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Authors

Talbot, Catherine

Madrid, Jesus

Del Rosso, Laura

et al.

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Rhesus monkey sociality is stable across time and linked to variation in the initiation but not receipt of prosocial behavior

Catherine F. Talbot^{1,2}, Jesus E. Madrid^{3,4,5}, Laura A. Del Rosso¹, John P. Capitanio^{1,6}, Joseph P. Garner^{4,7}, Karen J. Parker^{1,4,7}

¹California National Primate Research Center, Davis, California, USA

²Department of Psychology, Florida Institute of Technology, Melbourne, Florida, USA

³Neurosciences Program, Stanford University, Stanford, California, USA

⁴Department of Psychiatry and Behavioral Sciences, Stanford University, Stanford, California, USA

⁵Department of Psychology, Cornell University, Ithaca, New York, USA

⁶Department of Psychology, University of California, Davis, Davis, California, USA

⁷Department of Comparative Medicine, Stanford University, Stanford, California, USA

Abstract

Rhesus monkeys and humans are highly social primates, yet both species exhibit pronounced variation in social functioning, spanning a spectrum of sociality. Naturally occurring low sociality in rhesus monkeys may be a promising construct by which to model social impairments relevant to human autism spectrum disorder (ASD), particularly if low sociality is found to be stable across time and associated with diminished social motivation. Thus, to better characterize variation in sociality and social communication profiles, we performed quantitative social behavior assessments on $N = 95$ male rhesus macaques (*Macaca mulatta*) housed in large, outdoor groups. In Study 1, we determined the social classification of our subjects by rank-ordering their total frequency of nonsocial behavior. Monkeys with the greatest frequency of nonsocial behavior were

Correspondence: Catherine F. Talbot, Department of Psychology, Florida Institute of Technology, 150 W. University Blvd, Melbourne, FL 32901, USA. ctalbot@fit.edu Karen J. Parker, Department of Psychiatry and Behavioral Sciences, Stanford University, 1201 Welch Rd, MSLS P-104, Stanford, CA 94305, USA. kjparker@stanford.edu.

AUTHOR CONTRIBUTIONS

Catherine F. Talbot and Jesus E. Madrid led the behavioral data collection efforts. Laura A. Del Rosso performed behavioral reliabilities and day-to-day project management. Joseph P. Garner conducted the statistical analyses. Catherine F. Talbot, Jesus E. Madrid, Joseph P. Garner, and Karen J. Parker wrote the first draft of the manuscript. John P. Capitanio and Karen J. Parker procured project funding and site access and oversaw all aspects of scientific data collection. All authors reviewed and approved the submission of this manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

ETHICS STATEMENT

No animals were handled in this study. We collected all data unobtrusively from outside of each animal's home corral. Animal husbandry followed the Guide for the Care and Use of Laboratory Animals. The CNPRC is fully accredited by the Association for Assessment and Accreditation of Laboratory Animal Care, International. All procedures were ethically reviewed and approved by the Institutional Animal Care and Use Committee of the CNPRC, University of California, Davis, as well as the Administrative Panel on Animal Laboratory Care of Stanford University. All procedures complied with the National Institutes of Health policies on the care and use of animals and the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates.

classified as low-social ($n = 20$) and monkeys with the lowest frequency of nonsocial behavior were classified as high-social ($n = 21$). To assess group differences in social communication profiles, in Study 2, we quantified the rates of transient social communication signals, and whether these social signals were initiated by or directed towards the focal subject. Finally, in Study 3, we assessed the within-individual stability of sociality in a subset of monkeys ($n = 11$ low-social, $n = 11$ high-social) two years following our initial observations. Nonsocial behavior frequency significantly correlated across the two timepoints (Studies 1 and 3). Likewise, low-social versus high-social classification accurately predicted classification two years later. Low-social monkeys initiated less prosocial behavior than high-social monkeys, but groups did not differ in receipt of prosocial behavior, nor did they differ in threat behavior. These findings indicate that sociality is a stable, trait-like characteristic and that low sociality is linked to diminished initiation of prosocial behavior in rhesus macaques. This evidence also suggests that low sociality may be a useful construct for gaining mechanistic insight into the social motivational deficits often observed in people with ASD.

Keywords

autism spectrum disorder; rhesus macaque; social communication; social functioning; social motivation; threat behavior

1 | INTRODUCTION

Sociality is central to primate social organization as all primates are social for at least some portion of their lives (Sussman & Chapman, 2017), making it highly advantageous to recognize and remember conspecifics with whom one has interacted, respond appropriately to social cues, and glean information about the social relationships of others. Thus, one's ability to navigate the complexities of social life should be under strong selection pressure. Despite the evolutionary and everyday importance of navigating society, however, there is a wide natural variation in the ability to attend to, process, and respond appropriately to social information even within the same species of primate (Clark & Ehlinger, 1987; Phillips et al., 2014). Yet, there is little systematic research on the variation of social functioning in nonhuman primates.

