses were conducted using R software (R Core Team, version 4.0.1). The dominance rank of all the individuals in each group (excluding infants, who were assigned their mother's rank) was determined with the Elo method ("EloRating" package; Neumann & Kulik, 2020). The values obtained were averaged throughout the study periods and standardized to range from 0 to 1 (with 0 indicating lowest and 1 highest rank). Elo-ranks were highly stable in both groups throughout the study period (*S* index = 0.977 for JM; 0.982 for MM).

TABLE 2 Species, sex, age (in years), and rank of each study subject (immature monkeys, *n* = 34).

Species	Subject	Sex	Age	Rank
Japanese macaques	Takana	Female	1	0.653
	Botan		2	0.169
	Pan		2	0.352
	Yotsuba		2	0.434
	Mochi		2	0.583
	Pichi		3	0.217
	Hiba		3	0.497
	Tabu		3	0.653
	Hado		4	0.509
	Tsutsuji		4	0.645
	Hirame	Male	1	0.497
	Yumin		2	0.234
	Mekki		2	0.264
	Haku		2	0.509
	Noko		2	0.548
	Komatsu		2	0.592
	Shida		2	0.627
	Bon		4	0.169
	Yomogi		4	0.434
	Kote		4	0.592
	Shiira		4	0.627
	Yuu		5	0.234
Moor macaques	Lida	Female	0	0.416
	Bolet		1	0.125
	Bira		1	0.286
	Taro		1	0.415
	Ciro		2	0.115
	Sahril		3	0.415
	Crow	Male	1	0.119
	Foc		1	0.215
	Coko		1	0.322
	Suco		1	0.386
	Singa		2	0.322
	Kopi		5	0.322

To confirm the different dominance styles of the study species, we directly assessed the steepness of the dominance hierarchy in each study group ("steepness" package; Leiva & De Vries, 2014). As the proportion of unknown relationships differed across species, we randomly removed dyads with known relationships from the JM dominance matrix to reach the same proportion as MM, and averaged the values obtained over 1000 iterations to calculate the adjusted steepness of the dominance hierarchy (Klass & Cords, 2011). Moreover, for each study group, we assessed the proportion of agonistic interactions against the hierarchy (i.e., interactions in which the aggressor is a lower-ranking individual than the target of aggression; de Vries et al., 2006; Young & Isbell, 2002). We assessed these measures in two different ways: (i) including all the juveniles, subadults, and adults in the group, and (ii) only including subadults and adults, as social networks for juveniles may not be yet completely established. In line with literature, we expected steepness values to be higher in less tolerant JM than in MM, and the proportion of agonistic interactions against the hierarchy to be higher in more tolerant MM than in JM (see de Vries et al., 2006; Thierry, 2000, 2007; Thierry et al., 2008; Young & Isbell, 2002).

We analyzed maternal and offspring behavior using generalized linear mixed models (GLMMs; Baayen et al., 2008) with the "glmmTMB" package (Magnusson et al., 2021). First, we assessed whether dominance style predicts developmental changes in maternal behavior, using four models with a binomial distribution. Model 1 examined whether the offspring's probability of being in proximity to their mother was predicted by the two-way interaction of species with offspring age (Prediction 1, Table 1), while controlling for offspring sex, maternal rank, and observation effort (i.e., the log-transformed time within the 20-min focal sample in which the focal subject was visible). We further included the mother's identity as a random effect and the focal subject's identity as a random effect nested in mother's identity (McCullagh & Nelder, 1989). Models 2–4 were identical to Model 1, except that we used as dependent variables the offspring's probability of receiving maternal grooming (Prediction 2, Model 2), maternal restraint (Prediction 3, Model 3), and maternal rejective–aggressive behavior (Prediction 4, Model 4) during the focal sample (Table 1). Although maternal behavior may vary non-linearly through offspring development (e.g., with some maternal behaviors peaking during the first months of the offspring's life: Kulik et al., 2016; Maestripieri, 2002), we included age as a linear predictor in the models, because our study sample ($n = 34$) only included one offspring younger than 1 year (Table 2).

