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# Personality Assessment of Synanthropic Rhesus Macaques: Implications and Challenges

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## ABSTRACT

Answers to the question of what characteristics allow animals to thrive in human-dominated environments remain elusive. Consistent interindividual differences or personalities can potentially explain the functional significance of habitat-specific traits that enable animals to coexist with humans. Rhesus macaques (*Macaca mulatta*) are the most successful nonhuman primates in the Anthropocene, living in diverse climatic and environmental conditions. Studying the personalities of *synanthropic* rhesus macaques, that is, those that thrive in anthropogenic habitats, can provide insights into the biological traits facilitating their success. We planned a multi-method "bottom-up" approach of behavioral observations and novelty experiments, standardized for assessing captive nonhuman primates, to evaluate the personalities of adult rhesus macaques ($N = 52$). Novelty experiments encountered significant challenges, limiting their effectiveness. So, we continued with behavioral observations in the form of focal sampling, that revealed two repeatable traits, subjectively labeled as *social tension* and *meekness*. We found an association of sex with social tension, where males exhibited higher social tension than females. In an additional analysis, we found that individuals that obtained food through contact provisioning had higher scores for the meekness trait than individuals that obtained food through noncontact provisioning. We discuss how the observed personality traits may offer adaptive advantages in human-dominated environments, where despotic rhesus macaques face both benefits and costs (including social) of living in an anthropogenic setting. We also emphasize that protocols designed for captive conditions may not be directly applicable to free-living animals. The study underscores the need to reconsider behavioral experiments to obtain comparable measures between captive and non-captive populations. This would enhance the ecological validity of personality assessments. Nevertheless, empirically identifying traits using observations in synanthropic species can provide valuable insights into the mechanisms that enable certain animals to thrive amidst a rapid expansion of anthropogenic activities.

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**Abbreviations:** KNR, Kamla Nehru Ridge Biodiversity Park; MSCA-IF, Marie Sklodowska-Curie Actions Individual Fellowship; PCA, principal component analysis; UGC, University Grants Commission.

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**Summary**

- Studying personalities of synanthropic animals can shed light on the biological traits that help them thrive in human-dominated environments.
- A "bottom-up" multi-method approach, standardized for assessing captive nonhuman primate personalities, was used to study a population of synanthropic rhesus macaques.
- Behavioral observations yielded two repeatable traits, namely *social tension* and *meekness*, where comparatively more meek individuals obtained food through contact provisioning. Novelty experiments faced significant challenges.

## 1 | Introduction

Anthropogenic activities (e.g., urbanization, deforestation, land encroachment, industrial activities, and agricultural expansion) have intensified in recent years, breaking down the barriers that separate humans and wildlife (Dirzo et al. 2014). One of the critical questions remains: what makes some animals thrive in human-dominated environments? Considerable scientific advancements have been made in addressing this question, like the presence of behavioral plasticity in animals (Sih et al. 2004), yet answers are inconclusive. In contrast to the view of behavioral plasticity, personality or consistent interindividual differences suggest that behavioral responses are rather "non-flexible" and are somewhat constrained (Réale et al. 2007; Réale et al. 2010). Although the extent to which biological traits have plasticity is an ongoing topic of research (Dingemanse et al. 2010), interindividual differences in the phenotypic expression of specific traits and their variations can potentially explain the "selective" advantages with regard to specific environmental conditions and habitats (Belgrad and Griffen 2018; Leclerc et al. 2016; Santicchia et al. 2018). Due to the associations of personality traits with adaptive and survival benefits (Moiron et al. 2020; Smith and Blumstein 2008), studying these traits and their variations in animals living close to humans can provide insights into their potential functional advantages.

Several nonhuman primates have been coexisting in and around human settlements, but rhesus macaques are the most successful species in the Anthropocene (Cooper et al. 2022). Rhesus macaques are adapted to a wide range of climatic (from temperate to tropical) and environmental (from mountainous and forested to semi-deserts and swamps) conditions (Cooper et al. 2022). Likewise, their geographical range covers Central, South, and Southeast Asia (Brandon-Jones et al. 2004). In human-dominated environments, rhesus macaques may thrive as a *synanthropic* species (Klegarth 2017). Synanthropic animals may benefit from humans, both indirectly (such as by utilizing anthropogenic subsidies and experiencing low to no natural predation pressure) as well as directly (such as by getting provisioned) (McLennan et al. 2017). However, there are costs, too. Synanthropes are exposed to anthropogenic stressors (such as noise pollution and conflict with humans) that can impact their survival (Ilham 2024; Marty et al. 2020). For instance, empirical studies have shown that interactions with humans can directly influence the social networks and behavioral dynamics of animals living in human-dominated environments (Bhattacharjee and Bhadra 2020; Bhattacharjee and Bhadra 2021; Balasubramaniam et al. 2021; Lowry et al. 2013; Kaburu et al. 2019). Nonetheless, despite the trade-offs, rhesus macaques have successfully coexisted with humans (Cooper et al. 2022). Therefore, assessing the personalities of synanthropic rhesus macaques can expound on the biological traits and their variations that potentially help them thrive in human-dominated environments.