We and others have been studying naturally occurring variation in primate sociality for a number of years, employing multiple and diverse methodologies, with a focus on rhesus monkeys. These efforts have included use of instantaneous and scan sampling (to study the type and frequency of social and nonsocial behaviors) (Gunter et al., 2022; Kovacs-Balint et al., 2021; Parker et al., 2018), a personality rating instrument (to study variation in a personality dimension called Sociability) (Capitanio, 1999; Stevenson-Hinde et al., 1980), and a macaque-adapted version of a human instrument, the Social Responsiveness Scale (to study quantitative variation in social and autistic-like traits) (Constantino & Gruber, 2005, 2012; Feczko et al., 2016; Kovacs-Balint et al., 2021; Talbot et al., 2020, 2021). A consistent picture has now emerged showing that low-social monkeys initiate fewer affiliative interactions (Capitanio, 1999), spend less time in contact and grooming with conspecifics (Capitanio, 1999; Parker et al., 2018), and demonstrate deficiency in

species-typical social information processing (including face recognition and gaze aversion) compared to high-social monkeys (Capitano, 2002; Sclafani et al., 2016).

Naturally occurring low sociality in rhesus monkeys bears some similarity to the behavioral features observed in humans with autism spectrum disorder (ASD) (Parker, 2022). ASD is a neurodevelopmental disorder characterized by persistent social communication and interaction impairments (American Psychiatric Association, 2013; Maenner et al., 2020), which have been hypothesized to be motivational in nature (Chevallier et al., 2012; Dawson & Bernier, 2007; Itskovich et al., 2021). ASD remains poorly understood, in part, because there has been an overreliance on animal models which fundamentally lack the sophisticated cognitive and behavioral skills required to effectively model ASD symptoms. Naturally occurring low sociality in rhesus monkeys thus may represent a particularly compelling model by which to gain a better understanding of ASD's core social impairments, particularly if the low-social phenotype is found to be a characteristic that is stable within individuals and associated with diminished social motivation.

The present study therefore sought to better understand several aspects of naturally occurring variation in rhesus monkey social functioning. We first performed quantitative social behavior observations on monkeys housed in large outdoor groups to identify individuals at the behavioral extremes of our study sample (Study 1). Next, we quantified the rates and direction of transient visual social communication signals to assess group differences in social communication profiles (Study 2). Finally, in a subset of these monkeys, we assessed the within-individual stability of social functioning two years following our initial observation (Study 3). Given previous evidence that individual differences in social information processing abilities in infant rhesus monkeys predict later social classification (low-social versus high-social) (Sclafani et al., 2016), we hypothesized that social functioning would exhibit trait-like consistency over time. Although there is currently no systematic evidence regarding differences in the initiation and receipt of social communication behavior based on one's sociality as defined by behavioral frequencies, individuals with greater social impairment (as measured by the macaque Social Responsiveness Scale-Revised, or mSRS-R) have poorer Social Motivation factor scores (Talbot et al., 2021). Therefore, we hypothesized that low-social and high-social monkeys would differ in their social communication profiles, and specifically, that low-social monkeys would initiate (and possibly receive) less prosocial interaction. Finally, although dependent on context, low-social monkeys initiate more threats than high-social monkeys early in group formations and in response to videos depicting unfamiliar animals displaying affiliative and aggressive behavior (Capitano, 1999). Possibly due to these inappropriate social responses, low-social monkeys also experience a higher rate of traumatic injury than high-social monkeys (Myers et al., 2021). Thus, we hypothesized that low-social monkeys would initiate and receive a higher frequency of threat behavior compared to high-social monkeys.

2 | METHODS

2.1 | Subjects and housing

Subjects were $N = 95$ male rhesus macaques (*Macaca mulatta*) born and reared at the California National Primate Research Center (CNPRC). Selection criteria included: male, 1–7 years of age, socially housed in any of the 24 outdoor field corrals, medically healthy, not simultaneously enrolled in another CNPRC project, and previously enrolled in the CNPRC BioBehavioral Assessment Program as infants (Capitanio, 2021). All individuals that met these criteria were included in Study 1. Each subject lived in 1 of 15 outdoor, half-acre (0.19 ha) field corrals, measuring 30.5 m wide \times 61 m deep \times 9 m high. Each corral contained between 67 and 141 monkeys of mixed age and sex (see Table 1 for the distribution of subjects across corrals). Mean (SD) age of subjects was 3.72 (1.20) years with a range of 1.25–6.27 years at the time the study was initiated. Individuals were tattooed soon after birth and were periodically dye-marked to facilitate identification. Monkeys had ad libitum access to Lixit-dispensed water. Primate laboratory chow and seed mixture were provided twice daily, and fruit and vegetable supplements were provided once weekly. Various toys, swinging perches, along with outdoor social housing, provided a stimulating physical and social environment for all subjects.

