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The ability to inhibit impulses is related to social behavior in long-tailed macaques

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Abstract

Performance in cognitive tasks has been linked to differences in species' social organization, yet to understand its function its relationship to within-species variation in behavior should also be explored. One important cognitive capacity, the ability to inhibit impulses, is typically better in egalitarian than despotic primate species and in primate species with strong fission-fusion dynamics. A different line of research indicates that a high ability to inhibit impulses is related to less aggressive behavior and more socio-positive behavior. However, within species the relationship between performance on cognitive inhibition tasks and variation in social behavior remains to be explored. Here we investigate how performance in a typical inhibition task in cognitive research is related to aggressive and socio-positive behavior in despotic long-tailed macaques. Twenty individuals living in two naturalistic mixed-sex groups were tested with the Plexiglass Hole Task. Aggressive behavior and three types of socio-positive behavior (neutral/friendly approaches, socio-positive signaling, and grooming others) among group members were measured. Individuals differed in their ability to inhibit impulses. Individuals that were not good at inhibiting impulses showed higher rates of aggressive behavior, but also more socio-positive signals, whereas inhibition was not related to neutral/friendly approaches and grooming. These results confirm the positive link between impulsiveness and aggression. In addition, the results indicate that some social-positive behavior may be enhanced when inhibition is limited. In this species, benefits potentially derived from aggression and socio-positive signals match a low ability to inhibit impulses, suggesting that a low ability to inhibit impulses may actually be advantageous. To understand differences between species in cognitive skills, understanding the benefits of variation in a cognitive capacity within a species is crucial.

KEYWORDS
dominance style, impulsivity, primates, social cognition, social competence, social strategies

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CNS, central nervous system; BPRC, Biomedical Primate Research Center.

1 | INTRODUCTION

Inhibition, the ability to inhibit impulses, is considered an important cognitive capacity (Barrett et al., 2003; Loyant et al., 2021; MacLean et al., 2014) that primates may employ to address both social (social or Machiavellian intelligence hypothesis: Dunbar, 1998; Humphrey, 1976; Jolly, 1966) and ecological (ecological-intelligence hypothesis: de Petrillo et al., 2022) challenges (Herrmann et al., 2010). Comparative studies of primate cognition employ batteries of behavioral tests (Herrmann et al., 2007). Among them, inhibition is one of the cognitive capacities that is regularly studied (Amici et al., 2008; Fichtel et al., 2020; Joly et al., 2017). In behavioral cognition tasks measuring inhibition (Amici et al., 2008), species show differences in the ability to inhibit impulses. This variation has been linked to species differences in social behavior, such as fission-fusion dynamics (Amici et al., 2008) and social tolerance (Joly et al., 2017; Loyant et al., 2023), and to differences in dietary breadth (MacLean et al., 2014). While this highlights species differences, it does not address within species variation in cognitive capacities. Within species variation to inhibit impulses may be connected to sex differences (rhesus monkeys, *Macaca mulatta*: Loyant et al., 2021) and within-species variation in general intelligence (chimpanzees, *Pan troglodytes*: Beran & Hopkins, 2018). To unravel the functional relevance of the ability to inhibit impulses, its connection with variation in behavior is needed. Here we aim to address this question by investigating the relationship between interindividual variation in performance in a cognitive inhibition task and variation in social behavior.

In the literature, the terms impulsiveness and inhibition describe the same behavior but in the reverse scale: high impulsiveness means low inhibition and vice versa. While inhibitory control (Amici et al., 2008) or self-control (Beran & Hopkins, 2018; MacLean et al., 2014) are terms typically used when describing behavior in cognitive tasks, impulsivity (Krakowski, 2003); or: social impulsivity (Fairbanks, 2001); or: impulsive behavior (Higley et al., 1996) is often used to describe social behavior. To acknowledge the different terms used in research on cognition and on social behavior, we use the term *the ability to inhibit impulses* or *inhibition*. The ability to inhibit impulses can be measured in several ways. In comparative cognitive research, physical inhibition tasks measure the ability to inhibit impulses (Amici et al., 2012; Herrmann et al., 2008; Joly et al., 2017; Loyant et al., 2023). To our knowledge this type of physical inhibition tasks have not yet been linked to individual differences in social behavior. Studies linking the ability to inhibit impulses to within species variation in social behavior use different paradigms. First, several studies have used natural fluctuations (Fairbanks et al., 2001; Higley & Linnoila, 1997; Westergaard et al., 1999) or experimentally manipulated levels of CNS serotonin as a proxy to impulsivity (Fairbanks et al., 2001; Raleigh et al., 1980, 1985). Furthermore, to study behavior during confrontations with unknown conspecifics near the home cage, the Intruder Challenge Test, has been used to assess inhibition (Fairbanks, 2001; Fairbanks et al., 2021; Fairbanks, Jorgensen, et al., 2004; Fairbanks, Newman, et al., 2004).

Primates are social animals that experience both competition as well as cooperation and regulate these processes with social behavior (e.g., Seyfarth, 1977; Sterck et al., 1997) by employing both aggression and socio-positive behavior (e.g., Seyfarth, 1977; Vermande & Sterck, 2020). Aggression can be used to obtain resources (e.g., bonnet macaques, *Macaca radiata*: Boccia et al., 1988; comparative research: Isbell, 1991; capuchin monkeys, *Cebus apella*: Janson, 1985; long-tailed macaques: Overduin-de Vries et al., 2020; long-tailed macaques, *M. fascicularis* and Thomas langurs, *Presbytis thomasi*: Sterck & Steenbeek, 1997) and a high dominance position (e.g., vervet monkeys, *Cercopithecus aethiops*: Fairbanks, Jorgensen, et al., 2004). A high dominance position has been related to fitness benefits that can be provided through (the threat of) aggression (male primates: Alberts, 2012; Davidian et al., 2022; female primates: Pusey, 2012; long-tailed macaque males: de Ruiter et al., 1992; long-tailed macaque females: van Noordwijk & van Schaik, 1999). In addition, socio-positive behavior may be important to obtain cooperation (e.g., Kummer, 1978), can provide access to resources (Overduin-de Vries et al., 2020) and can lead to good relationships (Massen et al., 2010; Seyfarth & Cheney, 2012; Silk, 2002). These good relationships have also been related to fitness benefits (e.g., baboons, *Papio cynocephalus*: Silk, Alberts, et al., 2006; Silk, Altmann, et al., 2006; Silk et al., 2010a, 2010b; rhesus macaques: Kulik et al., 2012; Massen et al., 2012). Thus, both aggression and socio-positive behavior are important components of primate social behavior. These different types of social behavior may be correlated (rhesus macaques: Wooddell et al., 2019; children: Hawley, 2007; Vermande et al., 2018) or independent (long-tailed macaques: Overduin-de Vries et al., 2020; rhesus macaques: Wooddell et al., 2017).

Comparative research in primate cognition has investigated the connection between the ability to inhibit impulses and species differences in social organization. High fission-fusion dynamics may require a need to inhibit impulses, since enhanced social complexity may require caution (Amici et al., 2008) and fusion events may be risky (Aureli & Schaffner, 2007) because information on other individuals may be incomplete (Aureli et al., 2022). Accordingly, species with a high level of fission-fusion dynamics are better at inhibiting their impulses than species living in more cohesive groups (Amici et al., 2008, 2018). Also, in tolerant primate species a high level of inhibition may be advantageous, since social interactions may require more communication and coordination (Joly et al., 2017). Indeed, egalitarian macaques are better at inhibiting their impulses than despotic ones (Joly et al., 2017; Loyant et al., 2023). This also indicates that a low level of inhibition will be found in despotic species with coherent groups. Correspondingly, research that takes CNS serotonin levels as a proxy to the ability to inhibit impulses report outcomes consistent with this idea. Relatively egalitarian pig-tailed macaques (*Macaca nemestrina*) have higher serotonin levels, and thus a better ability to inhibit impulses, than the more despotic rhesus macaques (Westergaard et al., 1999). However, these studies do not connect the ability to inhibit impulses to within-species variation in social behavior.