The study of animal personality has advanced considerably in the last two decades, encompassing taxa ranging from insects to mammals, including nonhuman primates. In particular, for nonhuman primates, testing environments vary, such as captive and free-ranging living conditions and existing social settings or isolation from social groups. Whereas captive animals can be tested in existing social settings or in isolation, and researchers have discussed the trade-offs (*sensu* ecological validity) (Koski 2011; Koski and Burkart 2015; Šlipogor et al. 2016), free-living conditions typically do not allow testing animals in isolation. Besides, testing gregarious species in their natural social setting may have advantages in terms of ecological relevance. There are also methodological differences, ranging from questionnaire-based ratings to observational and/or experimental approaches (Freeman et al. 2011; Koski 2011; Massen et al. 2013; Šlipogor et al. 2016). Although each method has advantages and disadvantages (Freeman et al. 2013; Šlipogor et al. 2020; Vazire et al. 2007), the combined multi-method approach of behavioral observations and experiments is utilized less. It has been highlighted that observations and experiments as standalone methodologies may provide evidence of unrelated and independent personality traits (Martinig et al. 2022). Therefore, a multi-method approach can comprehensively reveal consistent salient and 'rare' traits (Bhattacharjee et al. 2024a; Campbell and Fiske 1959; Kluiver et al. 2022).

Rhesus macaques have been studied for their personalities predominantly using questionnaire-based ratings and observational approaches in both socially housed captive settings and natural free-ranging populations (Adams et al. 2015; Altschul et al. 2019; Kohn et al. 2016; Robinson et al. 2018; Sussman et al. 2013; von Borell et al. 2016). In previous studies, traits like *sociability/friendliness*, *confidence*, *dominance*, *openness*, *anxiety/equable/excitable*, and *activity* were identified (Capitanio 1999; Capitanio and Widaman 2005; Weinstein and Capitanio 2008; Robinson et al. 2018; Simpson et al. 2019; Weiss et al. 2011). Some of these traits were found to be associated with dominance status (Kohn et al. 2016), social style (Adams et al. 2015; Sussman et al. 2013), health and welfare (Robinson et al. 2018), and facial dimensions (Altschul et al. 2019). In the current study, we implemented a multi-method "bottom-up" approach standardized for assessing captive nonhuman primates (Bhattacharjee et al. 2024a; Kluiver et al. 2022) to determine the personalities of synanthropic rhesus macaques. The bottom-up approach involves extracting trait structure pertaining to variability after considering an assortment of behaviors (Vonk and Eaton 2018). Our multi-method approach included continuous focal observations and novelty experiments (novel objects, novel food items, food puzzles, predator model exposure; cf. Bhattacharjee et al. 2024a; Kluiver et al. 2022; Massen et al. 2013) conducted in macaques' social and free-living environmental conditions. While several studies have examined the personalities of nonhuman primates in the wild (Arnaud et al. 2016; Bergvall et al. 2011; Blaszczyk 2017; Carter et al. 2014; Forss et al. 2015; Neumann et al. 2013; Pritchard et al. 2014), little is known about the personalities of synanthropic nonhuman primates and how they predict species social dynamics as well as inter-specific interactions with humans (Pritchard et al. 2024).

Due to the "bottom-up" nature of the methodology, informed predictions on personality traits were challenging to make. However, given the despotic social style, steep linear hierarchies, and frequent aggressive interactions in rhesus macaques (Thierry 2000), we expected to find traits like tension and submissiveness that previous observational studies have reported (Adams et al. 2015; Bolig et al. 1992; Brent et al. 2014; Capitanio 1999; Capitanio and Widaman 2005; von Borell et al. 2016; Weiss et al. 2011). In addition, the matrilineal hierarchical system of rhesus macaques fosters strong social associations among philopatric females (Sterck et al. 1997). Thus, we expected traits like openness and sociability to be present, with females showing higher openness or sociable tendencies than males. In line with previous studies, based on the novelty experiments, we expected to observe traits like exploration or persistence, and boldness (Arnaud et al. 2016; Bhattacharjee et al. 2024d Carter et al. 2014; Forss et al. 2015; Nord et al. 2022). Although synanthropic animals are well-adapted to human-dominated environments, they may still experience a "landscape of fear" (Gallagher et al. 2017), where traits like vigilance and cautiousness are expected to play a significant role. Finally, because engaging in interactions with humans, such as acquiring food directly, requires a potentially high cost of initiating interactions (Jaman and Huffman 2013), we expected bolder individuals to interact more with humans than shy individuals in the events of interspecific interactions. However, the last prediction was not part of our initial study design, and we conducted a post-hoc analysis to examine this relationship.

