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Personality, social behavior, and the maintenance of cohesion in a multilevel-society primate (*Rhinopithecus roxellana*)

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ABSTRACT

Understanding how individual personality traits impact social interactions and cohesion in complex animal societies remains a critical challenge, particularly in wild populations of nonhuman primates. This study investigated personality in a free-ranging population of golden snub-nosed monkeys (*Rhinopithecus roxellana)*, a high-altitude temperate forest species organized in a multilevel social system. Personality structure was quantified using the Hominoid Personality Questionnaire, and its relationship to group cohesion was assessed through 12 behavioral variables and female transfer status. A behavioral experiment was designed to evaluate the tendency of individuals to temporarily depart from collective movement. Factor analysis of 41 questionnaire items revealed four distinct personality dimensions—Assertiveness, Openness, Neuroticism, and Sociability—that accounted for substantial inter-individual variation. Personality scores varied significantly by sex and dominance rank: males exhibited higher Assertiveness, females exhibited higher Sociability, and Neuroticism was negatively associated with dominance rank. Personality traits were linked to cohesion-related behavior, with Assertiveness positively associated with both affiliative and aggressive interactions, and Sociability predicting higher grooming rates. Moreover, Sociability and Openness showed opposing but insignificant influences on female transfer, with Openness additionally associated with temporary separations, suggesting that personality shapes both intra-unit cohesion and inter-unit fluidity in multilevel societies. These findings demonstrate that personality is a determinant of social organization and dynamics in primates, providing new insights into the evolutionary processes that influence and maintain complex social systems.

Keywords: Personality; Primates; Group cohesion; Multilevel society; Sociality

INTRODUCTION

Personality in nonhuman animals refers to stable inter-individual differences in behavior that persist across time and contexts (Réale et al., 2007; Sih et al., 2004). The expression of personality is impacted not only by genetics and environmental factors but also by social selection pressures, particularly in group-living species where social dynamics can influence behavioral consistency (Dingemanse & Araya-Ajoy, 2015; Webster & Ward, 2011). Far from representing random variation around an optimal fitness peak, personality exerts profound effects on social interactions, coordination, and overall group functioning (Gartland et al., 2022; Martin et al., 2023; Sih et al., 2015). Research on nonhuman primate personality forms a critical bridge between human and animal studies, with tools such as the Hominoid Personality Questionnaire (HPQ), adapted from the human Five-Factor Model, allowing standardized measurement of underlying latent variables explaining individual behavioral variation across species with diverse social systems (Adams et al., 2015; Freeman & Gosling, 2010; King & Figueredo, 1997; Robinson et al., 2016; Uher & Asendorpf, 2008; Weiss et al., 2006; Wilson et al., 2018). Employing a consistent set of traits

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across multiple taxa offers a robust framework for elucidating the evolutionary connections between personality and social structure.

Throughout social evolution, the emergence of personality has been regarded as a critical factor in coordinating interactions among social partners, particularly in aggression and cooperation (Wolf & Weissing, 2012). In the stable one-male units (OMUs) of mountain gorillas (*Gorilla beringei*), high Dominance scores are positively associated with conflict intervention and approach behaviors, while high Sociability scores are linked to grooming rates (Eckardt et al., 2015). In male-dominated chimpanzee (*Pan troglodytes*) societies, the Dominance trait underpins both intense social competition and the maintenance of durable affiliative bonds (Freeman et al., 2013). The relationship between personality and social rank has been widely studied, revealing diverse patterns across primate species (Clarke & Boinski, 1995). Bonobos (*Pan paniscus*) exhibit a female-centered fission-fusion system characterized by Agreeableness as the dominant dimension, with Dominance absent and Aggressiveness only weakly correlated with social rank (Garai et al., 2016). In Hanuman langurs (*Semnopithecus entellus*), Agreeableness, Confidence, and Extraversion promote dominance acquisition, extensive social integration, and higher activity levels (Konečná et al., 2008). Similarly, in rhesus macaques (*Macaca mulatta*), Confidence, alongside Anxiety, reflects dominance hierarchy and predicts heightened social tension and risk of injury (Robinson et al., 2018; Thierry et al., 2000). Collectively, these patterns indicate that primate personality structures are closely attuned to the organizational demands, competitive dynamics, and hierarchical gradients inherent to each social system.