Within-species variation in the ability to inhibit impulses has been found in several primate species (Amici et al., 2008; Fairbanks, 2001; Joly et al., 2017; Loyant et al., 2021; Westergaard et al., 1999). The connection between the ability to inhibit impulses and social behavior has been explored for aggressive behavior in particular. A low ability to inhibit impulses has been related to aggression in several mammalian species (golden hamsters, *Mesocricetus auratus*: Cervantes & Delville, 2007; Lister hooded rats: Rudebeck et al., 2007). Similarly, low CNS serotonin levels, indicating low inhibition, have been associated with a high rate of aggression both in natural fluctuations (rhesus macaques: Higley & Linnoila, 1997; Higley et al., 1996; Mehlman et al., 1995) and manipulated levels (vervet monkeys: Raleigh et al., 1980; long-tailed macaques; Shively et al., 2014; a cichlid species, *Neolamprologus pulcher*: Stettler et al., 2021). However, an effect on aggression is not always found (Raleigh et al., 1980, 1991). An individual's level of impulsivity and aggression in an Intruder Challenge Test were found to be correlated and to have a genetic component (male vervet monkeys: Fairbanks, Jorgensen, et al., 2004). In this species, impulsivity of adolescents in an Intruder Challenge Test leads to later obtaining a higher dominance position (Fairbanks, Jorgensen, et al., 2004). However, dominant males that maintain their position show intermediate impulsivity in this test (Fairbanks, 2001; Fairbanks, Jorgensen, et al., 2004) and in rhesus macaques performance at inhibition tasks does not correlate with dominance (Loyant et al., 2021). In adult humans, a low ability to inhibit impulses has been related to an increase in aggression (Garcia-Forero et al., 2009). Youth that cannot well inhibit impulses have difficulty suppressing anger (Calkins & Dedmon, 2000; Vigil-Colet & Codorniu-Raga, 2004) and show more often aggression (Calkins & Dedmon, 2000; Coccaro, 1992; Dolan et al.,2001; Virkkunnen et al., 1995). In addition, youth with a low ability to inhibit impulses more often exhibit social problem behavior such as delinquency (White et al., 1994; Zhang et al., 2017). Altogether, a low ability to inhibit impulses is usually linked with aggression. Yet a low ability to inhibit impulses may (vervets: Fairbanks, Jorgensen, et al., 2004) or may not be associated with high dominance. Altogether, it is unclear how these three factors, that is, impulsivity, aggression and dominance, interact.

The ability to inhibit impulses has also been studied in relation to socio-positive behaviors. High CNS serotonin levels, related to a high ability to inhibit impulses, have been linked to a high rate of grooming in despotic rhesus macaques (Mehlman et al., 1995). In addition, experimentally increased levels of serotonin have resulted in more socio-positive behavior such as approaching, proximity and grooming (vervets: Raleigh et al., 1980; Raleigh et al., 1991; long-tailed macaques: Shively et al., 2014; cichlid species: Stettler et al., 2021). Similarly, a high level of impulse control allows young humans to inhibit aggressive behavior, and switch to a more thoughtful prosocial way of interacting with their environment (Moilanen, 2007; Rydell et al., 2003). Therefore, whereas a low ability to inhibit impulses seems to be linked with higher levels of aggression, a high ability to inhibit impulses seems to be linked to socio-positive behavior.

However, to our best knowledge there are no studies that link performance in inhibition tasks as those used in cognitive studies to either aggressive or socio-positive behavior.

The aim of the current study is to investigate the relationship between the ability to inhibit impulses and social (i.e., both aggressive and socio-positive) behavior in group-living captive male and female long-tailed macaques, taking dominance level into account. The ability to inhibit impulses was measured with the Plexiglass Hole Task, a physical inhibition task that is regularly used in comparative research on cognitive abilities (Amici et al., 2012; Herrmann et al., 2008; Joly et al., 2017). The despotic long-tailed macaques (Thierry, 2007) have a relatively low ability to inhibit their impulses (Amici et al., 2012; Joly et al., 2017; but see Loyant et al., 2023). In this species aggression and socio-positive behavior form important categories of social behavior. Based on the literature described above, we predict that a low ability to inhibit impulses will relate to high levels of aggression. In addition, we predict that a high ability to inhibit impulses will relate to high levels of socio-positive behaviors.

2 | METHODS

2.1 | Subjects

The study was approved by the Animal Ethical Committee of the BPRC (DEC746). All applicable international, national, and/or institutional guidelines for the care and use of animals were followed, including the EU Directive 2010/63/EU for animal experiments. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. All authors state compliance with the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates.

Twenty long-tailed macaques housed at the Biomedical Primate Research Center, The Netherlands, participated in this study. Subjects were housed in two naturalistic mixed sex groups: 13 subjects (eight females; five males) were housed in a group of 25 animals (the Haas-group) and seven subjects (six female; one male) were housed in a group of 24 individuals (the Roza-group). Their age ranged from 3 to 20 years. Subjects participated in the experiment on a voluntary basis. Although important from the standpoint of animal welfare, this opens the possibility for a self-selection bias (i.e., poorer or better inhibitors tended to participate). However, we found considerable variation in impulsivity within the selection of participants. The overall variation within the complete monkey group may be even larger than documented in this study.

The monkeys were housed in interconnected indoor and outdoor enclosures. Observations were conducted in their home cage. During observations monkeys could walk freely between inside and outside compartments. A linear dominance rank was based on the direction of unprovoked submission, i.e. bared-teeth display, make room and give ground (Altmann, 1974) (h′ = 0.51, 0.83; p = 0.001, 0.0001; directional consistency index = 0.90, 0.98)

MatMan: (de Vries et al., 1993; de Vries, 1995, 1998) and was scored 1 for the highest-ranking individual to 24 or 25 for the lowest ranking individual in each of the groups.
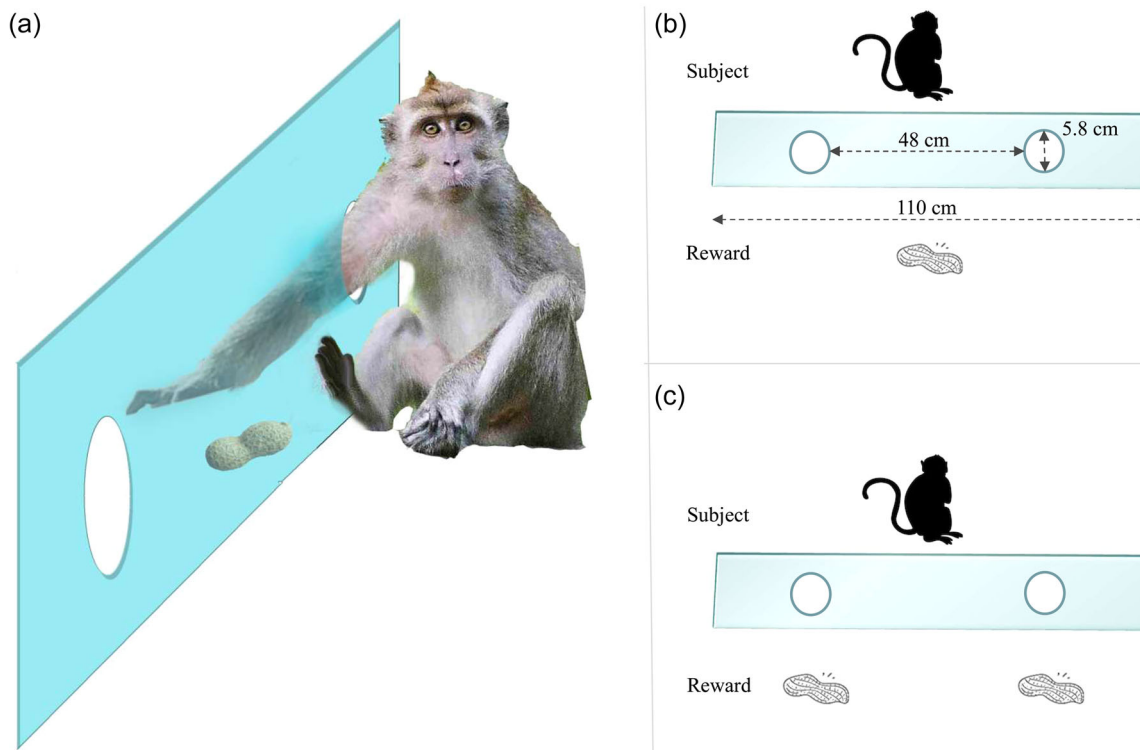
2.2 | Inhibition experiment

Preceding the experiment, animals were trained to position themselves close to a target (a red plastic shoehorn, approximately 5 by 45 cm), and upon touching the target were rewarded with a clicker sound and a preferred food item (raisin or peanut). This way we were able to control the position of the animal during the experiment. The experimenters wore protective clothing and avoided direct contact with the animals.