2.2 | Behavioral assessment overview

For each of the three studies described below (see Figure 1 for study design), the following common elements applied, and are summarized here. All subjects were observed unobtrusively in their home field corrals. Observations were conducted during the nonbreeding season (a period which spans approximately from February through September at the CNPRC) to minimize the impact of mating activities on social behavior. Before conducting behavioral assessments, observers became reliable on data collection with 90% agreement (number of agreements divided by the [number of agreements + number of disagreements]) on all behavioral categories. To collect behavioral data for each study, a given observer watched, twice daily, a maximum of nine subjects, residing in one to three corrals. The order in which subjects were observed was randomized, and the same randomized order for a given assessment day was used in both morning and afternoon sessions. Once monkeys had been classified as low-social or high-social in Study 1 (see details below), observers were blinded to subjects' social classification while performing the two subsequent behavioral assessments.

2.3 | Study 1: Social classification

Subjects ($N = 95$) were observed between June and August of 2016. Each observer conducted 10-min focal samples on subjects in their home corrals during two observation periods per day (0830–1030 and 1045–1300), over eight nonconsecutive days, within a two-week observation period. We used instantaneous sampling (Altmann, 1974) in which we recorded, at 15-s intervals, whether the subject was engaged in any of the following behaviors: nonsocial (subject is not within an arm's reach of any other animal and is not engaged in play), proximity (subject is within an arm's reach of another animal), contact (subject is touching another animal in a nonaggressive manner), groom (subject is engaged in a dyadic interaction with one animal inspecting the fur of another animal using its

hands and mouth), or play (subject is involved in chasing, wrestling, slapping, shoving, grabbing, or biting accompanied by a play face [wide eyes and open mouth, without bared teeth] and/or a loose, exaggerated posture and gait; the behavior must have been deemed unaggressive to be scored) (Parker et al., 2018).

After completion of data collection, total frequency of nonsocial behavior was summarized across the 16 behavioral observations for a total of 160 min of observation time per subject. Monkeys were then rank ordered on frequency observed in nonsocial behavior. Frequency of nonsocial behavior followed a continuous, unimodal, normal distribution, and the normal distribution was the best fit to the data versus bimodal or skewed alternatives, as assessed by akaike information criterion (AICc) and Bayesian information criterion (BIC). Monkeys with the greatest frequency of nonsocial behavior were classified as low-social ($n = 20$), and monkeys with the lowest frequency of nonsocial behavior were classified as high-social ($n = 21$).

2.4 | Study 2: Group differences

To assess group differences in social communication profiles, we observed the low-social ($n = 20$) and high-social ($n = 21$) monkeys identified in Study 1 one year later, between June and September of 2017. As before, to account for time-of-day differences in behavior, the observer conducted focal samples on subjects during two observation periods per day (0800–1130 and 1230–1600), over eight nonconsecutive days, within a two-week observation period. During each focal sample, the subject was observed for 15 min. Throughout the 15-min focal sample, subjects' social behavior frequencies were continuously sampled. We designed our ethogram to quantify the rates of transient social communication signals, and whether the social signals were initiated by, or directed towards, the focal subject. These thus included initiation or receipt of proximity, contact, groom-presents, lip-smacks, fear grimaces, and threats (see Table 2 for detailed ethogram). After completion of data collection, the total behavioral frequencies were summarized across the 16 behavioral observations for a total of 240 min of observation time per subject. Behaviors that were difficult to record at a distance reliably (i.e., lip-smacks and fear grimaces) were omitted from further analysis.

2.5 | Study 3: Behavioral stability

To assess within-individual stability of social classification (low-social versus high-social), a subset of the monkeys observed in Study 2 were again observed one year later, between March and May of 2018. This sample included $n = 11$ low-social and $n = 11$ high-social monkeys that were available for study (i.e., were living in the same social group, medically healthy, and not enrolled in another CNPRC project). We employed the same methodology as in Study 1, except here we conducted a total of eight, 15-min observations, occurring over four nonconsecutive days in a one-week observation period for a total of 120 min of observation time per subject. The 11 individuals with the highest non-social behavior frequency were classified as low-social in 2018, and vice versa.

2.6 | Statistical analysis

All analyses were performed in JMP16 Pro for Windows. We first tested whether rank, age at observation, corral, and social classification status predicted nonsocial behavior using a general linear model (GLM). Because these models test for unique contributions of each effect, if, for example, rank was mediating the relationship between social classification status and nonsocial behavior, then rank would be significant, and social classification would not.