Variation in individual personality composition within a group can profoundly influence social cohesion, reshaping patterns of association and driving the formation of non-random social structures (Ma et al., 2011; Majolo et al., 2008). In coordinated decision-making, members must reconcile personal preferences with social cues, with groups that effectively integrate these inputs more likely to maintain cohesion (Miller et al., 2013). Empirical evidence across taxa has shown that personality impacts group stability via multiple pathways, including the structuring of interaction networks, modulation of affiliative and leadership roles, and maintenance of subgroup integrity (Briard et al., 2015; Nakayama et al., 2016; Ren et al., 2024). The functional impact of specific traits often depends on the prevailing social context: bolder individuals frequently assume leadership roles during collective movement, whereas highly sociable members are pivotal when cooperation and partner coordination are required (Bevan et al., 2018). In vervet monkeys (*Chlorocebus pygerythrus*), persistent grooming behavior has been linked to long-term cohesion among male subgroups within social networks (Blaszczyk, 2018). Personality can also influence social network topology through homophily effects (Carter et al., 2015). For instance, Assamese macaques (*Macaca assamensis*) form stronger affiliative bonds with partners exhibiting similar personality traits, while in female baboons (*Papio ursinus*), kinship exerts a stronger influence than personality on coalition formation (Ebenau et al., 2019; Seyfarth et al., 2014). The extent to which personality contributes to cohesion is ultimately shaped by the broader social architecture, underscoring the need for integrative studies that explicitly link personality variation, social behavior, and structural features of social systems to elucidate the evolutionary basis of primate social complexity.

Multilevel societies (MLSs) represent one of the most complex and evolutionarily derived forms of social organization, defined by hierarchical arrangements in which modular core units are nested within larger, higher-order groupings (Grueter et al., 2020). The golden snub-nosed monkey (*Rhinopithecus roxellana*) exemplifies this system. Inhabiting the high-altitude temperate forests of central China, this species is thought to have evolved its aggregated social structure—composed of multiple OMUs integrated into a stable breeding band—as an adaptation to prolonged, severe winters (Qi et al., 2014, 2023; Zhao et al., 2024). Social interactions occur at two scales. Within OMUs, typically composed of 2–10 adult females, cohesion is maintained through affiliative behaviors such as grooming, embracing, and coordinated defense against external threats (Zhang et al., 2008a). At the band level, 8–14 OMUs coexist in a relatively stable structure with a degree of linear dominance among units, although conflicts rarely escalate to serious injury (Zhang et al., 2008b). Females may engage in extra-unit mating and transfer between OMUs (Qi et al., 2009), while resident males occasionally cooperate to repel bachelor males approaching the band but otherwise exhibit limited affiliative behavior at the band level (Qi et al., 2017). Social network analyses indicate that female transfer plays a significant role in maintaining social cohesion, thereby enhancing overall group stability (Fang et al., 2018, 2022). Although personality has been examined in captive golden snub-nosed monkeys, the absence of complex social interactions in captivity limits such assessments (Jin et al., 2013).

To better understand how personality contributes to social cohesion, the present study investigated the personality structure of free-ranging golden snub-nosed monkeys and assessed how individual traits relate to sex and dominance rank, variation in social behavior, female transfer status, and responses to externally induced disruptions of OMU cohesion. Personality was assessed using a modified HPQ tailored to the species-specific behavioral repertoire of the golden snub-nosed monkey (Freeman et al., 2013). Drawing on the ecological constraints and social organization of golden snub-nosed monkeys, this study hypothesized that specific personality dimensions would emerge. Frequent affiliative interactions among individuals were expected to promote Sociability as a key trait, whereas sensitivity to resource competition and the need for inter-unit transfer to avoid inbreeding under harsh and seasonal environmental conditions were expected to foster elevated levels of Neuroticism and Openness (Eckardt et al., 2015; Koski, 2011). In contrast, given that conflicts occur primarily between units and rarely escalate within OMUs, no clearly defined Dominance trait was expected. Furthermore, these distinct personality dimensions were predicted to be linked to cohesion within units and patterns of coexistence among units. Relationships between personality and long-term cohesion were measured based on behavioral variables and female transfer status, while short-term responses in social cohesion were evaluated via an experimental assay in which individuals were temporarily separated from collective unit movement. This integrative framework offers a novel lens through which to examine how stable individual traits shape social cohesion across hierarchical levels in a primate multilevel society.