We made use of an existing physical inhibition task to test the ability to inhibit impulses in our subjects, namely the Plexiglass Hole Task (Amici et al., 2008). The experimental apparatus (Figure 1) consisted of a plexiglass screen (110 x 32 cm) with two holes with a diameter of 58 mm, 48 cm apart. The animals had ample experience with transparent objects, since windows were always present in their enclosures. The size of the hole was sufficient for all monkeys to reach through. The plexiglass screen was mounted on a separated compartment of the monkeys' home cage instead of the wire mesh between the monkey and the experimenter. On the experimenter's side of the plexiglass, a table was situated on which the rewards were placed. Each subject received eight experimental sessions in total.

Each experimental session consisted of six training trials followed by one test trial.

In a training trial, a monkey was trained to reach for a reward (raisin) through one of the holes. The experimenter held the target through one of the holes semi-randomly alternating between the left and right hole. When the subject touched the target, the clicker was sounded and the experimenter placed the reward on the table just behind the hole. In training trials, if the monkey did not take the raisin immediately, the experimenter moved the reward back and forth through the hole until the monkey grabbed the reward by reaching with its arm through the hole.

In the experimental trial, the target was held against the plexiglass in the middle of the two holes. Upon touching the plexiglass with the reward, the reward was immediately placed on the table behind the plexiglass. We noted whether monkeys (1) impulsively reached for the food by a straightforward move, bumping against the plexiglass; (2) inhibited their impulse, relocated themselves to one of the holes and tried to reach for the food through the hole; or (3) showed none of the above reactions within 30 s. If monkeys reached through the hole, but did not stretch all the way through to take the reward, it was given the reward by the experimenter. When 30−60 s passed (depending on the perseverance of the monkey), without the subject reaching through any of the holes, subjects released. Since eight experimental trials were conducted, the monkeys could learn that they could reach through one of the holes, thereby increasing the number of individuals that

FIGURE 1 The experimental apparatus for the plexiglass hole task. (a) a visual representation of the setting; (b) the training setting; (c) the setting during tests.

eventually were able to show inhibition of the impulse. Without allowing for learning, only 4.2% of the long-tailed macaques are able to inhibit its impulse and reach through the hole (Amici et al., 2008).

We measured the ability to inhibit impulses by counting the number of times, within 8 experimental trials, that an animal inhibited its impulse: the animal did not bump into the plexiglass, relocated to one of the holes and tried to reach for the food through the hole. This number indicates the number of trials an individual inhibited its impulse (of immediately reaching straight to the food) and is a measure of how easily an individual can inhibit impulsive behavior.

We measured the time from the start of the experiment, when the reward was placed on the table, until the first attempt of reaching through a hole.

Experimental trials started twice every day directly after feeding in the morning and after feeding in the afternoon. The rewards in the training and experimental trials were not part of their regular diet.

2.3 | Social behavior observations

All subjects were observed in their social group during 15 min focal sampling sessions, totaling 7.5 h per individual. The behavioral data were also part of a publication measuring determinants of resource access (Overduin-de Vries et al., 2020). Two observers were trained by the same expert. The interobserver reliability was calculated for two observers consecutively observing the same monkey group. The interobserver reliability varied from fair to substantial (socio-positive signals: Spearman: $\rho = 0.530$, $p < 0.035$, $df = 14$; Grooming given: Spearman: $\rho = 0.808$, $p < 0.0002$, $df = 14$; Aggression: Spearman: $\rho = 0.9616627$, $p < 2.9 \times 10^{-9}$, $df = 14$). Focal sessions of a particular subject were separated by at least 30 min. During focal observations we noted aggression (chase, pull, push, slap, bite, open mouth display, stare, lunge, and point), and socio-positive behavior (neutral/friendly approaches of conspecifics; socio-positive signals, i.e. lip-smacking, eyebrow lifting; grooming) by the focal individual. Approaches were counted as neutral/friendly only if the approach was not followed by aggressive behavior from the approacher. Since aggression was rare during focal observations, all occurrence observations (two 1 h observations per day, at the end of morning and afternoon; 80 h in the Haas group, 65 h in the Roza group) were conducted focusing only on these rare behaviors. The individuals in the Haas and Roza group were visible for an average of 38 ± 3.9 h and 57 ± 2.3 h of the all occurrence observations, respectively. The total time each monkey was actually observed was used to calculate behavior rates.

The rate of aggression was calculated by counting the number of aggressive acts during focal and all occurrence observations and dividing by the summed duration of focal sessions and observation time of an individual during all occurrence sessions. The rate of neutral/friendly approach was calculated by counting the number of approaches that were not followed by aggression and dividing it by the total focal time. The rate of socio-positive signals was calculated by dividing the sum of the total amount of lip-smacking and eyebrow lifting behavior by the total focal time. The rate of grooming was

calculated by dividing the total duration of grooming behavior given by the focal animal by the total focal time.

2.4 | Statistics

First, correlations among behaviors and demographic factors were calculated using the "rcorr" function from the Hmisc library in R (R Core Team, 2020).

As described in the Introduction, research manipulating the level of inhibition with medication in primates suggests that a change in inhibition will lead to changes in aggression and social-positive behaviors. In line with this proposition, we regressed four social behavior measures (outcome variables) on inhibition (explanatory variable or predictor) using multiple linear regression. The four social behavior dependent measures were: (1) aggression; (2) neutral/friendly approach; (3) socio-positive signals; and (4) grooming (dependent variables). These behaviors were expressed as rates per individual ($N = 20$). Age, dominance rank, sex and group of the subject were also entered in the full models as explanatory variables. Since the number of predictors was relatively large given the number of cases, best subset selection was carried out to deal with the problem of overfit (James et al., 2021, p. 22). Each dependent variable was regressed on all possible combinations of predictors and for each dependent variable, the predictor subset with the smallest leave-one out cross-validation prediction error was selected. Mallow's C_p was used to measure prediction error because it adjusts for the number of predictors. In the present context, Mallow's C_p is proportional to the AIC. Multiple linear regression and best subset selection were done using the function regsubsets() of the leaps R package. There was a cubic relation in the data between aggression and inhibition. Therefore, for the models of physical aggression and threat, quadratic and cubic terms were included for inhibition.

3 | RESULTS

3.1 | Ability to inhibit impulses

Within the eight experimental trials in the plexiglass hole task, subjects varied in the number of times they inhibited their impulses and reached through a hole in the plexiglass (Figure 2). Whereas two subjects never showed successful inhibition of their impulses, the two most successful inhibitors inhibited their impulses in six out of eight trials (Mean = $2.85 \pm$ SD = 1.87). Subjects that did not inhibit their initial impulse in an experimental trial, eventually reached through the hole soon after bumping into the plexiglass. We videotaped 160 test trials. In 16 (10%) of these trials the monkeys did not try to reach for the treat within 30 s after the start of the experiment. In the majority of the trials (90%) there was reaching behavior within 30 s after the start of the experiment (Supporting Information). In 53.8% of the trials, the subjects impulsively reached straight ahead and bumped into the plexiglass. In 36.2% of the trials the subjects inhibited their impulses and reached through one of the
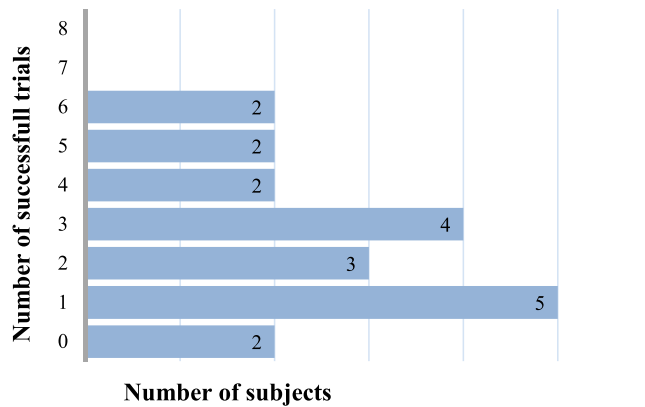
FIGURE 2 The ability to inhibit impulses varied between subjects.