Second, we assessed whether dominance style is associated with the link between maternal and offspring behavior. For this purpose, we ran three further models with a binomial distribution. Model 5 explored whether immatures' probability of engaging in grooming interactions with individuals other than their mothers was predicted by the three two-way interactions of species with maternal grooming, species with maternal restraint, and species with maternal rejective–aggressive behavior (i.e., as the z-transformed proportion of focal samples in which each behavior was observed at least once; Predictions 5 and 7, Table 1). We further controlled for the immature's age, immature's sex, maternal rank, and observation effort, including the focal subject identity as a random effect. Models 6 and 7 were identical to Model 5, except that the dependent variables were respectively the probability of engaging in social play with individuals other than their mothers (Predictions 5 and 7, Model 6) and the probability of engaging in solitary play (Predictions 6 and 8, Model 7) during the focal sample (Table 1).

We used likelihood ratio tests (Dobson & Barnett, 2008) to compare full models containing all predictors with null models including only control predictors, conditional effects, and random effects. The two-way interactions also included the main effects, which were however not interpreted if the interactions were significant. When two-way interactions did not improve model fit, the full model was re-run without them, while retaining the main effects of each predictor involved. For each model, we checked residual diagnostics and overdispersion using the "DHARMa" package (Florian, 2022), and multicollinearity using the "performance" package (Lüdecke et al., 2021). We detected no problems and very low multicollinearity in all our models (maximum variance inflation factors across models = 3.00; Miles, 2005).

3 | RESULTS

3.1 | Differences in dominance styles between the two study groups

We found differences between MM and JM in their dominance styles. Steepness values were higher in JM than in MM, although the difference became minimal after adjusting for the proportion of missing dyads in each group (Table 3). The proportion of agonistic interactions against the hierarchy was instead clearly higher in MM than in JM, in line with our predictions (Table 3).

3.2 | Changes in maternal behavior with offspring age

In Models 1–4, the full models significantly outperformed their respective null models (GLMM, Model 1: $\chi^2 = 19.563$, $df = 3$, $p < 0.001$; Model 2: $\chi^2 = 25.056$, $df = 3$, $p < 0.001$; Model 3: $\chi^2 = 6.914$, $df = 2$, $p = 0.032$; Model 4: $\chi^2 = 11.588$, $df = 2$, $p = 0.003$). First, the probability of being in proximity to mothers was lower in older offspring in both species, but it more quickly decreased in MM than in JM (Model 1 in Table 4; Figure 1). Second, the probability of receiving maternal grooming was relatively constant through the first 5 years of age in JM, but it clearly decreased over the same period in MM (Model 2 in Table 4; Figure 2). Third, the probability of receiving maternal restraint was lower in older offspring in both species (Model 3 in Table 4; Supporting Information: Figure SI1). Finally, the probability of receiving rejective–aggressive behavior from their mothers was predicted by species and offspring age (Model 4 in Table 4; Supporting Information: Figure SI2). In particular, the probability of maternal rejective–aggressive behavior was lower in older offspring in both species, and it was overall more likely to occur in JM than in MM (Model 4 in Table 4; Supporting Information: Figure SI2).

TABLE 3 For each study group, values of the steepness of the dominance hierarchy and proportion of agonistic interactions against the hierarchy; both measures have been calculated in two different ways: (i) including all individuals except infants, and (ii) only including subadults and adults

Measure	Japanese macaques	Moor macaques
Steepness for all individuals (except infants):		
Without corrections for missing dyads	0.280	0.163
With corrections for missing dyads (61%)	0.183	0.163
Steepness for subadults and adults:		
Without corrections for missing dyads	0.436	0.160
With corrections for missing dyads (62%)	0.164	0.160
Interactions against the hierarchy for all individuals (except infants)	193/2116 = 9%	68/346 = 20%
Interactions against the hierarchy for subadults and adults	144/1460 = 10%	46/245 = 19%

Note: The steepness is presented with and without corrections for missing dyads (as the proportion of unknown relationships was greater in moor macaques than in Japanese macaques).