MATERIALS AND METHODS

Study site and subjects

This study was conducted on a habituated, free-ranging troop of golden snub-nosed monkeys in the Guanyinshan National Nature Reserve, Qinling Mountains, China (E107°52′–108°02′, N33°20′–33°44′), where long-term behavioral research has been ongoing (Wang et al., 2023; Yang et al., 2022; Zhao et al., 2021). The monkeys were provisioned twice daily with small quantities of seeds to facilitate close observation, but behavioral data were collected only during natural activity periods after provisioning had ended. The study troop ranged through deciduous broad-leaved forest and theropencedrymion at elevations between 1 200 and 2 000 m a.s.l., with a mean annual temperature of 11.5 °C (−14.3 °C in January to 36.4 °C in July) (Wang et al., 2020).

The focal group included seven OMUs within a breeding band, totaling 69 individuals: seven resident adult males, 28 adult females, and eight subadults. As only four subadult females were sufficiently familiar to the raters, analyses were based on 39 individuals, comprising all adults in the breeding band plus the four recognizable female subadults. Juveniles and bachelor males in surrounding areas were excluded from the study.

Ethics

All research protocols adhered to regulatory requirements and were approved by the Animal Care Committee of the Wildlife Protection Society of China (SL-2012-42). All experiments followed the ASAB/ABS Guidelines for the Treatment of Animals in Behavioral Research and Teaching.

Personality assessment

Personality was evaluated using a modified version of the HPQ, a standardized instrument consisting of 54 items, each associated with one to three descriptive statements contextualized for nonhuman primate behavior (Garai et al., 2016; Weiss et al., 2009, 2011). The macaque version of the HPQ was used, with behavioral descriptors absent in golden snub-nosed monkeys replaced with functionally equivalent behaviors. For example, in the item “Fearful”, grimacing and running away were replaced with crouching and retreat: “FEARFUL: Subject reacts excessively to real or imagined threats by displaying behaviors such as screaming, crouching, retreat, or other signs of anxiety or distress”.

All items were translated into Chinese with reference to the Chinese Big Five Personality Inventory by a back-translation procedure (Wang et al., 2010). Each item was rated on a 7-point Likert scale, with 1 indicating that “the trait is entirely absent or negligible” and 7 indicating that “the trait is highly characteristic of the individual”. Raters were instructed to omit scoring for individuals with whom they lacked adequate familiarity and to avoid discussing their evaluations with others during the rating process.

Ratings were conducted between June and August 2021 by five trained observers, each of whom had conducted field research on the study troop for 9–20 months. All observers demonstrated reliable identification ability and possessed sufficient familiarity with the behavioral repertoires of the focal subjects to provide informed personality ratings.

Social behavior observations

Behavioral observations were conducted from September to December 2020 and from March to June 2021. Data collection followed a focal animal sampling protocol (Altmann, 1974), with each observation bout consisting of 60 min of continuous recording. Subjects were selected randomly without resampling to ensure equal sampling distribution across individuals. Observations were carried out daily from 0930h to 1630h, with two bouts scheduled in the morning and two in the afternoon. The observer responsible for behavioral data collection did not participate in personality assessments, and no individual was observed more than once per day. Over the entire study period, 294 h of focal data were recorded, yielding a mean of 7.54 h per subject (SD=1.66, Supplementary Table S1). Twelve behavioral variables were systematically coded (Table 1), encompassing affiliative, aggressive, submissive, and self-directed categories. These behaviors were selected to represent direct behavioral correlates of social cohesion (Labarge et al., 2020; Seebacher & Krause, 2017). For each focal subject, behavioral frequency was calculated as the number of observed occurrences of a given behavior divided by the total observation time.

In addition, demographic data on female transfers were also recorded. A transfer event was defined as a female departing her original OMU (“female leaving”) and joining a different OMU within the same breeding band (“female entering”). Based on transfer status during the study period, females were classified as either transferred or non-transferred.