holes. They did so on average 4.2 ± SE 4.7 s after the start of the test trial. The ability to inhibit impulses did not correlate significantly with age (spearman correlation: $\rho = 0.40$, $N = 20 = 18$, $p = 0.08$), or with dominance rank (Pearson correlation: $\rho = -0.19$, $N = 20$, $p = 0.41$), and it did not differ between the sexes (Wilcoxon rank sum test: $W = 43.5$, $N = 6,14$, $p = 0.93$) or between groups (Wilcoxon rank sum test: $W = 28$, $N = 13,7$, $p = 0.17$).

3.2 | Correlations between variables

We calculated whether the rates of social behavior, age and dominance rank were related (Table 1). Aggression was significantly correlated with dominance rank (Table 1), indicating that higher ranking individuals (with a lower rank number) more often employed aggression. Aggression and socio-positive behaviors were not significantly correlated, yet dominant individuals gave significantly less grooming, while dominance rank did not significantly correlate with the other socio-positive behaviors. In addition, socio-positive behaviors did not correlate significantly with each other. Age did not correlate significantly with any behavior.

3.3 | Ability to inhibit impulses and social behavior

Individuals with a relatively high ability to inhibit their impulses had significantly lower rates of aggression (Table 2 and Figure 3). Moreover, these individuals showed significantly less socio-positive signals (Table 2 and Figure 3). However, the ability to inhibit impulses did not significantly predict the rate of neutral/friendly approaches or the rate of grooming (Table 2).

In the selected models, also other factors significantly influenced social behavior. Higher ranking individuals showed more aggression than low-ranking ones. Groups differed in the rate of socio-positive signals, neutral/friendly approaches and grooming, and females had a lower rate of neutral/friendly approaches than males. Older

TABLE 1 Spearman correlation among social behaviors, age, and dominance rank.

	Aggression	Neutral/ friendly approach	Socio-positive signals	Grooming given	Age
Neutral/ friendly approach	0.06	-			
Socio-positive signals	0.41	−0.21	-		
Grooming given	−0.29	−0.32	0.20	-	
Age	0.25	−0.36	0.35	0.34	-
Dominance rank	−0.80**	−0.27	−0.31	0.58**	0.06

Note: Significance is indicated: **correlation is significant at the 0.01.

TABLE 2 Results of the best subset selection regressions.

Final model/factor (R^{2*})	ß	SE	T	p
Aggression ~ poly(inhibition,3) + age + rank ($R^2 = 0.819$)				
Intercept	1.635	0.261	6.266	<0.001
Inhibition	−0.997	0.355	−2.806	0.014
$Inhibition^2$	0.298	0.135	2.213	0.044
$Inhibition^3$	−0.027	0.014	−1.834	0.088
Age	0.004	0.001	2.805	0.014
Rank	−0.094	0.022	−4.166	<0.001
Socio-positive signals ~ inhibition + group ($R^2 = 0.415$)				
Intercept	0.687	0.170	4.041	<0.001
Inhibition	−0.099	0.045	−2.178	0.044
Group	0.478	0.176	2.716	0.015
Neutral/friendly approach ~ group + age +sex ($R^2 = 0.570$)				
Intercept	12.380	1.018	12.157	<0.001
Group	−2.716	0.974	−2.789	0.013
Age	−0.018	0.007	−2.401	0.029
Sex	−2.788	1.026	−2.719	0.015
Grooming given ~ group + age + rank ($R^2 = 0.502$)				
Intercept	−0.028	0.023	−1.210	0.244
Group	0.040	0.019	2.158	0.046
Age	0.000	0.000	2.433	0.027
Rank	0.007	0.002	3.137	0.006

Note: For each dependent variable and all possible predictor subsets the model with the lowest Mallows Cp leave-one out cross validation prediction error was selected.
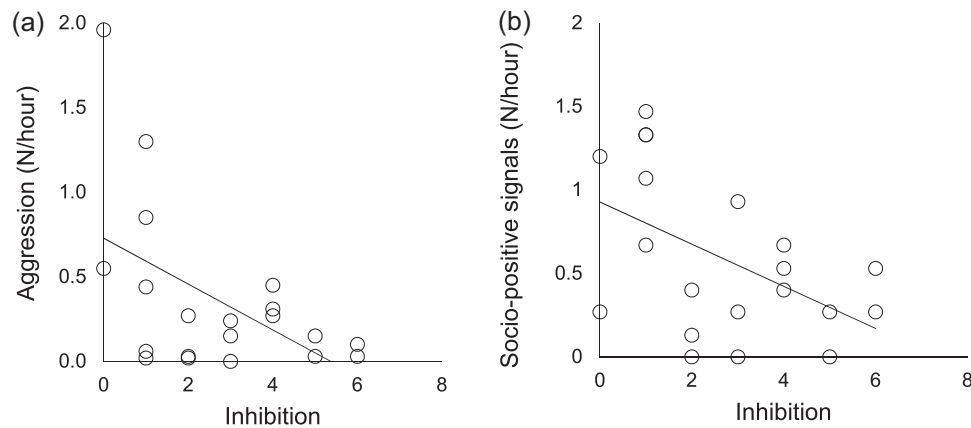
FIGURE 3 The ability to inhibit impulses (x-axis, number of successful trials out of eight) was related to (a). The rate of aggression (N/h); and (b). The rate of socio-positive signals (N/hour) (i.e., lip-smacking and eyebrow lifting).

individuals showed more aggression, but less neutral/friendly approaches than young individuals.

Except for the quadratic and cubic terms for inhibition in the model for aggression, there was no evidence of multicollinearity. That is, all tolerance values were above 0.1 and all values of the variance inflation factor were below 10.

4 | DISCUSSION

The ability to inhibit behavior is an important cognitive skill (Barrett et al., 2003; MacLean et al., 2014) and within species variation in this ability may be expressed in differences in social behavior (primates: Higley et al., 1996; Mehlman et al., 1995; e.g., humans: Calkins & Dedmon, 2000; García-Forero et al., 2009). This was investigated in long-tailed macaques by linking performance in the Plexiglass Hole Task, a physical inhibition task regularly employed in comparative studies of primate cognitive skills, to variation in aggressive and socio-positive behavior within this species. The results support the often-found connection between a low ability to inhibit impulses and high levels of aggression. Additionally, the ability to inhibit impulses was also related to socio-positive signals, but contrary to expectations, a low ability to inhibit impulses seems to be related to high rates of socio-positive signals. The rate of neutral/friendly approaches or grooming showed no relation with inhibition. The results indicate that both aggressive behavior and some socio-positive behavior may be related in a similar way by the ability to inhibit impulses, whereas other socio-positive behaviors are not related. This is only partly consistent with our predictions based on extant literature.

4.1 | Within species variation in inhibition and social behavior

The 20 subjects showed a wide range of responses to a food item placed behind a transparent barrier in front of them. After eight trials the majority of animals was eventually able to inhibit their impulses to

bump against the plexiglass, choosing an indirect route through a hole in the plexiglass. The inability to inhibit their impulses was not due to an inability to reach through the hole, since in training trials all individuals were able to reach for food through the hole in the plexiglass. Moreover, after impulsively bumping into the plexiglass, subjects often immediately reached through the hole. In addition, the level of inhibition in our study is in consistence with the relatively poor inhibiting skills of long tailed macaques compared to other species (Amici et al., 2012; Joly et al., 2017; but see Loyant et al., 2023). Still, the subjects clearly differed in impulsivity and this may be linked to social behavior.