3.3 | Link between maternal behavior and offspring behavior

In Model 5, the comparison between the full and the null model was not significant, only showing a statistical trend (GLMM: $\chi^2 = 10.381$, $df = 5$, $p = 0.065$). In the full model, a higher proportion of maternal grooming predicted a higher probability of immatures grooming with other partners, but only in MM (in JM, a higher probability of being groomed by mothers slightly decreased the probability of immatures grooming with others; Model 5 in Table 4; Supporting Information: Figure SI3). Moreover, in both species, higher maternal restraint seemed to predict a lower probability of immatures engaging in grooming interactions with partners other than mothers (Model 5 in Table 4; Supporting Information: Figure SI4). As the full model did not significantly outperform the null, however, these results should be taken with special caution.

In Models 6 and 7, both full models significantly outperformed their respective null models (GLMM, Model 6: $\chi^2 = 26.342$, $df = 5$, $p < 0.001$; Model 7: $\chi^2 = 41.580$, $df = 6$, $p < 0.001$). In particular, we observed that a higher proportion of maternal grooming predicted a higher probability of immatures engaging in social play with other partners in MM, with the opposite being found in JM (Model 6 in Table 4; Figure 3). Furthermore, a higher proportion of maternal grooming predicted more solitary play in MM immatures but less in JM (Model 7 in Table 4; Figure 4). Similarly, a lower proportion of maternal rejective–aggressive behavior predicted more solitary play in MM immatures but had no clear effect on JM (Model 7 in Table 4; Figure 5).

4 | DISCUSSION

In this study, we assessed whether dominance style (i) predicts differences in maternal behavior according to offspring age, and (ii) predicts the link between maternal behavior and offspring behavior, by comparing less tolerant JM and more tolerant MM.

First, in line with literature, we found differences in the dominance styles of both species: although the steepness of the dominance hierarchy was only slightly higher in less tolerant JM, the proportion of agonistic interactions against the hierarchy was visibly higher in more tolerant MM. Our results showed that maternal behavior consistently differed between these species, with maternal protectiveness decreasing with offspring age generally more quickly in MM than in JM, and maternal rejection being overall higher in JM (Table 1). Moreover, we observed that dominance style predicted the link between maternal and offspring behavior. Only in MM, maternal grooming was generally linked to more playful and socially integrated offspring, whereas higher maternal rejection predicted lower frequencies of solitary play behavior (Table 1). In JM, in contrast, maternal grooming appeared to be associated with a lower social and solitary play in offspring, whereas maternal rejection had no apparent relation with offspring behavior.

Largely in line with our predictions, maternal behavior differed between JM and MM. Mothers were less likely in proximity and grooming interactions with their offspring as the latter aged, especially in MM (in line with Predictions 1 and 2; Table 1). Furthermore, the probability of maternal rejection-aggression also decreased with offspring age in both species, and it was overall higher in JM than in MM (in line with Prediction 4; Table 1). These results have at least three implications. First, they support previous studies suggesting that less tolerant species have more "controlling" maternal styles than more tolerant species, being characterized by both higher maternal protectiveness (at least in terms of maternal proximity and grooming) and rejection (Bardi, Shimizu, Barrett, et al., 2003; Bardi, Shimizu & Borgognini-Tarli, 2003; Kaufman & Rosenblum, 1969; Maestripieri, 1994b; Mason et al., 1993; Thierry, 1985). By confirming previous findings through a direct comparison of free-ranging groups and the inclusion of a tolerant species whose maternal behavior had not been previously investigated (MM), our study provides new evidence that the link between dominance styles and maternal behavior may hold across different species and living