Behavioral experiment

A controlled field experiment was designed to quantify

Table 1 Definitions of behavioral variables in golden snub-nosed monkeys

Behavior type	Variable	Definition
Self-directed behavior	Scratching	Rapid scratching of own body.
	Self-grooming	Grooming directed toward own body.
Affiliative behavior	Perform grooming	Initiator sits and separates the fur of another individual with both hands.
	Receive grooming	Passive acceptance of grooming, often in seated or reclining posture following solicitation.
	Embracing	Arms extended to embrace another individual; may be accompanied by soft whimper vocalizations.
	Holding	Grasping of the lumbar region of another induvial from behind, sometimes with repeated pulling.
Aggressive behavior	Supplanting	Approaching and displacing another from a preferred position (e.g., shaded, warm, or food-adjacent area).
	Threatening	Non-contact aggressive display, including fixed staring and “gu-gu” vocalizations directed at another individual.
	Chasing	Persistent following of another individual, who continues to retreat; no physical contact involved.
	Fighting	Physical contact involving hitting, scratching, or grabbing; low likelihood of injury.
Submissive behavior	Avoiding	Withdrawing by more than 1 m in response to an approach.
	Retreating	Stepping back or turning away from an aggressor in response to threat or attack.

individual propensity to temporarily disengage from collective OMU movement, simulating a mild disruption to unit cohesion. Each focal subject participated in four trials—two in spring and two in summer—conducted during daily non-provisioning periods. At the conclusion of each day of behavioral observations, one subject from each OMU was randomly selected for testing. Consecutive trials for the same subject were separated by a minimum interval of 30 days to minimize habituation to the experimental context. All trials were video-recorded using a DJI OSMO Action camera, and behavioral coding and individual identification were conducted by a trained observer.

The experimental setup consisted of a 0.5 m^2 natural stone slate positioned beyond the natural foraging range of the monkeys (Figure 1). Trials began when the focal OMU approached the designated site during routine foraging activity. When the focal subject was within 3 m of the slate, the experimenter, stationed inside the experimental area, discreetly placed two unshelled peanuts at the rear edge of the slate to elicit approach. Peanuts were selected as the incentive based on previous cognitive studies, which showed that they reliably triggered motivation sufficient to interrupt ongoing social or foraging behaviors. When multiple group members were present, peanuts were placed in synchrony with the gaze and orientation of the focal subject to limit visual cues to other individuals and maintain experimental control. Once the focal subject approached the slate, the peanuts were removed to terminate the incentive phase and reduce the risk of attracting other group members through feeding-related cues. Latency from initial visual detection of the reward to physical contact with the slate was recorded. A trial was defined as successful if the subject remained on the slate for more than 3 s, coded as “Y” in the binary outcome model (Y/N); all other outcomes were coded as “N”.

Statistical analysis

All statistical analyses were performed using R v.4.2.1 (R Core Team, 2022), with data visualizations established using the ggplot2 package (Wickham, 2016).

Interrater reliability: Interrater reliability for each HPQ item was assessed using intraclass correlation coefficients (ICCs) following the framework of Shrout & Fleiss (1979), implemented via the irr package (Gamer et al., 2019). Two ICC forms were calculated: ICC (3,1), estimating the reliability of ratings from a single rater, and ICC (3,k), estimating the reliability of the mean ratings aggregated across all raters (k=5 in this study) (Shrout & Fleiss, 1979). Items yielding ICC values with 95% confidence intervals spanning zero were excluded from further analysis due to insufficient interrater agreement.

HPQ data reduction: Prior to conducting factor analysis, the Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy and Bartlett’s test of sphericity were applied to verify the appropriateness of the dataset for factor extraction. Once suitability was established, the optimal number of factors was determined using four complementary, automated approaches implemented via the “nfactors” and “fa.parallel” functions in the psych package, including Very Simple Structure (VSS), empirical Bayesian information criterion (Empirical BIC), standardized root mean square residual (SRMR), and parallel analysis (Revelle, 2023). These approaches provided a