We then tested the degree to which nonsocial behavior was a trait-like characteristic (i.e., consistent across time), incorporating Study 1 and Study 3 data. To do so, we performed a GLM predicting nonsocial behavior frequency in Study 3 ($n = 22$), from nonsocial behavior frequency in Study 1. As our subsequent analyses for Study 2 relied on monkeys' social classification (low-social versus high-social), based on nonsocial behavior frequency in Study 1, we also used logistic regression to test whether social classification status in Study 1 predicted social classification status in Study 3, in these same $n = 22$ animals.

To test if low-social and high-social monkeys differed in initiation and/or receipt of social communication signals, in Study 2 we observed $n = 41$ of the monkeys classified in Study 1. We calculated the total counts of initiating versus receiving: (1) prosocial behavior (this included proximity, contact, and groom-presents which were all highly correlated and therefore combined into a single category), and separately, (2) threat behavior. We then analyzed these data with a restricted maximum likelihood repeated-measures mixed model, where the subject was nested within social classification (low-social versus high-social); behavior was coded by type (prosocial or threat) and direction (initiate or receive). Suitable subject interaction and nesting terms were included as random effects to calculate appropriate error terms for mixed models following (Littell et al., 2002; Newman et al., 1997). The third-order interaction of social classification \times behavior type \times behavior direction tests whether the behavioral counts differ overall between low-social and high-social animals. Given a significant finding, we then used custom tests to evaluate whether there were significant social classification \times behavior direction interactions for each behavior type, and if so, which behavior direction differed between low-social and high-social monkeys. These post hoc tests were Bonferroni corrected for multiple comparisons. Thus this “winnowing strategy,” by having gatekeeper tests at each stage, minimizes the number of tests performed, maximizing power while maintaining correction for multiple comparisons. The data were square-root transformed (as would be expected for approximately Poisson distributed data) to meet the assumptions of linear methods (homogeneity of variance, normality of error, and linearity; Grafen & Hails, 2002). The repeated measures approach uses each animal as its own control and thus inherently controls for confounds such as rank, age, and so forth (please see Supporting Information for step-by-step SAS code, accompanied by annotation of the analysis).

SUPPORTING INFORMATION

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

3 | RESULTS

Nonsocial behavior frequency was not significantly predicted by age ($F_{1,28} = 0.2614$; $p = 0.6132$), rank ($F_{1,28} = 0.2426$; $p = 0.6262$), or corral ($F_{1,28} = 0.3147$; $p = 0.9763$), but did differ by social classification ($F_{1,28} = 134.2887$; $p < 0.0001$), confirming that the potential confounds of age, rank, and corral were not driving nonsocial behavior frequency or social classification.

Nonsocial behavior frequency was significantly correlated in the $n = 22$ monkeys observed in Study 1 and Study 3 ($F_{1,20} = 6.464$; $p = 0.0194$; $r = 0.4942$). Similarly, low-social versus high-social classification in Study 1 predicted low-social versus high-social classification in Study 3 (LR-Chisq = 4.717; $p = 0.0299$; Accuracy = 73%; Table 3), demonstrating the trait-like consistency of this behavioral measure, both at the individual and group level.

Low-social versus high-social classification in Study 1 significantly predicted prosocial behavior in Study 2 ($F_{1,39} = 8.731$; $p = 0.0053$), such that prosocial behavior differed in direction (initiates and receives) between low-social and high-social monkeys ($F_{1,68.94} = 5.288$; $p = 0.0245$), but threat behaviors did not show the same interaction ($F_{1,68.94} = 1.075$; $p = 0.3035$). Further examination of prosocial behavior revealed that low-social monkeys initiated less prosocial behavior compared to high-social monkeys ($F_{1,117.6} = 7.2939$; $p = 0.0079$), but no difference was observed between low-social and high-social monkeys in prosocial behavior received ($F_{1,117.6} = 0.0186$; $p = 0.8918$) (see Figure 2).

4 | DISCUSSION

To advance our understanding of the low-social phenotype in an animal model of ASD, this study investigated the trait-like consistency of social functioning in rhesus monkeys and whether low-social monkeys differed in their initiation and receipt of social communication signals compared to high-social monkeys. We found that nonsocial behavior frequency (i.e., sociality) was stable across a two-year period, as evaluated both within-individuals and at the group (i.e., low-social versus high-social) level. In addition, low-social monkeys initiated less prosocial behavior than high-social monkeys, but no difference was observed in the receipt of prosocial behavior, suggesting that low sociality may be driven, at least in part, by a motivational deficit. Finally, these social communication differences were restricted to prosocial behavior, as low-social and high-social monkeys did not differ in the initiation or receipt of threat behavior.