## 2 | Materials and Methods

### 2.1 | Study Site and Subjects

We conducted the study at the Kamla Nehru Ridge Biodiversity Park (KNR) (28°40′50"N, 077°13′01"E) in North Delhi, India. KNR is a part of the highly weathered Aravalli hill range and is spread out across an 87-hectare area surrounded by motorable roads and dense urban residential areas. The flat hilltops and relatively shallow valleys give the area an undulating topography. The natural vegetation resembles that of tropical dry and mixed deciduous forests. A major biodiversity reintroduction and restoration drive is in place to eradicate 'invasive' species like the Mexican weed *Prosopis juliflora*. In KNR, five water bodies are present. People use KNR as a walking park, and the area is known to attract tourists due to its striking biodiversity profile (Sinha 2014). Among the fauna, free-living rhesus macaques are present (Figure 1). However, comprehensive information on the population size and other demographic properties, like age and sex, is unavailable. The macaques are provisioned daily by local people (Supporting Information S1: Figure S1), typically between 9 AM and 11 AM (T.G., personal observations, 2021–2022). We chose a group randomly with an estimated size of 100, including 52 adults and ~48 juveniles. We sampled all 52 adults (female = 43, male = 9) from the group for the current study. We selected only adults as correctly identifying and sampling sub-adults or juveniles in a free-ranging population is challenging without long-term monitoring.

### 2.2 | Data Collection for Personality Assessment

We aimed to use a standardized multi-method bottom-up approach of behavioral observations and novelty experiments to assess personality (Bhattacharjee et al. 2024a; Campbell and Fiske 1959; Kluiver et al. 2022; Koski 2011; Massen et al. 2013). The study lasted between early November 2021 and late July 2022. The first 4 months (November 2021–February 2022) included identifying individuals using facial features and scars, as well as habituation of the group to the experimenters.

#### 2.2.1 | Behavioral Observations

Twenty-minute-long continuous focal observations were conducted following an extensive ethogram (Supporting Information S1: Table S1). The ethogram consisted of 87 behaviors, state (durational), and point (frequency) behaviors (which became 110 after including the passive behaviors, that is, behaviors where a focal individual was the recipient). During focal observations, we also collected data on human-macaque interactions with regard to obtaining food through contact and noncontact provisioning (cf. Table 1). Observations were performed 5 days a week at different times of the day between 9 AM and 5 PM using a pseudo-randomized order, such that an individual was not observed more than once on the same day or two consecutive days. After correcting for the time individuals were out of sight, a total of 5560 min of observational data were obtained (mean ± standard deviation = 107.68 ± 21.22 min per focal individual). Thus, it is important to note that the mean observation time per individual may be relatively low. Nonetheless, the data set included a relatively large number of individuals, ensuring a broad population-level representation. To investigate temporal consistency, focal data were split into two approximately equal nonoverlapping phases (cf. Bhattacharjee et al. 2024a; Bhattacharjee et al. 2024b; Kluiver et al. 2022). The first phase consisted of data collected until April 2022, and the second phase included data collected between May and July 2022. All focal observations were filmed by a handheld Sony HDR-CX405 HD video camera.

#### 2.2.2 | Novelty Experiments

The experimental approach followed the standardized protocol for testing captive nonhuman primates (see Bhattacharjee et al. 2024a; Kluiver et al. 2022; Koski 2011; Massen et al. 2013). The standardized behavioral experiments used to measure personality rely on predetermined variables such as engagement duration, approach latency, number of manipulations, and proximity duration. This can assist in quantifying traits such as exploration, persistence, and boldness, which are difficult to measure through

**FIGURE 1** | Synanthropic rhesus macaques at the Kamla Nehru Ridge Biodiversity Park, New Delhi, India. (a) Some individuals from the study population, along with a free-ranging dog (b) Rhesus macaque presence in human-dominated environments in the study area. [Photo credit: Taniya Gill, 2022].

**TABLE 1** | The rotated principal components or rhesus macaque personality traits with variable loadings and their percentages of variance, and percentages of attribute communalities of the behavioral variables.

| Variables | Social tension | Meekness | % Communalities |
|---|---|---|---|
| Look around | **0.87** | −0.10 | 72.99 |
| Approach | **0.81** | 0.12 | 71.99 |
| Avoid | −0.12 | **0.91** | 79.30 |
| Attention | 0.30 | **0.70** | 67.86 |
| **% Variance** | 38.20 | 33.60 | |

*Note:* Variable loadings of > ± 0.5 are in bold.

behavioral proxies from focal observations. For each experimental category, two types of objects/food items/puzzles/predator models were used on different days to assess contextual consistencies in behavior (cf. Bhattacharjee et al. 2024a; Kluiver et al. 2022; Koski 2011; Massen et al. 2013). Furthermore, for each type of experiment, except for the predator models, we provided multiple novel objects of the same type to avoid monopolization by dominant individuals. Experiments were conducted within the existing social group setting of the macaques in a pseudo-randomized order, ensuring that the same category tests were not repeated consecutively. We recorded all the experiments with a video camera at least 20 m from the experimental setups. Focal observations were not conducted on the days of novelty experiments.