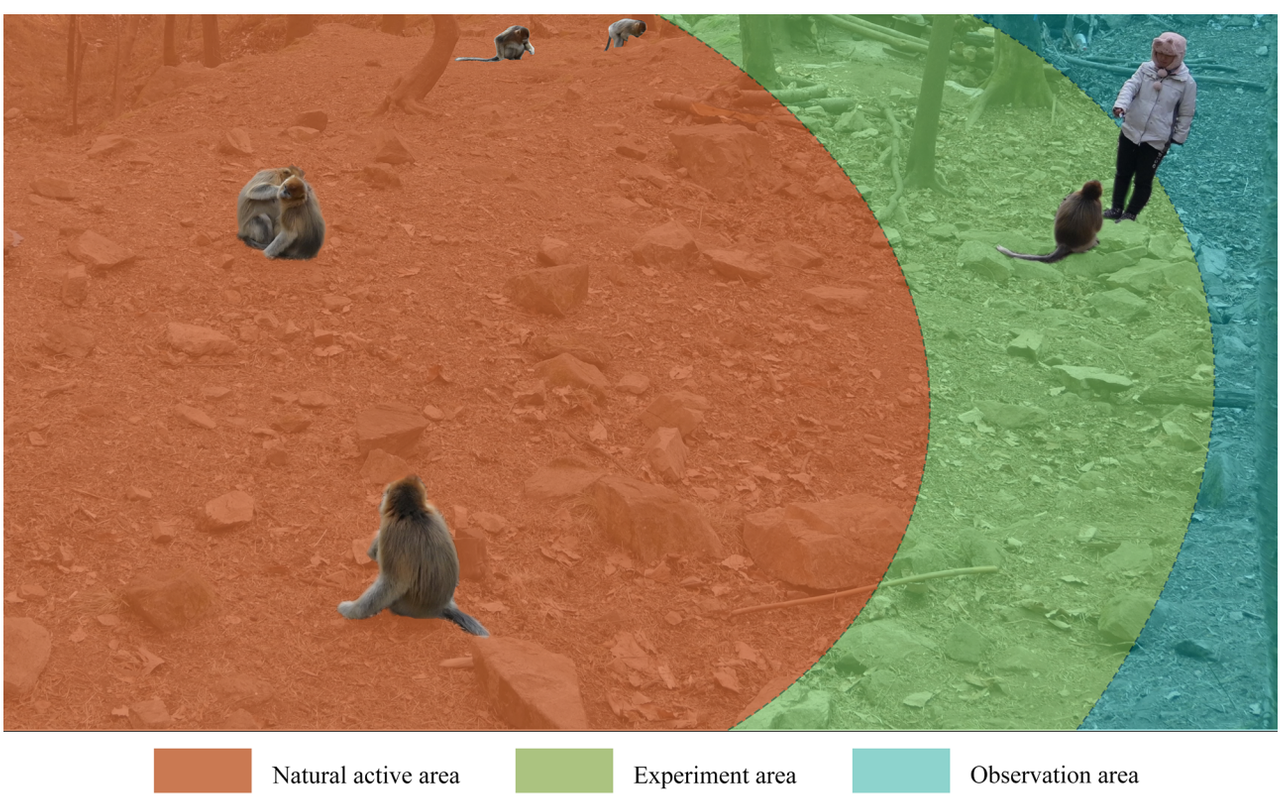

Figure 1 Experimental setup for behavioral assay in a one-male unit

One researcher positioned inside the experimental area, facing the slate platform, used peanuts to attract the outermost member of an OMU approaching the boundary between the activity and experimental areas. Simultaneously, a second researcher, located in the observation area, recorded the procedure using a video camera. The trial ended once the focal individual stood steadily on the slate platform.

statistically rigorous and data-driven framework for determining latent factor structure and are considered more robust than traditional reliance on Kaiser's criterion or scree plot inspection (Morton & Altschul, 2019).

Factor extraction was performed using principal axis factoring with the "fa" function in the psych package (Revelle, 2023). Both promax (oblique) and varimax (orthogonal) rotations were applied. When promax rotation revealed strong inter-factor correlations or substantially altered structure, the promax solution was retained; otherwise, varimax rotation was adopted for interpretability (Weiss, 2017). Factor labels were assigned through content-based interpretation, drawing preferentially from existing studies of golden snub-nosed monkeys and, when unavailable, from broader nonhuman primate and human personality research.

For subsequent analyses, factor scores for each subject were calculated using the Bartlett method in accordance with the identified factor structure (DiStefano et al., 2009; Gorsuch, 1983). Items were retained when the absolute loading exceeded 0.40 and the highest loading corresponded to a single factor. This procedure produced statistically precise estimates of latent traits by incorporating unique variance and inter-item correlations, yielding personality dimension scores for all 39 subjects.