Individuals commonly vary in their response to the same environmental and social stimuli, and this variation is often consistent. These individual differences in suites of correlated traits comprise a limited number of dimensions (often referred to as “personality”) that are surprisingly consistent across species (Capitanio, 2004; Gosling, 2001). As noted above, humans and rhesus monkeys exhibit pronounced individual differences in social functioning (Chan et al., 2017; Constantino & Gruber, 2012; Constantino et al., 2007; Talbot et al., 2020). The present study extended these findings in rhesus monkeys to show that an individual’s sociality, as measured by behavioral frequencies, is a trait-like characteristic similar to prior findings on the personality dimension, Sociability, using a

rating methodology. In fact, we have previously found strong correlations between nonsocial behavior frequency and ratings-derived Sociability scores (Parker et al., 2018; Talbot et al., 2021), suggesting that these two measures are tapping into the same underlying construct. In rhesus macaques, Sociability is stable across time and predicts behavior in situations different from the one in which the dimension was originally derived, up to four and a half years later (Capitanio, 1999; Capitanio & Widaman, 2005). Together, these findings suggest that degree of social engagement, broadly construed, is a characteristic of individuals that is consistent over time and across measurement tools.

The finding that low-social monkeys selectively initiate less prosocial communication behavior adds to our growing understanding of naturally occurring low sociality in this species. Prosocial behavior is a distinctive feature of nonhuman primates' social lives. Despite rhesus macaques' despotic society, they, too, display prosocial tendencies as evidenced by policing (Beisner & Mccowan, 2013), reconciliation behavior (de Waal & Yoshihara, 1983; de Waal & Ren, 1988), and sharing of resources (Dubuc et al., 2012). In the current study, we found that low-social monkeys initiated less proximity, contact, and groom-presents compared to high-social monkeys. In contrast, we found no group differences in prosocial behavior received. The lack of initiation of social interactions by low-social monkeys seems to suggest an underlying deficit in social motivation. This interpretation is consistent with our prior findings showing that the primary psychological factor underlying the mSRS-R is Poor Social Motivation, and higher scores on Poor Social Motivation (indicating greater social impairment) were strongly associated with nonsocial behavior frequency (Talbot et al., 2021).

People with ASD likewise exhibit diminished social interactions and communication. These social impairments manifest differently based on distinct patterns of social behavior, from which three ASD subtypes have been identified and studied, including aloof, passive, and active-but-odd (Beglinger & Smith, 2001; Wing & Gould, 1979). The aloof subtype represents individuals with severe social impairment and includes individuals who rarely initiate social interactions with others (except to satisfy needs) and tend to reject social approaches from others. The passive subtype also includes individuals who rarely initiate social interactions with others, but accept social approaches and can be led to participate in group activities in a passive role. In contrast, the active-but-odd subtype includes individuals who initiate spontaneous social approaches to others, but these interactions are often one-sided and individuals often exhibit inappropriate social behavior (Wing & Gould, 1979). In the current study, our finding that low-social monkeys initiate but do not receive fewer prosocial interactions is similar to the passive ASD subtype in which individuals exhibit impaired motivation to initiate social contact but may passively respond to social overtures. Indeed, the idea that lack of social motivation plays a key role in many ASD cases has gained increasing attention over the past two decades and has led to the development of the "social motivation hypothesis of ASD." Namely, individuals with ASD tend to have deficits in social reward processing which can cause diminished social orienting, lack of social initiation, and difficulty in fostering and maintaining social bonds (Chevallier et al., 2012; Dawson & Bernier, 2007). Further research is now warranted in a larger cohort of naturally low-social monkeys to determine whether they, too, exhibit distinct social engagement

subtypes. If so, this could provide a fruitful avenue for examining biobehavioral profiles underlying variation in social motivation relevant to ASD.

Although the biological underpinnings of motivated social behavior in primates are not well understood, emerging evidence suggests a role for the arginine vasopressin (AVP) signaling pathway (Parker, 2022). For example, deletion variants in the promoter region of the AVP receptor 1A-encoding gene may underlie within and between species differences in social personality, bonding, and response to social cues in chimpanzees and bonobos (*Pan paniscus*) (Anestis et al., 2014; Hopkins et al., 2014; Staes et al., 2014, 2015, 2016). In rhesus macaques, cerebrospinal fluid (CSF) AVP concentration is strongly associated with time spent in dyadic grooming (Parker et al., 2018), as well as quantitative social trait variation (as measured by mSRS-R scores) (Oztan et al., 2021). Pharmacological studies have further implicated a role for AVP in primate prosocial functioning, as AVP administration improves behavioral synchrony in rhesus monkeys (Jiang & Platt, 2018), and enhances cooperative behavior and social communication abilities in humans (Brunnlieb et al., 2016; Rilling et al., 2012; Thompson et al., 2004). Given that low CSF AVP concentration is associated with both low sociality in rhesus monkeys and ASD in humans (Oztan et al., 2018, 2020; Parker et al., 2018), low sociality in monkeys may be a useful construct for gaining mechanistic insight into the social motivational deficits found in people with ASD (Chevallier et al., 2012).