TABLE 4 Results of the models run, including estimates, standard errors (*SE*), confidence intervals (*CIs*), likelihood ratio tests (*LRT*), degrees of freedom (*df*), and *p* values for each test and control predictor (between parentheses, the reference category)

MODEL	Estimate	*SE*	95% *CIs*	*LRT*	*df*	*p*
Model 1: Probability of proximity with mothers						
Intercept	−6.734	0.648	−8.005 to −5.464	–	–	–
Species (MM)*Offspring age	−0.774	0.226	−1.275 to −0.272	8.733	1	0.003*
Species (MM)	1.109	0.623	−0.112 to 2.330	–	1	0.075
Offspring age	−0.147	0.157	−0.455 to 0.161	–	1	0.350
Offspring sex (male)	−0.235	0.269	0.763–0.292	0.557	1	0.455
Maternal rank	2.135	0.892	0.382–3.881	4.345	1	0.037
Model 2: Probability of maternal grooming						
Intercept	−7.360	0.510	−8.360 to −6.359	–	–	–
Species (MM)*Offspring age	−0.734	0.237	−1.200 to −0.269	10.685	1	0.001*
Species (MM)	0.0562	0.474	−0.873 to 0.985	–	1	0.906
Offspring age	0.0314	0.110	−0.185 to 0.248	–	1	0.777
Offspring sex (male)	−0.023	0.215	−0.445 to 0.397	0.012	1	0.911
Maternal rank	0.766	0.767	−0.738 to 2.270	0.968	1	0.325
Model 3: Probability of maternal restraint						
Intercept	−7.126	2.148	−11.335 to −2.916	–	–	–
Species (MM)	−0.824	1.111	−3.002 to 1.353	0.594	1	0.440
Offspring age	−1.243	0.695	−2.604 to 0.119	6.134	1	0.013*
Offspring sex (male)	−0.486	0.711	−1.879 to 0.908	0.460	1	0.498
Maternal rank	−3.686	2.951	−9.469 to 2.097	1.865	1	0.172
Model 4: Probability of maternal rejective–aggressive behavior						
Intercept	−8.038	1.134	−10.260 to −5.816	–	–	–
Species (MM)	−2.587	0.766	−4.088 to −1.087	10.740	1	0.001*
Offspring age	−0.618	0.265	−1.138 to−0.098	5.664	1	0.017*
Offspring sex (male)	0.560	0.514	−0.448 to 1.568	1.111	1	0.292
Maternal rank	−1.181	1.637	−4.390 to 2.028	0.448	1	0.485
Model 5: Probability of offspring grooming with others						
Intercept	−8.303	0.515	−9.312 to −7.293	–	–	–
Species (MM)*Maternal grooming	1.049	0.424	0.217–1.881	5.707	1	0.017*
Species (MM)	1.421	0.445	0.547–2.295	–	1	0.001*
Maternal grooming	−0.251	0.249	−0.739 to 0.236	–	1	0.313
Maternal restraint	−0.323	0.157	−0.631 to −0.015	4.059	1	0.044*
Maternal rejection-aggression	0.221	0.141	−0.056 to 0.498	2.387	1	0.122
Offspring age	0.209	0.118	−0.021 to 0.440	3.070	1	0.080
Offspring sex (male)	−0.407	0.262	−0920 to 0.106	2.372	1	0.123
Maternal rank	−0.243	0.784	−1.781 to 1.294	0.096	1	0.757
Model 6: Probability of offspring playing with others						
Intercept	−7.346	0.448	−8.304 to −6.389	–	–	–
Species (MM)*Maternal grooming	0.995	0.410	0.192–1.798	5.547	1	0.018*

TABLE 4 (Continued)