The predicted relationship between a low ability to inhibit impulses and relatively high rates of aggression was found. This is consistent with other studies on humans, nonhuman primates and other animals (humans: García-Forero et al., 2009; primates: Fairbanks, Jorgensen, et al., 2004; Mehlman et al., 1995; Raleigh et al., 1991; other animals: Cervantes & Delville, 2007; Rudebeck et al., 2007). Similarly, impulsive rhesus monkey adolescent males show higher rates of escalated aggression (Mehlman et al., 1994). We explored how aggression, impulsivity and dominance interact. In our data, inhibition and dominance were not related, similar to findings in other studies (Fairbanks, 2001; Fairbanks, Jorgensen, et al., 2004; Loyant et al., 2021). However, both more dominant individuals and less inhibited individuals showed higher rates of aggression. This suggests that part of the more dominant individuals can show high rates of aggression, possibly due to their dominance position (Overduin-de Vries et al., 2020), yet that only specific individuals, namely the individuals that are not particularly good at inhibiting their impulses, show these higher rates of aggression. These impulsive-aggressive individuals have been considered less socially competent (Mehlman et al., 1995). Also in humans, a low ability to inhibit impulses and the accompanying high rates of aggression are considered disadvantageous (White et al., 1994) and aggression may be excessive (Calkins & Dedmon, 2000; Coccaro, 1992; Dolan et al., 2001). However, in long-tailed macaques impulsive individuals may not be at a disadvantage. An earlier study in the same groups

indicated that high rates of aggressive behavior provide access to food sources (Overduin-de Vries et al., 2020). Thus, in long-tailed macaques high rates of aggression, connected to a low ability to inhibit impulses, may be beneficial.

The predicted relationships between a high ability to inhibit impulses and high rates of three types of socio-positive behavior were not found. No effect of inhibition on neutral/friendly approaches was found. This finding differs from studies that link high serotonin levels, i.e. a high level of inhibition, to higher rates of approaching (vervet monkeys: Raleigh et al., 1980; Raleigh et al., 1991). Second, we predicted that a high ability to inhibit impulses would relate to more socio-positive signals, yet the reverse was found: individuals that had a low ability to inhibit impulses seemed to show high rates of socio-positive signals. These signals were not correlated with dominance. The socio-positive signals lip-smacking and eyebrow lifting (Angst, 1974) indicate friendly intent, often when individuals encounter each other. However, neutral/friendly approaches did not show a similar pattern in occurrence and cannot explain the higher rate of socio-positive signals. This may indicate that less inhibited individuals signal more often. A high rate of socio-positive signals may enhance grooming and cooperation (chimpanzees: Fedurek et al., 2015; apes: Genty et al., 2020; vervets, *Chlorocebus pygerythrus*: van de Waal et al., 2013; Guinea baboons, *Papio papio*: Whitham & Maestripieri, 2003). Accordingly, a low ability to inhibit these signals may provide benefits. Third, we predicted that a high ability to inhibit impulses would relate to more grooming of others, yet no relationship was found. This result is different from studies where high serotonin levels were related to high rates of grooming (rhesus macaques: Mehlman et al., 1995; vervet monkeys: Raleigh et al., 1980, 1991), yet consistent with other studies that did not find a link between serotonin levels and grooming (pig-tailed and rhesus macaques: Westergaard et al., 1999). In all, our findings suggest that in long-tailed macaques socio-positive signaling—similar to aggression—is more impulsive, while the ability to inhibit impulses is not related to neutral/friendly approaches and grooming.

The relation between low levels of inhibition on the one hand and high rate of behavior on the other hand, may suggest an underlying relation between inhibition and general activity levels. However, neutral/friendly approach, which should depend on activity levels as it involves movement, was not related to inhibition. Possibly, the found results are caused by an increase in expressivity resulting from decreased inhibition. Moreover, one-time actions with a short temporal duration (like eye-brow raising or lip-smacking) may be more impulsive, and thus more related to low inhibition, than a longer duration behavior like grooming.

This study links performance on a cognitive task of inhibition to individual variation in social behavior. Although comparable in sample size to many studies on animal cognition (Amici et al., 2012; Herrmann et al., 2008; Joly et al., 2017; but see Fichtel et al., 2020), since training and performing cognitive tasks with primates is rather time consuming, the small sample size of 20 individuals is a limitation to our study. Therefore, exploring the connection between the ability to inhibit impulses and social behavior would benefit from additional

research to confirm both the relationships found and those not found. Also, the relationship between the control variables and the ability to inhibit impulses may be further explored, especially when they are not consistent with the literature. In our sample, age did not affect the ability to inhibit impulses, while in rhesus monkeys middle-aged were less good at inhibition (Loyant et al., 2021) and, in contrast, in vervets older individuals were better at inhibiting than younger ones (Fairbanks, 2001; Fairbanks, Jorgensen, et al., 2004; Fairbanks, Newman et al., 2004). Yet consistent with other research (Fairbanks, Jorgensen, et al., 2004; Fairbanks, Newman et al., 2004), high-ranking individuals had a lower ability to inhibit impulses than low-ranking ones. No clear sex differences were found, which contrasts with findings in rhesus macaques where males were less able to inhibit impulses than females (Loyant et al., 2021). These outcomes may be due to the composition of our sample, for example, the majority was female, while quite some research on impulsiveness has focused on males (e.g., Fairbanks, 2001; Mehlman et al., 1994, 1995). Altogether, we found that in long-tailed macaques more inhibited individuals show both less aggression and less socio-positive behavior. However, such a concerted effect was not found, since aggression and socio-positive behavior did not correlate. Apparently, in different individuals the ability to inhibit impulses has a different effect. This indicates that not one cognitive skill, or one neurotransmitter, related to the ability to inhibit impulses determines the outcomes of behavior, but in concert with other features. Future research may elucidate what these additional features may be.

4.2 | Between species differences

High levels of impulsive behavior have been related to social problem behavior and low social competence in humans (Krakowski, 2003; Zhang et al., 2017) and primates (Fairbanks, Jorgensen, et al., 2004; Mehlman et al., 1995). However, it may not be correct to generalize this and to assume that all species with a low ability to inhibit impulses show social incompetence. We propose that species differences in the ability to inhibit impulses may indicate species differences in benefits from impulsiveness. We found that in long-tailed macaques a low ability to inhibit impulses is related to a high rate of aggression and socio-positive signals. High aggression rates may be beneficial in this despotic species, since aggressive individuals obtain more resources (e.g., Overduin-de Vries et al., 2020). This may also apply to socio-positive behavior, since high rates of socio-positive signals may provide benefits (e.g., Fedurek et al., 2015). This may contrast with more egalitarian macaques, in which a better ability to inhibit impulses (cognitive tasks: Joly et al., 2017; Loyant et al., 2023; serotonin levels: Westergaard et al., 1999) and low levels of aggression may provide benefits.

Thus far, the evidence that differences in the ability to inhibit impulses between despotic and nepotistic primates translate in different rate of aggression is scarce and, at best, mixed. The differences to inhibit impulses between despotic and egalitarian

species would predict that levels of aggression are higher in more despotic species. This is indeed found in some comparisons (relatively egalitarian pig-tailed vs. despotic rhesus macaques: Westergaard et al., 1999), however the opposite is found in other studies (despotic macaques have less aggression than egalitarian macaques: review in Hemelrijk, 1999; Thierry, 2022). In addition, differences between species in the ability to inhibit impulses may also be reflected in differences in levels of socio-positive behavior. However, comparative data on grooming do not show a systematic difference between despotic and egalitarian macaque species (Westergaard et al., 1999). Altogether, a species' rate of aggressive and socio-positive behavior may not reflect its ability to inhibit impulses.