The novel objects were - (i) a hanging setup of glossy compact discs (CDs) and (ii) rubber toys. None of these objects contained food items inside. For the first object, a 230 cm long single string was threaded through 15–16 CDs (CD diameter = 12 cm). The two ends of the string were then tightly attached to existing structures (like wooden logs of park boundaries). We installed two such structures at distant locations approximately 120 cm above ground for the macaques to inspect and interact with (Supporting Information S1: Video S1). For the latter, locally made blue and red colored fish-shaped rubber toys were used (Supporting Information S1: Video S2). The rubber toys had a length of 7.6 cm and identical appearances. We provided five rubber toys to the macaques. The experimenter left the area after installing or placing the novel objects within a short duration (< 10 s). The tests were filmed for 60 min after the placement of objects.

Novel food items were selected by observing macaques' foraging activity (including provisioned items). We used gooseberries and kiwi as novel food items. As kiwi fruits are larger than gooseberries, we cut kiwi fruit into small pieces. Approximately 50 units or pieces of each food item were placed in an open area clearly visible to the macaques to avoid potential monopolization. After placing the food items on the ground, the experimenter left the area. We filmed the tests until all food items were eaten or for 60 min.

Two types of food puzzles were used–(i) a wooden maze box and (ii) a rotating plastic bottle. We installed three wooden maze boxes (60 cm × 12 cm × 60 cm) approximately 80 cm above ground at distant locations in the study area. The boxes had plexiglass fronts with strategic openings where individuals could insert their fingers to move tomatoes (8–10 intact tomatoes) placed inside (Supporting Information S1: Video S3). The tomatoes could be retrieved by moving them in a specific direction through a larger opening. Like the wooden maze box, we installed three rotating bottles of 50 cm lengths at different locations. Each bottle was loaded with two handfuls of chickpeas and had 28 holes of 2.5–3 cm diameter on one side. The bottles were horizontally placed using tightly attached ~200 cm strings, approximately 170 cm above ground. Originally, the holes were on the upper sides, but individuals could obtain the chickpeas through the holes by rotating and holding (often shaking) the bottles (Supporting Information S1: Video S4). The strings were attached in a way such that the bottles returned to their original positions (i.e., holes on the upper side) once individuals let go. After installing the puzzles, food items were loaded within 1 min, and the experimenter left the area. We filmed the tests until all food items were retrieved or for 60 min. For predator exposure experiments, we used snake and tiger models, which are known to elicit antipredator responses in macaques (Etting and Isbell 2014; Maestripieri 2010; van Dijk et al. 2023). A rubber snake model (~72 cm in length) with patterns resembling an Indian cobra was placed on a narrow path (Supporting Information S1: Video S5), which the study group frequently uses. The tiger model was a 108 cm-long plush toy in a sitting posture with patterns resembling a tiger (Supporting Information S1: Video S6). The tiger model was placed in the same position where the snake test took place. Unlike other experiments, each predator exposure experiment lasted for 30 min.

We intended to repeat the novelty experiments to test temporal consistencies in behavior; however, we found low participation rates and, therefore, decided not to do so.

## 2.3 | Data Coding

Focal and experimental videos were coded using Eudico Linguistic Annotator (ELAN) (version 6.2, 2021). We followed the ethogram provided in Supporting Information S1: Table S1 to code the focal observational data. Of the 87 behaviors described in the ethogram, 35 were exhibited by at least 30% (16 individuals) of the subjects. To avoid potential overestimation and/or skewness, we discarded behaviors with low occurrences across both phases (i.e., exhibited by < 30% of the individuals). The 35 retained variables were corrected for the varying observation durations of the individuals, and their rates were calculated (seconds per minute for durational variables and frequency per minute for event behaviors). The standardized values of these variables were used in the analyses. From the novelty experiments, we coded the following parameters–latency to approach (novel objects, novel food items, food puzzles, and predator models), duration in proximity (novel objects, food puzzles, and predator models), number of approaches (predator models), duration of handling (novel objects), duration of manipulation (food puzzles), and eating (novel food items and food items from puzzles). See Supporting Information S1: Table S2 for definitions of these parameters. T.G. coded all data, and D.B. coded ~15% of the total data (including focal observational and novelty experimental data) to check for reliability using Intraclass correlation tests (ICC). The overall reliability score was high (ICC (3,k) = 0.94, $p < 0.001$). We also checked the coder reliability using each focal observational behavior and dependent variable from novelty experiments (excluding the ones with low occurrences). The ICC values ranged between 0.35 and 1 (see Supporting Information S1: Table S3), indicating sufficiently high agreements. Due to low and inconsistent participation rates, we did not include dependent variables from the novelty experiments (such as latency to approach novel objects/food puzzles/predator models, number of approaches to predator models, time in proximity to novel objects/food puzzles/predator models, manipulation time for novel objects, and eating novel food items; cf. Supporting Information S1: Table S2) in the statistical analyses. Therefore, we limited our assessment of personality exclusively to the focal observational data.