MODEL	Estimate	*SE*	*95% CIs*	*LRT*	*df*	*p*
Species (MM)	1.684	0.420	0.861–2.508	–	1	0.037*
Maternal grooming	−0.493	0.236	−0.955 to −0.030	–	1	<0.001*
Maternal restraint	−0.261	0.149	−0.554 to 0.032	2.995	1	0.083
Maternal rejection-aggression	−0.056	0.141	−0.333 to 0.220	0.161	1	0.688
Offspring age	0.016	0.112	−0.203 to 0.235	0.020	1	0.887
Offspring sex (male)	−0.184	0.253	−0.679 to 0.311	0.527	1	0.468
Maternal rank	−0.105	0.769	−1.613 to 1.402	0.019	1	0.891
Model 7: Probability of offspring solitary play						
Intercept	−8.736	0.976	−10.649 to −6.823	–	–	–
Species (MM)*Maternal grooming	5.983	1.500	3.042–8.924	20.324	1	<0.001*
Species (MM)*Maternal rejection-aggression	−7.136	2.210	−11.469 to −2.803	12.293	1	<0.001*
Species (MM)	6.477	1.358	3.816–9.138	–	1	<0.001*
Maternal grooming	−0.395	0.406	−1.184 to 0.394	–	1	0.327
Maternal restraint	−0.189	0.324	−0.825 to 0.446	0.338	1	0.561
Maternal rejection-aggression	0.107	0.230	−0.344 to 0.559	–	1	0.641
Offspring age	−0.086	0.216	−0.509 to 0.337	0.155	1	0.693
Offspring sex (male)	0.641	0.477	−0.294 to 1.576	1.772	1	0.183
Maternal rank	1.596	1.421	−1.889 to 4.382	1.221	1	0.269

Note: The asterisks denote significant *p* values for the test predictors. Control predictors in italics. All models had a binomial distribution and included the log-transformed focal sample duration as conditional effect and subject identity as random effect. Models 1–4 also included mother identity as random effect. MM stands for moor macaques.

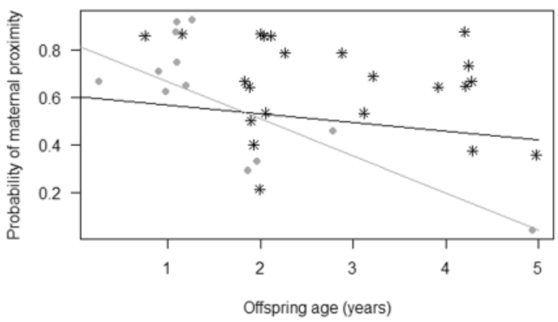

FIGURE 1 For each species (Japanese macaques in black, moor macaques in gray), probability of maternal proximity as a function of offspring age (see Model 1 in Table 4). Circles and asterisks represent the average values for the study subjects (immature monkeys, $n = 34$) and are jittered to avoid overlap. The lines depict the predicted probability of maternal proximity (separately for each species), which has been back-transformed from the log-odds ratio scale and contains standardized controls. Please note that the intercept values for the model are determined by the scale of the offset term (i.e., observational effort).

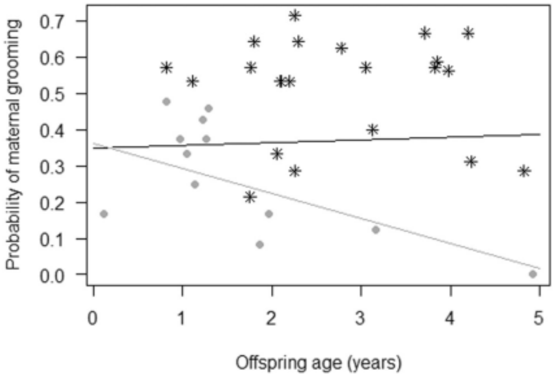

FIGURE 2 For each species (Japanese macaques in black, moor macaques in gray), probability of maternal grooming as a function of offspring age (see Model 2 in Table 4). Circles and asterisks represent the average values for the study subjects (immature monkeys, $n = 34$) and are jittered to avoid overlap. The lines depict the predicted probability of maternal grooming (separately for each species), which has been back-transformed from the log-odds ratio scale and contains standardized controls. Please note that the intercept values for the model are determined by the scale of the offset term (i.e., observational effort).