Alternatively, benefits of the ability to inhibit impulses can be determined within a species. In despotic macaques, a lack of inhibition may be beneficial through its link with benefits of higher rates of aggression and socio-positive signals, which is translated at species level in a relatively low ability to inhibit impulses. In other species, such as egalitarian macaques, primate species with much fission fusion dynamics and in relatively egalitarian (Boehm, 1999) and fission fusion (Chapais, 2013; Layton et al., 2012) humans, the ability to inhibit impulses may be beneficial, thereby selecting for a high ability to inhibit impulses. In humans the advantages of a high ability to inhibit impulses have been found (Cassotti et al., 2016; Cooper et al., 2009) and chimpanzees with high ability to inhibit show higher intelligence (Beran & Hopkins, 2018), yet in other egalitarian and fission-fusion primate species this remains to be established. This proposition needs to be assessed in a comparative way.

5 | CONCLUSION

In conclusion, this study indicates that a low ability to inhibit impulses is related to aggressive behavior, but also to socio-positive signals. In this despotic primate species, a low ability to inhibit impulses and high rates of both aggression and social signaling may be advantageous, for example in obtaining access to resources. This contrasts with views, albeit in egalitarian species, that a low ability to inhibit impulses may be disadvantageous. Determining within species the benefits of high or low inhibition is key to understand these species differences.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data are provided as Supporting Information.

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REFERENCES
Alberts, S. C. (2012). *Magnitude and sources of variation in male reproductive performance*. University of Chicago Press.

Altmann, J. (1974). Observational study of behavior - sampling methods. *Behaviour*, 49(3–4), 227–266. https://doi.org/10.1163/156853974x00534

Amici, F., Aureli, F., & Call, J. (2008). Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. *Current Biology*, 18(18), 1415–1419. https://doi.org/10.1016/j.cub.2008.08.020

Amici, F., Call, J., & Aureli, F. (2012). Aversion to violation of expectations of food distribution: The role of social tolerance and relative dominance in seven primate species. *Behaviour*, 149(3–l4), 345–368. https://doi.org/10.1163/156853912x637833

Amici, F., Call, J., Watzek, J., Brosnan, S., & Aureli, F. (2018). Social inhibition and behavioural flexibility when the context changes: A comparison across six primate species. *Scientific Reports*, 8(3067), 3067. https://doi.org/10.1038/s41598-018-21496-6

Angst, W. (1974). [The communicative behavior of the crab-eating monkey *Macaca fascicularis* Raffles 1821]. *Fortschritte der Verhaltensforschung*, 15, 5–31.

Aureli, F., & Schaffner, C. M. (2007). Aggression and conflict management at fusion in spider monkeys. *Biology Letters*, 3(2), 147–149. https://doi.org/10.1098/rsb.2007.0041

Aureli, F., Schaffner, C. M., & Schino, G. (2022). Variation in communicative complexity in relation to social structure and organization in non-human primates. *Philosophical Transactions of the Royal Society B*, 377, 20210306. https://doi.org/10.1098/rstb.2021.0306

Barrett, L., Henzi, P., & Dunbar, R. (2003). Primate cognition: from 'what now?' to 'what if?'. *Trends in Cognitive Sciences*, 7(11), 494–497. https://doi.org/10.1016/j.tics.2003.09.005

Beran, M. J., & Hopkins, W. D. (2018). Self-Control in chimpanzees relates to general intelligence. *Current Biology*, 28(4), 574–579. https://doi.org/10.1016/j.cub.2017.12.043

Boccia, M. L., Laudenslager, M., & Reite, M. (1988). Food distribution, dominance, and aggressive behaviors in bonnet macaques. *American Journal of Primatology*, 16(2), 123–130. https://doi.org/10.1002/ajp.1350160203

Boehm, C. (1999). *Hierarchy in the forest: The evolution of egalitarian behavior*. Harvard University Press.

Calkins, S. D., & Dedmon, S. E. (2000). Physiological and behavioral regulation in two-year-old children with aggressive/destructive behavior problems. *Journal of Abnormal Child Psychology*, 28(2), 103–118. https://doi.org/10.1023/a:1005112912906

Cassotti, M., Agogué, M., Camarda, A., Houdé, O., & Borst, G. (2016). Inhibitory control as a core process of creative problem solving and idea generation from childhood to adult-hood. *New Directions for Child and Adolescent Development*, 2016, 61–72. https://doi.org/10.1002/cad.20153

Cervantes, M. C., & Delville, Y. (2007). Individual differences in offensive aggression in golden hamsters: A model of reactive and impulsive aggression. *Neuroscience*, 150(3), 511–521. https://doi.org/10.1016/j.neuroscience.2007.09.034

Chapais, B. (2013). Monogamy, strongly bonded groups, and the evolution of human social structure. *Evolutionary Anthropology: Issues, News, and Reviews*, 22(2), 52–65. https://doi.org/10.1002/evan.21345

Coccaro, E. F. (1992). Impulsive aggression and central serotonergic system function in humans: An example of a dimensional brain-behavior relationship. *International Clinical Psychopharmacology*, 7(1), 3–12. https://doi.org/10.1097/00004850-199200710-00001

Cooper, B., Greenberg, M., & Domitrovich, C. (2009). The contribution of inhibitory control to preschoolers' social-emotional competence. *Journal of Applied Developmental Psychology*, 30(3), 310–320. https://doi.org/10.1016/j.appdev.2008.12.012

Davidian, E., Surbeck, M., Lukas, D., Kappeler, P. M., & Huchard, E. (2022). The eco-evolutionary landscape of power relationships between males and females. *Trends in Ecology & Evolution*, 37(8), 706–718. https://doi.org/10.1016/j.tree.2022.04.004

Dolan, M., Anderson, I. M., & Deakin, J. F. W. (2001). Relationship between 5-HT function and impulsivity and aggression in male offenders with personality disorders. *British Journal of Psychiatry*, 178(4), 352–359. https://doi.org/10.1192/bjp.178.4.352

Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology: Issues, News, and Reviews*, 6(5), 178–190. https://doi.org/10.1002/(sici)1520-6505(1998)6:5<178::aid-evan5>3.0.co;2-8

Fairbanks, L. A. (2001). Individual differences in response to a stranger: Social impulsivity as a dimension of temperament in vervet monkeys (Cercopithecus aethiops sabaeus). *Journal of Comparative Psychology*, 115(1), 22–28. https://doi.org/10.1037/0735-7036.115.1.22

Fairbanks, L. A., Jorgensen, M. J., Huff, A., Blau, K., Hung, Y. Y., & Mann, J. J. (2004). Adolescent impulsivity predicts adult dominance attainment in male. *American Journal of Primatology*, 64(1), 1–17. https://doi.org/10.1002/ajp.20057

Fairbanks, L. A., Melega, W. P., Jorgensen, M. J., Kaplan, J. R., & McGuire, M. T. (2021). Social impulsivity inversely associated with CSF 5-HIAA and fluoxetine exposure in vervet monkeys. *Neuropsychopharmacology*, 24(4), 370–378. https://doi.org/10.1016/S0893-133X(00)00211-6

Fairbanks, L. A., Newman, T. K., Bailey, J. N., Jorgensen, M. J., Breidenthal, S. E., Ophoff, R. A., Comuzzie, A. G., Martin, L. J., & Rogers, J. (2004). Genetic contributions to social impulsivity and aggressiveness in vervet monkeys. *Biological Psychiatry*, 55(6), 642–647. https://doi.org/10.1016/j.biopsych.2003.12.005

Fedurek, P., Slocombe, K. E., Hartel, J. A., & Zuberbühler, K. (2015). Bonobos and chimpanzees infer the target of another's attention. *Animal Behaviour*, 83(2), 345–353. https://doi.org/10.1016/j.anbehav.2011.10.026

Fichtel, C., Dinter, K., & Kappeler, P. M. (2020). The lemur baseline: How lemurs compare to monkeys and apes in the primate cognition test battery. *PeerJ*, 8, e10025. https://doi.org/10.7717/peerj.10025

García-Forero, C., Gallardo-Pujol, D., Maydeu-Olivares, A., & Andrés-Pueyo, A. (2009). Disentangling impulsiveness, aggressiveness and impulsive aggression: An empirical approach using self-report measures. *Psychiatry Research*, 168(1), 40–49. https://doi.org/10.1016/j.psychres.2008.04.002

Genty, E., Heesen, R., Guéry, J.-P., Rossano, F., Zuberbühler, K., & Bangerter, A. (2020). How apes get into and out of joint actions. *Shared intentionality as an interactional achievement. Interaction Studies*, 21(3), 353–386. https://doi.org/10.1075/is.18048.gen

Hawley, P. H. (2007). Social dominance in childhood and adolescence: Why social competence and aggression may go hand in hand. In P. H. Hawley, T. D. Little & P. C. Rodkin (Eds.), *Aggression and adaptation: The bright side to bad behavior* (pp. 1–30). Lawrence Earlbaum Associates.