It is somewhat surprising that we did not find any difference in threat behavior between low-social and high-social monkeys, especially since negative correlations have been reported between Sociability (as a ratings-derived personality characteristic) and threats initiated (Capitanio, 1999). The situations in which those prior relationships were found, however, were always in situations of challenge—in response to a video playback, or during the initial stages of a group formation. No relationship between Sociability and threats has been found in stable social situations, such as in the animals' natal groups (Capitanio, 1999), and as also studied in the present report. It is possible that, in an environment in which one's companions are relatively well-known, other mechanisms, such as avoidance, may mitigate the very real social deficiencies that have been demonstrated by low-social individuals (Capitanio, 1999, 2002; Capitanio et al., 2008). Nevertheless, in times of challenge, even in a familiar social environment, these social deficiencies may manifest themselves to an extent resulting in injury—as we have previously found (Myers et al., 2021). Clearly, more work is needed to understand the underlying psychological components of low sociality, and the contexts in which those components create social problems (and potential injuries) for the animals.

This study had several limitations that warrant discussion. First, in keeping with our broader goal of modeling ASD, which is male-biased in prevalence (Maenner et al., 2020), our sample was restricted to male rhesus macaques. Thus, whether these findings generalize to female monkeys remains to be determined. Second, we were unable to ascertain more nuanced social communication signals such as lip-smacks and fear grimaces in the large outdoor field corrals. These nuanced signals were challenging to capture in such a large space with a limited number of observers. Finally, we do not know the mechanics of how low-social and high-social animals interact with others—when a solicitation is made toward

an animal, the high-social animal may respond accordingly. But what does the low-social animal do—does it ignore the solicitation, walk away from it, or threaten the other animal? It thus would be ideal for future studies to take a transactional approach to ethological observations on low-social animals to better deduce underlying motivational components of their behavioral repertoires (Mason et al., 1980; Parker et al., 2006).

In conclusion, our findings add to the growing behavioral taxonomy of naturally occurring differences in rhesus monkey sociality. Specifically, we found that sociality is a stable trait-like characteristic, associated with variation in the initiation of social interactions, particularly prosocial behavior. As such, naturally occurring low sociality may be a valuable construct by which to understand the social deficits that characterize ASD. Additionally, research is now needed to better understand exactly why this wide natural variation in one's ability to attend to, process, and respond appropriately to social information exists, particularly in highly social species, and what underlying psychological and biological mechanisms govern this motivated behavioral variation.

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DATA AVAILABILITY STATEMENT

The data analyzed in the current study are available from the corresponding authors upon reasonable request.

ACRONYMS:

AICc	akaike information criterion
ASD	autism spectrum disorder
AVP	arginine vasopressin
BID	Bayesian information criterion
CNPRC	California National Primate Research Center
CSF	cerebrospinal fluid
GLM	general linear model
mSRS-R	macaque Social Responsiveness Scale-Revised