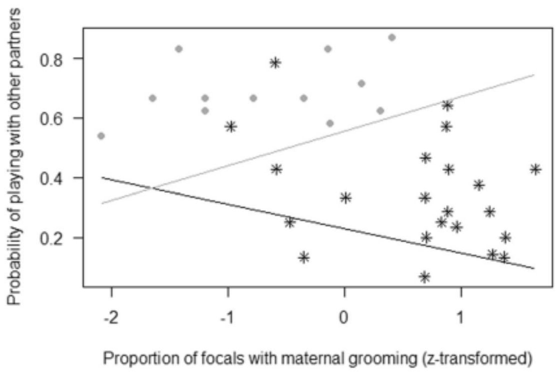

FIGURE 3 For each species (Japanese macaques in black, moor macaques in gray), probability of immatures engaging in social play with other partners as a function of maternal grooming (modeled as the *z*-transformed proportion of focal samples in which maternal grooming was observed at least once; see Model 6 in Table 4). Circles and asterisks represent the average values for the study subjects (immature monkeys, $n = 34$) and are jittered to avoid overlap. The lines depict the predicted probability of social play (separately for each species), which has been back-transformed from the log-odds ratio scale and contains standardized controls. Please note that the intercept values for the model are determined by the scale of the offset term (i.e., observational effort).

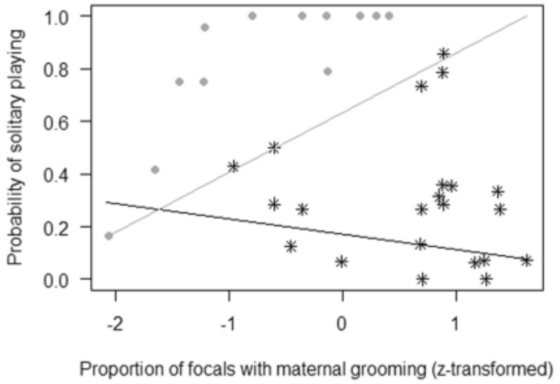

FIGURE 4 For each species (Japanese macaques in black, moor macaques in gray), probability of solitary play by immatures as a function of maternal grooming (modeled as the *z*-transformed proportion of focal samples in which maternal grooming was observed at least once; see Model 7 in Table 4). Circles and asterisks represent the average values for the study subjects (immature monkeys, $n = 34$) and are jittered to avoid overlap. The dashed lines depict the predicted probability of solitary play (separately for each species), which has been back-transformed from the log-odds ratio scale and contains standardized controls. Please note that the intercept values for the model are determined by the scale of the offset term (i.e., observational effort).

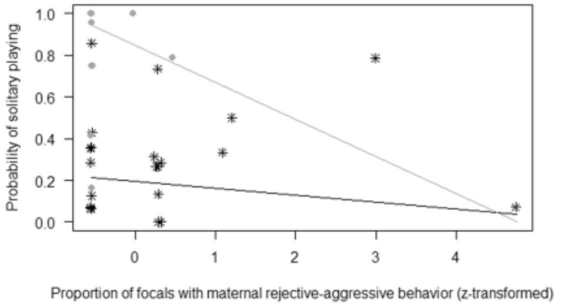

FIGURE 5 For each species (Japanese macaques in black, moor macaques in gray), probability of solitary play by immatures as a function of maternal rejection-aggression (modeled as the *z*-transformed proportion of focal samples in which maternal rejection-aggression was observed at least once; see Model 7 in Table 4). Circles and asterisks represent the average values for the study subjects (immature monkeys, $n = 34$) and are jittered to avoid overlap. The dashed lines depict the predicted probability of solitary play (separately for each species), which has been back-transformed from the log-odds ratio scale and contains standardized controls. Please note that the intercept values for the model are determined by the scale of the offset term (i.e., observational effort).

conditions, and is therefore unlikely to simply reflect the specific contingencies of particular study groups.