## 2.4 | Statistical Analyses

Statistical analyses were performed in R (version 4.3.0) (R Core Team 2022). The repeatability of the 35 standardized behavioral variables between the two phases was assessed using ICC (3,1) (ICC value > 0.2), that is, a two-way mixed model intraclass correlation test (Lessells and Boag 1987; McGraw and Wong 1996). In the next step, we calculated the mean values of the repeatable behavioral variables between the two phases and standardized them. Principal components analysis (PCA) was conducted using the mean values of the repeatable variables. We checked whether the overall Kaiser-Meyer-Olkin sampling adequacy (MSA) value (cut-off = 0.6) and attribute communality values (cut-off = 60%) were high enough (Hadi et al. 2016). In case the values were below their cut-offs, the corresponding behavioral variables were identified, and a step-by-step process further reduced the number of variables until the cut-offs were crossed (cf. Bhattacharjee et al. 2024a, 2024b; Kluiver et al. 2022). Once these criteria were met, a scree plot was generated based on an unrotated PCA, and the eigenvalue of each principal component (PC) was inspected. The number of PCs was decided depending on the eigenvalues (eigenvalue cut-off = ≥ 1) and by visual inspection of the scree plot. Additionally, we performed an automated model selection procedure. We computed Bartlett's sphericity test for correlation (Bartlett 1950). As personality traits can correlate with each other and form behavioral syndromes, we used an oblique rotation technique (direct oblimin) and checked the correlation coefficients using the phi matrix value. The component loadings $\geq |0.5|$ were considered salient (Budaev 2010). From each PC, individual factor scores (synonymously personality scores) were obtained following a regression method.

Both ICC and PCA were run using the *psych* package (Revelle and Revelle 2015). The PCA was performed using the "principal" function. The automated selection of PCs was checked using the "fa.parallel" function. We conducted linear models (LM) using the *glmmTMB* package to investigate the association of sex with personality (Brooks et al. 2017). We constructed separate models (depending on the number of personality traits) with Gaussian error distributions with "identity" link functions. Linear model diagnostics were investigated using the "testResiduals" function of the *DHARMa* package (Hartig 2020). Null versus full model comparisons were done using the "lrtest" function from the package *lmtest* (Zeileis and Hothorn 2002). We used a Bayesian elo-rating method for assessing the dominance rank relationships (Neumann and Fischer 2023). The significance value ($\alpha$) was set at 0.05 for all statistical analyses.

### 2.5 | Additional Analyses of Dominance Rank Relationships

We found 63 cumulative instances from three behavioral variables: *being displaced*, *fear grimace*, and *cover*. These variables were removed due to low occurrences, and we opportunistically utilized them to determine the dominance rank relationships of a subset of our sample ($n = 41$). We created a matrix corrected for directionality of the variables. A Bayesian elo-rating method was applied (cf. Neumann and Fischer 2023) to determine the steepness of dominance hierarchy and the ordinal ranks of the individuals. We investigated the associations between the personality scores of the individuals and their social ranks using Spearman correlation tests.

### 2.6 | Additional Analyses on Human-macaque Interactions

Although the behavioral variables *contact provisioning* and *non-contact provisioning* were dropped due to low occurrences, we performed additional post hoc analyses. These variables were identified after data collection as being important for synanthropic animals (Balasubramaniam et al. 2020; Balasubramaniam et al. 2022; Cox and Gaston 2018; Marty et al. 2020; Sengupta et al. 2015). Based on data from both phases, we checked the identity of individuals that obtained food through contact and noncontact provisioning. If an individual obtained food through both, we considered the response to be contact provisioning (securing food from human hands), as noncontact provisioning is considered the "default" way of obtaining food (cf. Supporting Information S1: Table S1). We found that 15 individuals obtained food through contact provisioning. The number was 17 for noncontact provisioning, suggesting that these individuals were never observed to obtain food through contact provisioning. We conducted Mann-Whitney U tests to compare the personality scores of individuals that obtained food through contact versus exclusively noncontact provisioning.

## 3 | Results

### 3.1 | Repeatability of Variables

Of the 35 variables, we found nine that were repeatable (ICC value > 0.2 and $p < 0.05$, Table S4). The ICC values ranged between 0.23 and 0.53, suggesting moderately low to relatively high repeatability; however, due to low overall MSA value (i.e., < 0.6) and inadequate attribute communality values (< 60%), the number of variables was reduced to four. The attribute communalities of the four remaining behavioral variables (*approach*, *attention*, *avoid*, and *look around*) ranged between 68% and 79%, with an overall MSA value of 0.61. All other assumptions of the PCA were fulfilled (eigenvalues of selected PCs ≥ 1; Bartlett test: $p < 0.001$). The automated selection process of PCs suggested one component to be strongly included, but the second component's eigenvalue was close to simulated and resampled lines. We decided to choose two components. The two PCs had a weak positive correlation (a value of 0.219 from the phi matrix), indicating they are independent.

### 3.2 | Personality Traits

We found two personality traits in synanthropic rhesus macaques based on behavioral observations. These components cumulatively explained 71.80% of the data variance. The labeling of traits was based on the variables loaded on them (Table 1). PC1 had two positively loaded variables: *look around* and *approach*. Look around was defined as an individual's side-by-side head movement without any clear focus. The behavior approach implied moving towards conspecifics in a neutral or affiliative manner, that is, without displacing them. A lack of clear focus on conspecifics and the tendency to initiate affiliative social interactions prompted us to label PC1 as "social tension." Thus, social tension could represent initiating positive social interactions yet being cautiously aware of potential within-group aggressive interactions. Social tension explained 38.20% of the variance of the data. Like social tension, PC2 included two positively loaded variables: *avoid* and *attention*. These behavioral variables included paying attention to conspecifics or within-group events. Avoid was defined as an individual's tendency to redirect themselves when (certain) conspecifics were within three meters. Attention was focused on within-group conflicts and vocalizations, without moving head, often coupled with a frozen body posture. The loading of these two variables together potentially represents individuals' tendencies to avoid within-group conflicts proactively. Accordingly, we labeled PC2 "meekness," that explained 33.60% of the data variance.