Hemelrijk, C. K. (1999). Effects of cohesiveness on inter-sexual dominance relationships and spatial structure among group-living virtual entities. *Advances in Artificial Life, Proceedings*, 1674, 524–534. https://doi.org/10.1007/3-540-48304-7_71

Herrmann, E., Call, J., Hernandez-Lloreda, M. V., Hare, B., & Tomasello, M. (2008). Comparing social skills of children and apes - response. *Science*, 319(5863), 570.

Herrmann, E., Call, J., Hernàndez-Lloreda, V., Hare, B., & Tomasello, M. (2007). Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science*, 317(5843), 1360–1366. https://doi.org/10.1126/science.1146282

Herrmann, E., Hare, B., Call, J., & Tomasello, M. (2010). Differences in the cognitive skills of bonobos and chimpanzees. *PlosOne*, 5(8), e12438. https://doi.org/10.1371/journal.pone.0012438

Higley, J. D., King, S. T., Hasert, M. F., Champoux, M., Suomi, S. J., & Linnoila, M. (1996). Stability of interindividual differences in serotonin function and its relationship to severe aggression and competent social behavior in rhesus macaque females. *Neuropsychopharmacology*, 14(1), 67–76. https://doi.org/10.1016/s0893-133x(96)80060-1

Higley, J. D., & Linnoila, M. (1997). Low central nervous system serotonergic activity is traitlike and correlates with impulsive behavior. A nonhuman primate model investigating genetic and environmental influences on neurotransmission. *Annals of the New York Academy of Sciences*, 836(1), 39–56. https://doi.org/10.1111/j.1749-6632.1997.tb52354.x

Humphrey, N. (1976). The social function of intellect. In P. Bateson & R. Hinde (Eds.), *Growing Points in Ethology* (pp. 303–317). Cambridge University Press.

Isbell, L. A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, 2, 143–155. https://doi.org/10.1093/beheco/2.2.143

James, G., Witten, D., Hastie, T., & Tibshirani, R. (2021). *An introduction to statistical learning with applications in R* (ISL, 2nd ed.). Springer.

Janson, C. (1985). Aggresive competition and individual food consumption in wild brown capuchin monkeys (Cebus apella). *Behavioral Ecology and Sociobiology*, 18, 125–138. https://doi.org/10.1007/bf00299041

Jolly, A. (1966). Lemur social behavior and primate intelligence: The step from prosimian to monkey intelligence probably took place in a social context. *Science*, 153(3735), 501–506. https://doi.org/10.1126/science.153.3735.501

Joly, M., Micheletta, J., De Marco, A., Langermans, J. A., Sterck, E. H. M., & Waller, B. M. (2017). Comparing physical and social cognitive skills in macaque species with different degrees of social tolerance. *Proceedings of the Royal Society B-Biological Sciences*, 284(1862), 20162738. https://doi.org/10.1098/rspb.2016.2738

Krakowski, M. (2003). Violence and serotonin: Influence of impulse control, affect regulation, and social functioning. *The Journal of Neuropsychiatry and Clinical Neurosciences*, 15(3), 294–305. https://doi.org/10.1176/appi.neuropsych.15.3.294

Kulik, L., Muniz, L., Mundry, R., & Widdig, A. (2012). Patterns of interventions and the effect of coalitions and sociality on male fitness. *Molecular Ecology*, 21(3), 699–714. https://doi.org/10.1111/j.1365-294X.2011.05250.x

Kummer, H. (1978). On the value of social relationships to nonhuman primates: A heuristic scheme. *Social Science Information*, 17(4–5), 687–705. https://doi.org/10.1177/053901847801700418

Layton, R., O'Hara, S., & Bilsborough, A. (2012). Antiquity and social functions of multilevel social organization among human hunter-gatherers. *International Journal of Primatology*, 33(5), 1215–1245. https://doi.org/10.1007/s10764-012-9634-z

Loyant, L., Waller, B. M., Micheletta, J., & Joly, M. (2021). Heterogeneity of performances in several inhibitory control tasks: Male rhesus macaques are more easily distracted than females. *Royal Society Open Science*, 8, 211564. https://doi.org/10.1098/rsos.211564

Loyant, L., Waller, B. M., Micheletta, J., Meunier, H., Ballesta, S., & Joly, M. (2023). Tolerant macaque species are less impulsive and reactive. *Animal Cognition*, 26, 1453–1466. https://doi.org/10.1007/s10071-023-01789-8

MacLean, E. L., Hare, B., Nunn, C. L., Addesso, E., Amici, F., Anderson, R. C., & Aureli, F. (2014). The evolution of self-control. *Proceedings of the National Academy of Sciences USA*, 111(20), E2140–E2148. https://doi.org/10.1073/pnas.1323533111

Massen, J., Sterck, E., & de Vos, H. (2010). Close social associations in animals and humans: Functions and mechanisms of friendship.

Behaviour, *147*(11), 1379–1412. https://doi.org/10.1163/000579510x528224

Massen, J. J. M., Overduin-de Vries, A. M., de Vos-Rouweler, A. J. M., Spruijt, B. M., Doxiadis, G. G. M., & Sterck, E. H. M. (2012). Male mating tactics in captive rhesus macaques (*Macaca mulatta*): The influence of dominance, markets, and relationship quality. *International Journal of Primatology*, *33*(1), 73–92. https://doi.org/10.1007/s10764-011-9552-5

Mehlman, P. T., Higley, J. D., Faucher, I., Lilly, A. A., Taub, D. M., Vickers, J., Suomi, S. J., & Linnoila, M. (1994). Low csf 5-hiaa concentrations and severe aggression and impaired impulse control in nonhuman-primates. *American Journal of Psychiatry*, *151*(10), 1485–1491. https://doi.org/10.1176/ajp.151.10.1485

Mehlman, P. T., Higley, J. D., Faucher, I., Lilly, A. A., Taub, D. M., Vickers, J., Suomi, S. J., & Linnoila, M. (1995). Correlation of csf 5-hiaa concentration with sociality and the timing of emigration in free-ranging primates. *American Journal of Psychiatry*, *152*(6), 907–913. https://doi.org/10.1176/ajp.152.6.907

Moilanen, K. L. (2007). The adolescent self-regulatory inventory: The development and validation of a questionnaire of short-term and long-term self-regulation. *Journal of Youth and Adolescence*, *36*(6), 835–848. https://doi.org/10.1007/s10964-006-9107-9

van Noordwijk, M. A. & van Schaik, C. P. (1999). The effects of dominance rank and group size on female lifetime reproductive success in wild long-tailed macaques, *Macaca fascicularis*. *Primates*, *40*(1), 105–130. https://doi.org/10.1007/bf02557705

Overduin-de Vries, A. M., de Vries, H., Vermande, M. M., Reijntjes, A. H. A., & Sterck, E. H. M. (2020). Both aggressive and affiliative behaviour facilitate resource access in high-ranking female long-tailed macaques (*Macaca fascicularis*). *Behaviour*, *157*(3–4), 267–287. https://doi.org/10.1163/1568539X-bja10001

De Petrillo, F., Nair, P., Cantwell, A., & Rosati, A. G. (2022). The evolution of cognitive control in Lemurs. *Psychological Science*, *33*(9), 1408–1422. https://doi.org/10.1177/09567976221082938

Pusey, A. (2012). *Magnitude and sources of variation in female reproductive performance*. University of Chicago Press.