Second, our study showed that these interspecific differences in maternal behavior dynamically emerged across offspring development (as shown by the significant interaction between age and species in Models 1 and 2), being weaker during infancy and strongly increasing as individuals approached sexual maturity, growing into the social roles that they have as adults (Amici et al., 2019; Fairbanks, 1996; Lonsdorf, 2017; Maestripieri, 2018). In less tolerant species, individuals may face a higher risk of severe aggression and lower reconciliation rates (e.g., De Waal & Luttrell, 1989; Demaria & Thierry, 2001; Petit et al., 1997), and mothers may thus exert more control over their offspring (Bardi, Shimizu, Barrett, et al., 2003; Bardi, Shimizu & Borgognini-Tarli, 2003; Kaufman & Rosenblum, 1969; Maestripieri, 1994a; Mason et al., 1993; Thierry, 1985). In more tolerant species, in contrast, mothers may show protectiveness toward younger offspring, but quickly decrease the frequency of these behaviors as immatures get older, because they may face lower risks during social interactions (see Thierry, 1990, 2007).

Third, the probability of maternal rejection-aggression was overall higher in JM than in MM. Although these results are in line with the hypothesis that mothers in less tolerant species show more rejection to improve their offspring's stress management skills (see Maestripieri, 2018), it is also possible that higher rejection in JM is a by-product of other species characteristics, such as the fact that less tolerant species are generally more aggressive and mothers may simply relate more aggressively to their offspring (Maestripieri, 1998). Future longitudinal studies will be necessary to contrast these different hypotheses.

Only partially in line with our predictions (Prediction 3; Table 1), the probability of maternal restraint decreased with offspring age in both species, with no significant differences between species. These results are in line with previous studies showing that restraint is usually directed only toward very young offspring (e.g., Bardi, Shimizu & Borgognini-Tarli, 2003; Li et al., 2013). Moreover, they suggest that maternal restraint, despite usually being considered a protective behavior similar to grooming or proximity (e.g., Bardi & Huffman, 2002; Fairbanks & McGuire, 1993; Maestripieri, 1999), may have a different function and be linked to other developmental outcomes (e.g., reducing rather than facilitating offspring interaction with others; see below).

Our results further suggest that dominance style mediated the link between maternal and offspring behavior, partially in line with our predictions (Table 1). Maternal grooming (but not lower maternal restraint) was associated with a higher probability that offspring interacted with other group members, but only in MM (partially in line with Prediction 5; Table 1). Therefore, maternal grooming may promote the integration of immatures in the social group, in line with an abundant literature on the topic (e.g., Kulik et al., 2016; Murray et al., 2014; Weaver & de Waal, 2003), but this effect may be stronger in more tolerant species, where individuals may have fewer constraints with regard to the social partners they can interact with (Beltrán Francés et al., 2020; Maestripieri, 1994a; Thierry, 1985, 1990). Partially in line with our predictions, higher maternal grooming (but not maternal restraint) predicted less solitary play in the offspring, but only in JM (Prediction 6; Table 1). In MM, in contrast, maternal grooming was linked to an increase in the probability that immatures engaged in solitary play. Therefore, these results suggest that maternal grooming may be related to developmental changes in offspring behavior, but differently depending on dominance style. In more tolerant species, maternal grooming appears to predict a higher tendency to play alone and interact with others, whereas in less tolerant species, maternal grooming might have the opposite effect.

Finally, maternal rejection failed to predict the occurrence of social interaction with others (Prediction 7, Table 1), providing support neither to the hypothesis that rejection may promote social independence of offspring (Bardi & Huffman, 2002, 2006; Schino et al., 2001), nor to the hypothesis that maternal rejection may decrease the likelihood that offspring engage in social interactions with others (Bardi & Huffman, 2006). However, maternal rejection was associated with a decrease in the likelihood that MM immatures engaged in solitary play (contrary to Prediction 8; Table 1).