Normalized David's scores: Because conflicts in golden snub-nosed monkeys primarily occur between OMUs and female support is critical during inter-unit aggression, dominance rank was evaluated at the OMU level. To quantify the hierarchical position of each OMU within the breeding band, a dominance matrix was constructed by recording the frequency of inter-unit agonistic interactions. Outcomes were coded as victories when one unit supplanted or chased another, and as defeats when a unit avoided or retreated. Normalized David's Scores (NDS) were then calculated for each OMU based on this matrix (de Vries et al., 2006).

Personality and behavior associations: Spearman rank correlation coefficients, computed with the "cor" function in R, were used to assess associations between individual scores on personality dimensions and frequencies of social behaviors. Behavioral frequency was defined as the number of occurrences of a focal behavior divided by the total observation time. Correlations were calculated between four personality dimensions and 12 social behavioral variables, with Benjamini-Hochberg correction applied to control the false discovery rate (FDR).

To examine whether personality traits were associated with female dispersal patterns, females were categorized as transferred or non-transferred based on their dispersal status during the observation period. Normality of personality scores within each group was tested with the "shapiro.test" function in R, and homogeneity of variance was assessed using the "leveneTest" function in the car package (Fox & Weisberg, 2019). For normally distributed data with equal variances, independent-samples *t*-test was applied; otherwise, Mann-Whitney *U* test was used. Effect sizes were calculated using the "cohen.d" function for the *t*-test and "wilcox-effsize" function for the Mann-Whitney *U* test, both from the effsize package (Torchiano, 2020).

Sex differences in personality were examined using independent-sample *t*-test or Mann-Whitney *U* test, depending on the normality of the data. Spearman rank correlation was used to assess associations between personality scores and OMU dominance rank.

Generalized linear mixed-effects models: To investigate whether personality traits influenced the probability of separation from the OMU during collective activity, a binomial generalized linear mixed model (GLMM) was implemented using the lme4 package in R (Bates et al., 2015). The response variable was a binary outcome for each trial, indicating whether the focal individual was successfully separated from its OMU during collective movement. The full model included sex, dominance rank, trial number, and individual factor scores as fixed effects, together with interactions between rank and each personality trait, while the null model included only the random intercept for individual identity. Individual identity was specified as a random effect in all models to account for repeated measures. Model selection followed a backward stepwise procedure, with comparisons based on changes in Akaike Information Criterion (AIC) values, delta AIC, and evidence ratios (ER). Non-significant interaction terms were sequentially removed, and nested models were compared using likelihood ratio tests with the 'anova' function in R (Burnham et al., 2011). Multicollinearity among predictors was assessed using variance inflation factors (VIFs>5), calculated with the 'vif' function from the car package in R (Fox & Weisberg, 2019).

RESULTS

Interrater reliability of questionnaire items

Thirteen items demonstrated poor interrater reliability, defined as ICC (3,k) values below 0.4 with 95% confidence intervals spanning zero, and were thus excluded from subsequent analyses to ensure measurement robustness (Supplementary Table S2). For the remaining 41 items, ICC (3,1) ranged from 0.127 (jealous) to 0.551 (aggressive) with a mean of 0.277 (SD=0.124), while ICC (3,k) ranged from 0.421 (jealous) to 0.860 (aggressive) with a mean of 0.626 (SD=0.135).

Personality structure

To test our first hypothesis that golden snub-nosed monkeys exhibit a multidimensional personality structure, a factor analysis of HPQ ratings was conducted. Prior to factor extraction, data suitability was confirmed by the KMO measure of sampling adequacy (Overall MSA=0.61) and Bartlett's test of sphericity (χ^2=4 136.93, P<0.01). Automated factor retention analyses consistently supported a four-factor solution, which was also corroborated by scree plot inspection (Supplementary Figures S1, S2). The four factors were identified according to salient loadings as: Assertiveness, Openness, Neuroticism, and Sociability (Table 2). Promax rotation of the four-factor model accounted for 68% of total variance and revealed one moderate inter-factor correlation between Neuroticism and Assertiveness (r=−0.33; Supplementary Table S3). Assertiveness encompasses emotional instability, impulsiveness, and aggressiveness, in contrast to stability and gentleness. Openness captures activity, cognitive exploration, and innovation. Neuroticism reflects anxiety, fearfulness, vulnerability, and submissiveness. Sociability represents the general tendency to engage in social relationships.