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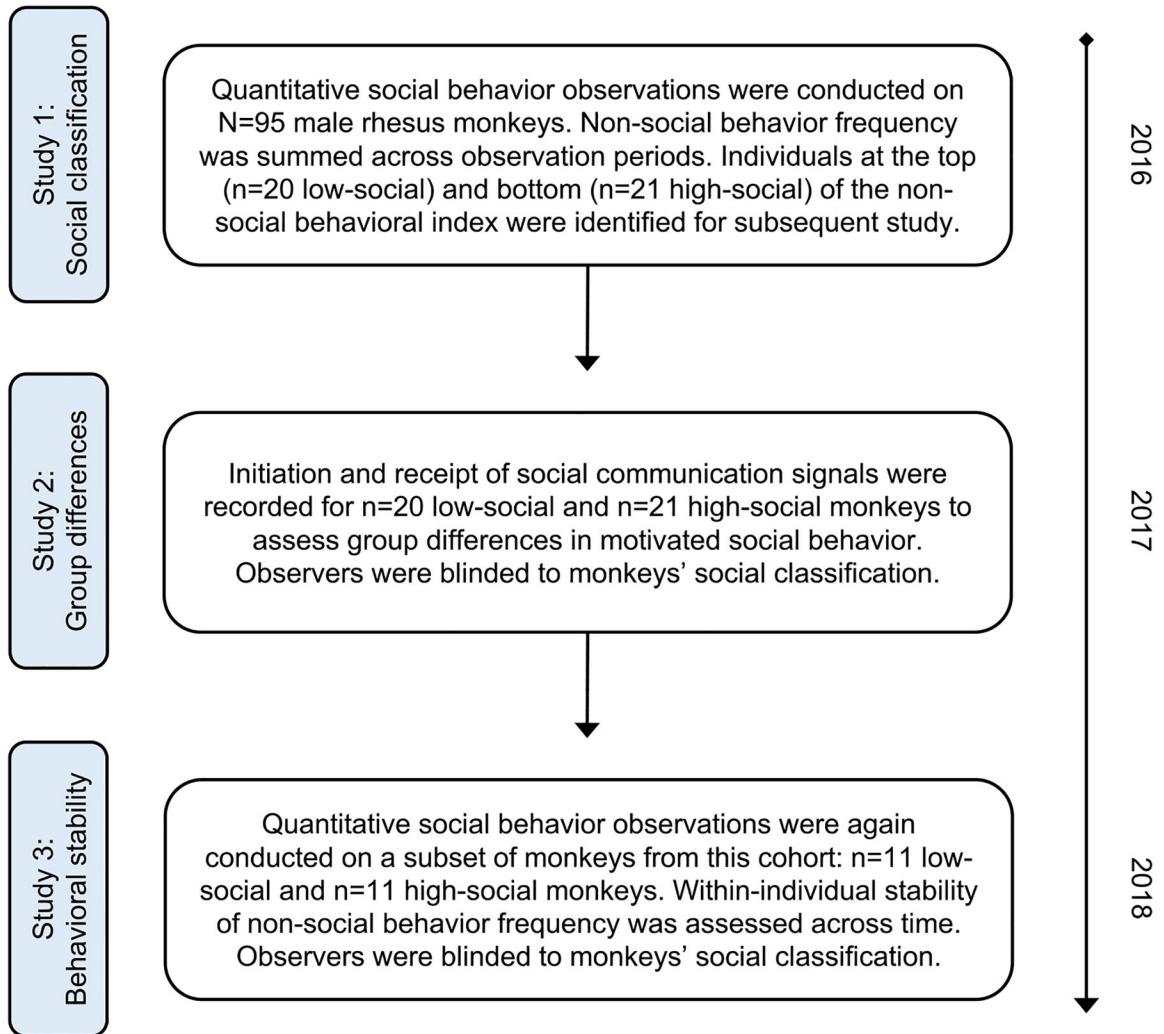


FIGURE 1.

Flow diagram of study procedures. The flow diagram details the progress from social classification (Study 1) through evaluation of group differences in social communication profiles (Study 2) and assessment of behavioral consistency in sociality at the individual and group levels across time (Study 3).