## 3.3 | Sex Differences

We found an association of sex with the social tension trait. Males were higher on social tension than females (LM: $z = 2.43$, Cohen's $d = 0.67$, 95% CI [0.13, 1.22], $p = 0.01$). This full model differed from the null model that lacked the fixed effect of sex ($p = 0.01$). We did not find any association of sex with meekness (LM: $z = -0.934$, Cohen's $d = 0.26$, 95% CI [−0.29, 0.80], $p = 0.35$).

## 3.4 | Associations of Social Ranks With Personality Traits

The steepness of the dominance hierarchy (steepness = 0.66, 89% credible interval = 0.58–0.74) confirms a despotic social style of our study population of rhesus macaques (cf. Thierry 2007). However, we found no significant associations between social tension and social ranks (Spearman correlation test: $rho = 0.03$, $p = 0.82$), and meekness and social ranks (Spearman correlation test: $rho = 0.21$, $p = 0.18$). These results suggest that the observed personality traits were largely dominance-independent.

## 3.5 | Response to Novelty Experiments

We found low participation in novelty experiments. Only a small proportion of the sample voluntarily approached or interacted (i.e., participated) with the presented stimuli (e.g., novel objects, novel food items, food puzzles, or predator models). Only six individuals (11.52% of the sample) interacted with the novel object CDs. In the second novel object experiment, only two individuals (3.84%) spent time in the proximity of the rubber toys without any active engagement with them. Both the novel food item tests had only four participants (7.69%). The food puzzles (wooden maze and rotating plastic bottle) had slightly higher participation rates than novel objects and novel food items. Nine individuals (17.30%) approached each of these puzzles. Of them, only seven and five individuals manipulated the wooden maze and rotating plastic bottles, respectively. In the predator experiment, a total of 10 individuals participated in the snake model (19.23%), whereas the tiger model had twelve participants (23.07%).

## 3.6 | Human-Macaque Interactions During Food Provisioning

We found no difference in social tension scores between individuals that obtained food through contact and noncontact provisioning (Mann Whitney U test: $U = 97$, $z = -0.89$, $p = 0.37$, Figure 2). Unlike social tension, we found a significant difference in meekness trait scores between individuals that obtained food through contact and noncontact provisioning (Mann-Whitney U test: $U = 67$, $z = -2.07$, $p = 0.03$, Figure 2). Individuals that obtained food through contact provisioning had higher meekness scores (mean ± standard deviation: $0.74 \pm 1.33$) than individuals that obtained food through noncontact provisioning ($-0.20 \pm 0.50$). The association of only one personality trait with contact food provisioning points towards the discriminant validity of the observed traits.

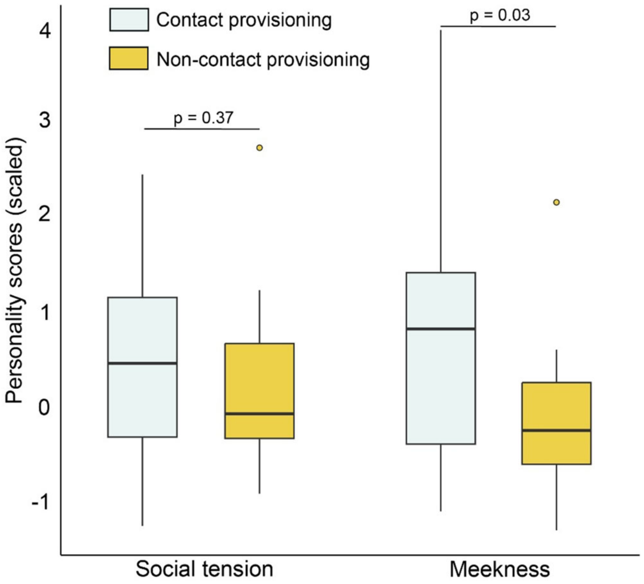

**FIGURE 2** | Personality traits and contact and noncontact food provisioning. Boxes indicate interquartile ranges, and whiskers represent the upper and lower limits of the data. The horizontal bars within the boxes represent the median values. Dots show outliers. Significance values ($p$ value) are provided.