Sex differences in personality

Sex differences were observed in personality scores (Figure 2). Males exhibited significantly higher Assertiveness scores compared to females (t=2.193, P=0.035), while females scored significantly higher on Sociability than males

Table 2 Promax-rotated factor loadings derived from reliable survey items

Item	Assertiveness	Openness	Neuroticism	Sociability	h^2
Excitable	**0.95**	−0.01	0.14	0.24	0.75
Impulsive	**0.94**	0.14	−0.01	0.21	0.82
Unemotional	**−0.92**	−0.12	**−0.41**	−0.19	0.68
Irritable	**0.90**	−0.23	0.03	0.06	0.86
Gentle	**−0.86**	0.25	−0.07	0.04	0.85
Erratic	**0.86**	0.26	0.31	−0.09	0.74
Defiant	**0.75**	−0.10	−0.14	0.10	0.65
Bullying	**0.70**	−0.31	−0.37	0.05	0.94
Aggressive	**0.61**	−0.22	**−0.52**	0.05	0.95
Friendly	**−0.59**	0.32	0.11	0.36	0.86
Stingy	**0.57**	0.18	−0.14	**−0.47**	0.70
Jealous	**0.52**	0.08	0.04	−0.19	0.35
Helpful	−0.35	0.24	−0.13	0.29	0.37
Active	−0.02	**0.88**	0.02	0.08	0.82
Imitative	−0.29	**0.84**	−0.01	−0.07	0.82
Curious	−0.08	**0.79**	−0.03	0.14	0.72
Innovative	0.04	**0.77**	0.16	−0.04	0.63
Playful	−0.07	**0.72**	0.16	0.15	0.66
Inventive	−0.09	**0.67**	−0.10	0.00	0.46
Reckless	**0.50**	**0.67**	0.03	−0.22	0.65
Inquisitive	−0.20	**0.62**	0.00	0.11	0.51
Lazy	−0.10	**−0.61**	0.00	−0.22	0.46
Cautious	−0.12	**−0.60**	0.22	0.17	0.37
Solitary	−0.30	**−0.50**	0.32	−0.44	0.70
Fearful	0.30	−0.15	**0.88**	0.10	0.66
Timid	−0.02	−0.39	**0.87**	0.33	0.81
Vulnerable	0.01	0.26	**0.83**	0.03	0.79
Anxious	**0.40**	−0.35	**0.81**	−0.12	0.80
Thoughtless	0.37	0.39	**0.75**	−0.12	0.76
Autistic	0.02	−0.13	**0.72**	−0.17	0.59
Submissive	−0.14	0.38	**0.72**	0.05	0.81
Manipulative	0.31	−0.22	**−0.55**	0.13	0.60
Dominant	**0.49**	−0.28	**−0.54**	−0.13	0.90
Affectionate	−0.02	0.08	−0.17	**0.73**	0.64
Independent	0.01	0.04	**−0.51**	**−0.72**	0.65
Sociable	0.30	0.25	−0.22	**0.70**	0.72
Sympathetic	**−0.42**	0.03	0.18	**0.54**	0.66
Individualistic	**0.43**	0.12	−0.06	**−0.53**	0.57
Depressed	−0.25	−0.22	**0.45**	**−0.47**	0.63
Protective	0.31	−0.24	−0.27	**0.43**	0.41
Unperceptive	−0.10	−0.11	0.21	−0.27	0.17

h^2: Communalities. Factor loadings greater than or equal to |0.4| are shown in bold.

(t=−2.373, P=0.023).

Rank differences in personality

Correlation analyses revealed that individuals in higher-ranking OMUs scored lower on Neuroticism (ρ=−0.660, P<0.01), while no significant associations were detected between dominance rank and other personality dimensions (Supplementary Table S4).