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org/

Raleigh, M. J., Brammer, G. L., McGuire, M. T., & Yuwiler, A. (1985). Dominant social status facilitates the behavioral effects of sero-tonergic agonists. *Brain Research*, *348*(2), 274–282. https://doi.org/10.1016/0006-8993(85)90445-7

Raleigh, M. J., Brammer, G. L., Yuwiler, A., Flannery, J. W., McGuire, M. T., & Geller, E. (1980). Serotonergic influences on the social-behavior of vervet monkeys (cercopithecus-aethiops-sabaeus). *Experimental Neurology*, *68*(2), 322–334. https://doi.org/10.1016/0014-4886(80)90089-8

Raleigh, M. J., McGuire, M. T., Brammer, G. L., Pollack, D. B., & Yuwiler, A. (1991). Serotonergic mechanisms promote dominance acquisition in adult male vervet monkeys. *Brain Research*, *559*(2), 181–190. https://doi.org/10.1016/0006-8993(91)90001-c

Rudebeck, P. H., Walton, M. E., Millette, B. H. P., Shirley, E., Rushworth, M. F. S., & Bannerman, D. M. (2007). Distinct contributions of frontal areas to emotion and social behaviour in the rat. *European Journal of Neuroscience*, *26*(8), 2315–2326. https://doi.org/10.1111/j.1460-9568.2007.05844.x

de Ruiter, J. R., Scheffrahn, W., Trommelen, G. J. J. M., Uiterlinden, A. G., Martin, R. D., & Van Hooff, J. A. R. A. M. (1992). Male social rank and reproductive success in wild long-tailed macaques. In R. D. Martin, A. F. Dixson, & E. J. Wickings (Eds.), *Paternity in primates: Genetic tests and theories* (pp. 175–191). Karger.

Rydell, A. M., Berlin, L., & Bohlin, G. (2003). Emotionality, emotion regulation, and adaptation among 5-to 8-Year-Old children. *Emotion*

(Washington, D.C.), *3*(1), 30–47. https://doi.org/10.1037/1528-3542.3.1.30

Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*, *65*, 671–698.

Seyfarth, R. M., & Cheney, D. L. (2012). The evolutionary origins of friendship. *Annual Review of Psychology*, *63*, 153–177. https://doi.org/10.1146/annurev-psych-120710-100337

Shively, C. A., Register, T. C., Higley, J. D., & Willard, S. L. (2014). Sertraline effects on cerebrospinal fluid monoamines and species-typical socioemotional behavior of female cynomolgus monkeys. *Psychopharmacology*, *231*(7), 1409–1416. https://doi.org/10.1002/ajp.1350020406

Silk, J. (2002). Using the 'F'-word in primatology. *Behaviour*, *139*(2–3), 421–446. https://doi.org/10.1163/156853902760102735

Silk, J. B., Alberts, S. C., & Altmann, J. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) II. variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology*, *61*(2), 197–204. https://doi.org/10.1163/156853902760102735

Silk, J. B., Altmann, J., & Alberts, S. C. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) I. variation in the strength of social bonds. *Behavioral Ecology and Sociobiology*, *61*(2), 183–195. https://doi.org/10.1007/s00265-006-0250-9

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2010a). Female chacma baboons form strong, equitable, and enduring social bonds. *Behavioral Ecology and Sociobiology*, *64*(11), 1733–1747. https://doi.org/10.1007/s00265-006-0250-9

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2010b). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology*, *20*(15), 1359–1361. https://doi.org/10.1016/j.cub.2010.05.067

Sterck, E. H. M., & Steenbeek, R. (1997). Female dominance relationships and food competition in the sympatric Thomas langur and long-tailed macaque. *Behaviour*, *134*(9–10), 749–774. https://doi.org/10.1163/156853997x00052

Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, *41*(5), 291–309. https://doi.org/10.1007/s002650050390

Stettler, P. R., F. Antunes, D., & Taborsky, B. (2021). The serotonin 1A receptor modulates the social behaviour within groups of a cooperatively-breeding cichlid. *Hormones and Behavior*, *129*(2021), 104918. https://doi.org/10.1016/j.yhbeh.2020.104918

Thierry, B. (2007). Unity in diversity: Lessons from macaque societies. *Evolutionary Anthropology: Issues, News, and Reviews*, *16*(6), 224–238. https://doi.org/10.1002/evan.20147

Thierry, B. (2022). Where do we stand with the covariation framework in primate societies. *American Journal of Biological Anthropology*, *178*(Suppl. 74), 5–25. https://doi.org/10.1002/ajpa.24441

Vermande, M. M., Gilholm, P. A., Reijntjes, A. H. A., Hessen, D. J., Sterck, E. H. M., & Overduin-de Vries, A. M. (2018). Is inspiring group members an effective predictor of social dominance in early adolescence? direct and moderated effects of behavioral strategies, social skills, and gender on resource control and popularity. *Journal of Youth and Adolescence*, *47*(9), 1813–1829. https://doi.org/10.1007/s10964-018-0830-9

Vermande, M. M., & Sterck, E. H. M. (2020). How to get the biggest slice of the cake. A comparative view of social behaviour and resource access in human children and nonhuman primates. *Frontiers in Psychology*, *11*, 584815. https://doi.org/10.3389/fpsyg.2020.584815

Vigil-Colet, A., & Codorniu-Raga, M. J. (2004). Aggression and inhibition deficits, the role of functional and dysfunctional impulsivity. *Personality and Individual Differences*, *37*(7), 1431–1440. https://doi.org/10.1016/j.paid.2004.01.013

Virkkunen, M., Goldman, D., Nielsen, D. A., & Linnoila, M. (1995). Low brain serotonin turnover rate (low CSF 5-HIAA) and impulsive violence. *Journal of psychiatry & neuroscience: JPNNeuroscience*, *20*(4), 271–275.

de Vries, H. (1995). An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour*, *50*(5), 1375–1389. https://doi.org/10.1006/anbe.1997.0708

de Vries, H. (1998). Finding a dominance order most consistent with a linear hierarchy: A new procedure and review. *Animal Behaviour*, *55*(4), 827–843. https://doi.org/10.1006/anbe.1997.0708

de Vries, H., Netto, W. J., & Hanegraaf, P. L. H. (1993). Matman: A program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour*, *125*(3–4), 157–175. https://doi.org/10.1163/156853993x00218

van de Waal, E., Spinelli, M., Bshary, R., Ros, A. F. H., & Noë, R. (2013). Negotiations over grooming in wild vervet monkeys (*Chlorocebus pygerythrus*). *International Journal of Primatology*, *34*(6), 1153–1171. https://doi.org/10.1007/s10764-013-9729-1

Westergaard, G. C., Mehlman, P. T., Westergaard, G. C., Suomi, S. J., & Higley, J. D. (1999). CSF5-HIAA and aggression in female macaque monkeys: species and interindividual differences. *Psychopharmacology*, *146*(4), 440–446. https://doi.org/10.1007/pl00005489

White, J. L., Moffitt, T. E., Caspi, A., Bartusch, D. J., Needles, D. J., & Stouthamer-Loeber, M. (1994). Measuring impulsivity and examining its relationship to delinquency. *Journal of Abnormal Psychology*, *103*(2), 192–205. https://doi.org/10.1037/0021-843x.103.2.192

Whitham, J. C., & Maestripieri, D. (2003). Primate rituals: the function of greetings between male Guinea baboons. *Ethology*, *109*(10), 847–859. https://doi.org/10.1046/j.0179-1613.2003.00922.x

Wooddell, L. J., Kaburu, S. S. K., & Dettmer, A. M. (2019). Dominance rank predicts social network position across developmental stages in rhesus monkeys. *American Journal of Primatology*, *82*(11), e23024. https://doi.org/10.1002/ajp.23024

Wooddell, L. J., Kaburu, S. S. K., Murphy, A. M., Suomi, S. J., & Dettmer, A. M. (2017). Rank acquisition in rhesus macaque yearlings following permanent maternal separation: The importance of the social and physical environment. *Developmental Psychobiology*, *59*(7), 863–875. https://doi.org/10.1002/dev.21555

Zhang, Z., Wang, Q., Liu, X., Song, P., & Yang, B. (2017). Differences in inhibitory control between impulsive and premeditated aggression in juvenile inmates. *Frontiers in Human Neuroscience*, *11*, 373. https://doi.org/10.3389/fnhum.2017.00373

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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