Overall, our results suggested important differences between the two study groups, not only in maternal behavior throughout offspring development, but also in the link between maternal and offspring behavior. This confirms the importance of considering variation in maternal style and its link to offspring development even in species sharing very close life histories and similar ecological characteristics (Bardi & Huffman, 2006). However, our study also has important limitations, and our conclusions should be taken with caution. First, we only included two study groups. Therefore, the interspecific differences we found may also be simply explained by socio-ecological factors other than dominance style. Maternal styles, for instance, may vary within species depending on group size and composition (e.g., Berman, 1992; Berman et al., 1997; Liu et al., 2018; Schino et al., 1995), food accessibility (e.g., Andrews et al., 1993; Hauser & Fairbanks, 1988; Rosenblum & Sunderland, 1982), risk of predation, infant kidnaping, or infanticide (e.g., Berman, 1992; Fairbanks & McGuire, 1987; Liu et al., 2018; Maestripieri, 2001; Sekizawa & Kutsukake, 2019). Therefore, more study groups would be needed to rule out alternative explanations. Second, the link between maternal and offspring behavior cannot inform us about the causal relationship between these two variables: without experimental manipulations, it is not possible to exclude that this link is explained by genetic factors or by previous experiences shared by mothers and offspring, which affect both maternal styles and immature behavior (see Schino et al., 2001; for a discussion). Similarly, it is also possible that offspring behavior partially explains specific maternal behavior (e.g., more strongly soliciting affiliative and agonistic support by mothers; see Maestripieri, 2018). Longitudinal studies and structural equation models may be useful, in the future, to better understand possible causal pathways linking maternal and offspring behavior. Finally, there are several factors other than offspring age and sex, or maternal rank, which may influence interindividual variation in maternal style, including a mother's emotional reactivity to stressful events (e.g., Bardi & Huffman, 2006; Maestripieri, 1993a, 1993b), her age (e.g., Hoffman et al., 2010; Schino et al., 1995), her physical condition (e.g., de la Torre et al., 2021) or her previous maternal experience (e.g., Holley & Simpson, 1981; Tanaka, 1989). Unfortunately, we could not test the role of these factors in our study, because we did not have information about such factors for the MM group. However, future studies should account for these possible sources of variation where possible.

In conclusion, our study suggested that dominance style might be an important factor modulating changes in maternal and offspring behavior. In more tolerant species, protectiveness may more strongly decrease during the first years of life, as individuals gradually grow into their adult social roles. Moreover, dominance style predicted the link between maternal style and offspring behavior, as higher maternal grooming and lower rejection were linked to more social and playful behavior in immatures, but only in more tolerant species. Although these findings need to be strengthened by the inclusion of more groups and species, and the use of longitudinal approaches, they seem to confirm dominance style as a crucial source of developmental variation.

AUTHOR CONTRIBUTIONS

Alba Castellano-Navarro: Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Víctor Beltrán Francés**: Data curation (equal); investigation (equal); writing – review and editing (supporting). **Anna Albiach-Serrano**: Conceptualization (equal); investigation (equal); methodology (equal); supervision (equal); writing – review and editing (equal). **Andrew J. J. MacIntosh**: Funding acquisition (equal); supervision (equal); writing – review and editing (equal). **Risma Illa Maulany**: Resources (equal); writing – review and editing (supporting). **Putu O. Ngakan**: Resources (equal); writing – review and editing (supporting). **Katja Liebal**: Writing – review and editing (equal). **Federica Amici**: Conceptualization (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); resources (equal); supervision (lead); writing – original draft (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available in "Supporting Information".

ETHICS STATEMENT

This study was observational. The protocols used were approved by the ethics committees and followed the nonhuman primate research regulations of the Primate Research Institute and Wildlife Research Centre of Kyoto University, as well as the Indonesian Foreign Research Permit Division, Ministry of Research and Technology/National Research and Innovation Agency. The authors 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.

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