## 4 | Discussion

Animal personality research allows us to examine the ecological and evolutionary implications of biological traits and their variations. Despite our initial aim to assess synanthropic macaque personality using a multi-method approach of behavioral observations and novelty experiments, low participation in experiments led us to rely solely on observational data. We identified two traits: social tension and meekness, that are relevant to the despotic nature of rhesus macaques (Brent et al. 2014). Males exhibited higher social tension than females. Individuals that obtained food through contact provisioning from humans had higher scores in the meekness trait than those obtaining food through noncontact provisioning. However, the extremely low participation of macaques prevented the successful implementation and completion of novelty experiments. As a result, sufficient data could not be obtained to assess personalities such as boldness, exploration, or persistence. We discuss how the observed personality traits and their variations can benefit a highly adapted nonhuman primate species living in human-dominated environments.

### 4.1 | Personality Traits Obtained Through Focal Observations

The observed traits of social tension and meekness align with previous findings on rhesus macaque personalities using similar observational approaches. However, while Brent et al. (2014) used the label meek for variables approach and submit, our study identified it through different behavioral indicators, highlighting methodological variation in personality construct among these studies. For instance, the current study used a comprehensive ethogram of 110 behaviors (incl. passive behaviors), whereas others used ~12 variables. Besides, we used a "bottom-up" method instead of grouping multiple behaviors into predefined categories (such as physical aggression and submissiveness). Although grouping behaviors into predefined categories may help tackle data of low representation, the approach is not free from inherent biases (such as lack of validity checks and presence of species/population-specific behaviors), which has been discussed previously (Freeman et al. 2013; Uher 2008). Irrespective of the methodological approach, labeling traits is still subjective, generating ambiguity on the interpretability of constructs among researchers. Nonetheless, we believe that animal personality research can benefit from carrying out methodological comparisons.

Both personality traits reported in our study have elements of within-group-level social interactions and can be interpreted as "social personality traits" (Koski 2011). Like several other nonhuman primates and generally gregarious animals, rhesus macaques show complex social dynamics (Sade 2017), where social personality traits may play a role. Consistency in sociality (i.e., an individual's position in the social network) can be linked to interindividual variations in social tension in rhesus macaques (Brent et al. 2013), implying how social tension as a personality trait may shape dyadic interactions. Variations in social tension further hold the potential to explain dominance structure and affiliative social interactions (Altschul et al. 2019; Bhattacharjee et al. 2024b; Gartland et al. 2022). Rhesus macaques are considered a despotic species (Thierry 2007), where higher social tension may provide advantages to individuals in terms of within-group aggression avoidance (Chapais 1983). Individuals, especially philopatric females with lower social tension and higher tolerance, may engage in interactions that are beneficial to maintaining strong social bonds (cf. Bhattacharjee et al. 2023; Gartland et al. 2022; Sterck et al. 1997). Our findings are in line with this sex difference in the social tension trait. Additionally, higher social tension in males than in females could be attributed to the necessity of males to form alliances with unrelated males (Higham and Maestripieri 2010), exposing them to competition within a group. However, due to the low representation of males in our sample, conclusions should be drawn with caution. The presence of a relatively stable dominance hierarchy could also be the reason for low social tension among females (Forkman and Haskell 2004). The general variations in social tension could be explained by life-history trade-offs (pace-of-life syndrome, Réale et al. 2010), social niche specialization (Bergmüller and Taborsky 2010), and state-behavior feedback (social niche hypothesis, Sih et al. 2015).

Variations in the meekness trait might be associated exclusively with the despotic social style of rhesus macaques, where within-group aggressive interactions are frequent (Thierry 2007). Individuals can avoid potential conflicts by exercising caution. This could be achieved proximately by collecting spatiotemporal information on nearest neighbors (Cameron and du Toit 2005; Sinha 1998). Alternatively, by being less meek, individuals may allocate their time and energy to other activities, like resting, feeding, or engaging in social interactions. In our study, dominance rank relationships were not determined, which could have assisted in understanding how personality traits are associated with sociality patterns (Konečná et al. 2012).

### 4.2 | Challenges Associated With Experimental Approach and Proposed Improvements

Replicating laboratory protocols of behavioral and cognitive experiments on wild animals in their natural habitat can provide us with information on their ecological validity. Although some studies successfully replicated laboratory protocols in the wild with more than 60% participation (Arnaud et al. 2016; Carter et al. 2012; Herborn et al. 2010), others encountered challenges (Schuppli et al. 2022). Our experimental approach was fairly inefficient, as evidenced by the low (~13% for the eight tasks) and inconsistent participation rates. Several factors, such as lack of motivation, relatively large group size, and conservative thresholds of coded variables, might have contributed to this. We discuss these challenges in detail and propose improvements for future studies.