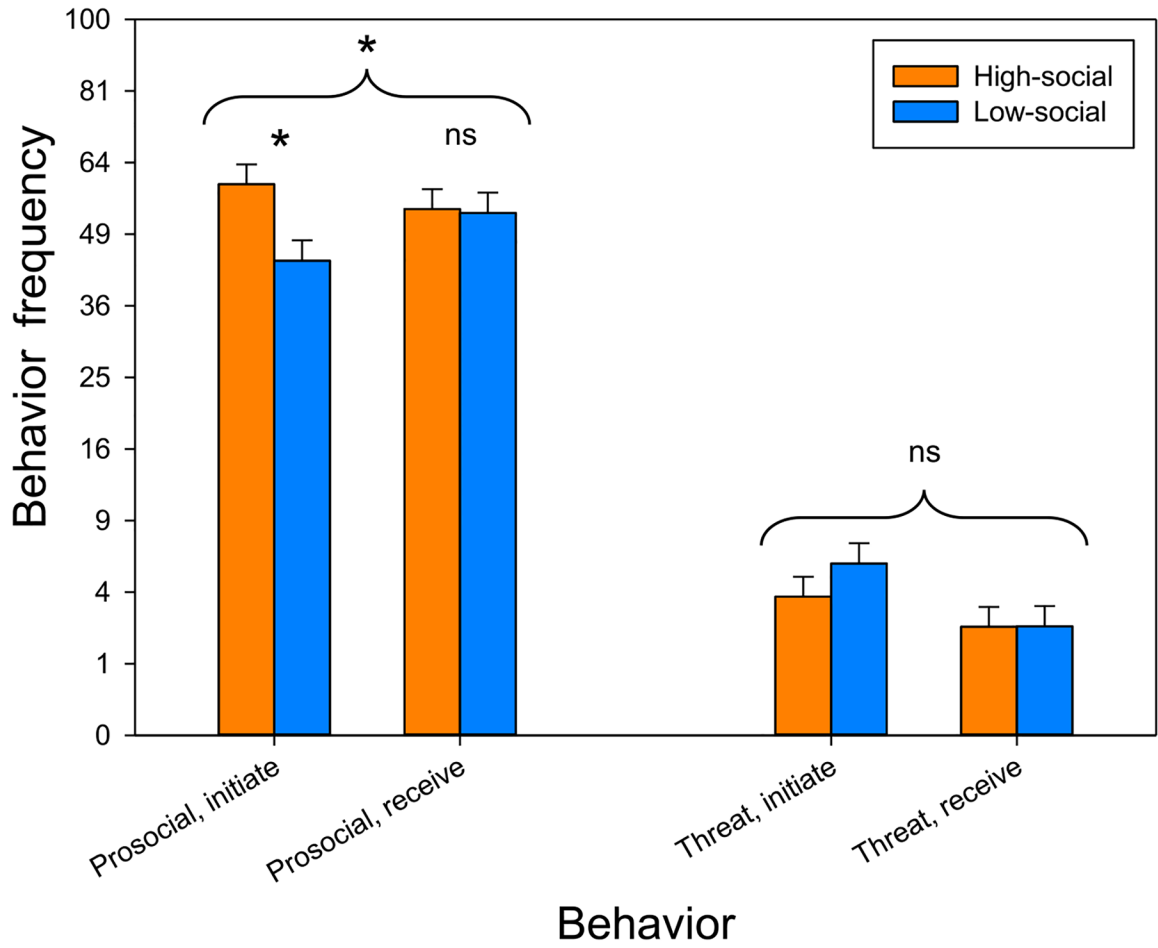


FIGURE 2. Naturally occurring differences in rhesus monkey sociality are linked to variation in social communication profiles. Low-social male rhesus monkeys ($n = 20$) initiated significantly less prosocial behavior than high-social male monkeys ($n = 21$) but did not differ from high-social monkeys in receipt of prosocial behavior. This motivated behavior effect was specific to the prosocial behavior domain, as low-social and high-social monkeys did not differ in threat behavior, either initiated or received. Data were square root transformed for analysis. $LSM \pm SEM$ is plotted.

TABLE 1

Distribution of study subjects across the 15 outdoor field corrals

Corral	Study 1	Study 2		Study 3	
	All subjects	Low-social	High-social	Low-social	High-social
A	4	1	1	1	1
B	6	0	0	0	0
C	4	0	2	0	0
D	6	2	2	1	1
E	7	0	0	0	0
F	17	2	6	2	3
G	1	0	0	0	0
H	10	3	3	1	2
I	10	0	0	0	0
J	4	4	0	2	0
K	9	1	5	0	2
L	5	3	1	1	1
M	3	2	0	1	0
N	4	1	1	1	1
O	5	1	0	1	0
Total	<i>N</i> = 95	<i>n</i> = 20	<i>n</i> = 21	<i>n</i> = 11	<i>n</i> = 11

Note: The columns detail the number of subjects initially observed for social classification in Study 1 ($N = 95$), the number of individuals classified as either low-social ($n = 20$) or high-social ($n = 21$), which were then evaluated one year later for group differences in social communication profiles in Study 2, and the number of individuals that were assessed for behavioral consistency in sociality in Study 3 at the individual and group levels two years after the initial assessment.

TABLE 2

Study 2: Ethogram for assessment of social communication signals

Behavior	Description
Proximity (i/r)	The core region (i.e., head, trunk, thighs, upper arms) of the focal subject is within an arm's length radius of a conspecific
Contact (i/r)	Physical, nonaggressive touch observed between the focal subject and a conspecific involving the core region (i.e., head, trunk, thighs, upper arms)
Groom-present (i/r)	Exaggerated and rigid presentation lasting several seconds of an animal's head, neck, ventrum, dorsum, or flank at the beginning or within a grooming bout between the focal subject and a conspecific
Lipsmack (i/r)	Rapid lip movement accompanied by a smacking sound demonstrated between the focal subject and a conspecific
Fear grimace (i/r)	Exaggerated grin prominently displaying the teeth and demonstrated between the focal subject and a conspecific
Threat (i/r)	Agonistic signals demonstrated between the focal subject and a conspecific which include the following: open-mouth stare, head-bobbing, grunts, and lunges

Note: Behavior frequencies were continuously sampled over each 15-min observation period. i = focal subject initiated the behavior, r = focal subject received the behavior.

TABLE 3

Study 1 and Study 3: Social classification is stable across two years

Study 3	Study 1	
	Low-social	High-social
Low-social	8	3
High-social	3	8

Note: Social classification (low-social versus high-social) in Study 1 predicted social classification in Study 3 with 73% accuracy. The confusion matrix reports the number of individuals that were true positives, $N = 8$ low-social, and true negatives, $N = 8$ high-social, and the number of individuals that were misclassified ($N = 3$) from each group out of the $N = 11$ low-social and $N = 11$ high-social monkeys originally classified in Study 1.

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