Living in enriched human-dominated environments may lead animals to be less neophobic toward human artifacts (Bhattacharjee et al. 2024c; Griffin et al. 2017). We suspect the "novel" objects were not novel enough to elicit behavioral responses, resulting in a lack of engagement. Similar patterns were observed in semi free-ranging Japanese macaques (*Macaca fuscata*), where individuals did not have the inclination to interact with novel objects (Personal observations, J.J.M.M., D.B., 2021–2023). In the current study, we found that juveniles inspected and interacted with novel objects more than the adults, which could be explained by their relatively higher tendency to explore and innovate (Kendal et al. 2005). However, we only focused on adults in this study. The primary reason for low participation in novel food tasks could be due to the regular provisioning of our study group with highly rewarding food items, like apples, bananas, and peanuts. Provisioning may negatively influence animals' tendencies to explore (Berman and Li 2002; Sengupta et al. 2015). Nonetheless, larger food items (such as dragon fruits and durians, if they are potentially novel) could generate more attention from synanthropic animals. We also think conducting novel food item tests in multiple locations simultaneously would be beneficial in capturing the behavioral responses of a large population. In contrast, the food puzzle tests garnered relatively higher participation. Yet, the fast-depleting nature of food items in the puzzles potentially led to less overall involvement. A relatively costly alternative would be remotely controlled food dispensers, as such devices have proved fruitful in capturing animals' behavioral and cognitive responses in the wild (Rosati et al. 2022). Additionally, "impossible" or "unsolvable" tasks could be used to examine traits like persistence (Rao et al. 2018). Finally, for predator exposure experiments, we coded variables (especially the distances) used for captive populations, that is, avoidance based on limited spatial proximity (cf. Bhattacharjee et al. 2024a; Kluiver et al. 2022; van Dijk et al. 2023). We found ~20% participation in the predator experiments, more data could have been obtained by making the variables less conservative, that is, by increasing the distance of approach, proximity, etc. Life-sized predator models could elicit more intense antipredator behaviors (cf. Kluiver et al. 2022).

### 4.3 | Implications of Macaque Personality on Human-Macaque Interactions

Our additional analyses revealed an association between personality and human-macaque interactions during provisioning. Although social tension did not differ, individuals obtaining food through contact provisioning were more meek than individuals that obtained food through noncontact provisioning. Notably, meekness as a personality trait was measured at the level of within-group interactions. It is known that such a response could indicate higher risk-taking or bolder traits in more 'submissive' individuals. By contrast, as humans are a stable part of the synanthropic macaques' environment, it is no longer a novel situation for individuals (cf. Bergvall et al. 2011). Our results also indicate that the observed personality traits are independent of social rank. This suggests that consistent individual behavioral tendencies, such as meekness and social tension, may exist separately from hierarchical positioning within the group. However, the frequencies of recorded interactions for the assessment of dominance rank relationships were limited. Thus, these results should be interpreted with caution. Subsequently, if more meek individuals are the low-ranking individuals in a group, obtaining food by making contact with humans can be beneficial. It can help secure provisioned food items using an alternate yet effective strategy by not waiting for the food items to be placed on the ground, where more dominant individuals can exhibit aggression. In a comparative study using despotic Japanese macaques, slightly less despotic barbary macaques (*Macaca sylvanus*), and more egalitarian moor macaques (*Macaca maura*), researchers found that subordinates in the more despotic societies use alternate "opportunistic" strategies to maximize food intake (Gomez-Melara et al. 2021). Meanwhile, bolder individuals may be less likely to obtain food this way, as they take more risks and explore alternative foraging strategies, such as stealing food or competing with other monkeys. This highlights how personality traits influence monkeys' interactions with humans and their reliance on human-provided resources. More systematic observations in the future would be valuable for a nuanced understanding of how variations in traits are linked to intra- and inter-specific interactions.

## 5 | Conclusion

We identified two personality traits - social tension and meekness. Using post-hoc analyses, we found that only meekness was associated with macaques' inter-specific interactions with humans, particularly during food provisioning, thus highlighting the role of personalities in interspecies dynamics. Our findings have implications for the 'One Health' perspective. Provisioning can severely affect human-animal coexistence as the act of provisioning influences the behavioral dynamics of animals in human-dominated environments (and beyond) and can also foster the transmission of zoonotic diseases (Shutt and Lees 2021; Strandin et al. 2018). Growing human-macaque conflicts in Asia and Africa, as well as macaques' tendencies to "bargain" in several Asian countries, are classic examples of "provisioning gone wrong" (Fuentes et al. 2008; Priston and McLennan 2013; Radhakrishna et al. 2013; Riley 2007). Unfortunately, how these behavioral dynamics relate to personalities is poorly understood. Therefore, more studies on synanthropic nonhuman primate personalities would be valuable for managing populations and mitigating conflicts between humans and nonhuman primates.

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### Author Contributions

**Taniya Gill:** investigation, data curation, formal analysis, writing – original draft. **Anshul Gautam:** investigation, data curation. **Jorg J. M. Massen:** conceptualization, methodology, resources, writing – review and editing. **Debottam Bhattacharjee:** conceptualization, formal analysis, supervision, resources, visualization, writing – original draft, writing – review and editing. All authors gave their final approval for publication and agreed to be held accountable for the work performed therein.

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### Ethics Statement

Ethical approval for the study was obtained from the Department of Forests and Wildlife, Government of NCT of Delhi, India (Approval No.: F.No.CF/LC/105/07/HQ/PartFile-/833-37). All experiments were noninvasive, and the participation of animals was completely voluntary. We adhered to the ethical guidelines of the American Society of Primatologists for the study.

### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

All data generated in the study and the code for analyses (R-script) have been deposited in the Open Science Framework repository and can be accessed using the link: https://doi.org/10.17605/OSF.IO/XT53Z.

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section.