Personality and social cohesion

Behavioral variables: To evaluate whether distinct personality dimensions correspond to behavioral tendencies underlying social cohesion, correlations between factor scores and observed affiliative, aggressive, and submissive behaviors were assessed. The correlation matrix between personality trait scores and 12 behavioral variables is shown in Table 3. Assertiveness was negatively correlated with self-directed behavior (self-grooming: ρ=−0.508, P<0.05) and positively correlated with affiliative behaviors other than grooming (embracing: ρ=0.517, P<0.05; holding: ρ=0.497, P<0.05), as well as with aggressive behaviors (threat: ρ=0.368, P<0.05; chasing: ρ=0.365, P<0.05). Neuroticism was negatively associated with embracing (ρ=−0.429, P<0.05), and strongly negatively associated with aggressive behaviors (threat: ρ=−0.611, P<0.01; chasing: ρ=−0.454, P<0.05; fighting: ρ=−0.461, P<0.05), while showing strong positive correlations with submissive behaviors (avoiding: ρ=0.647, P<0.01; retreating: ρ=0.624, P<0.01). Sociability was positively associated with grooming behaviors (self-grooming: ρ=0.424, P<0.05; perform grooming: ρ=0.408, P<0.05). Openness did not exhibit significant associations with any measured

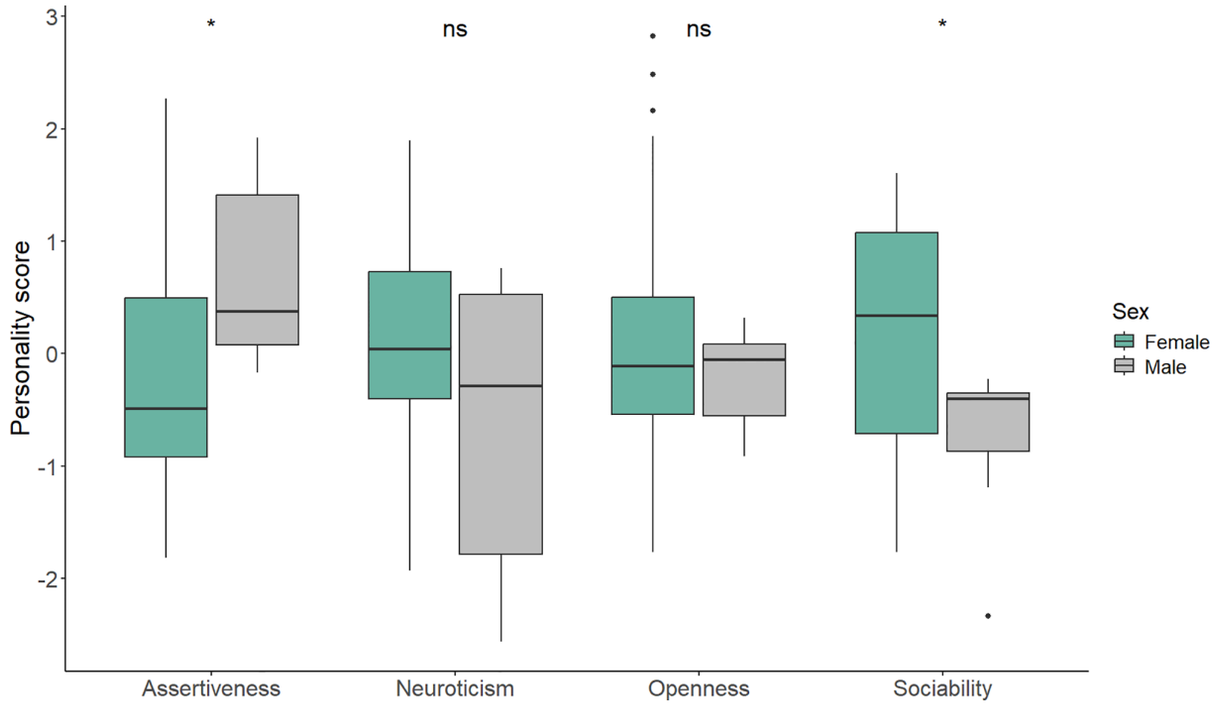

Figure 2 Distribution of personality scores by sex

Significant indicators are shown above boxes: *: P<0.05; ns: Not significant.

Table 3 Spearman rank correlations between behavioral variables and personality scores

Behavior type	Variable	Assertiveness	Openness	Neuroticism	Sociability
Self-directed behavior	Scratching	−0.236	−0.005	0.362	0.049
	Self-grooming	−0.508*	−0.100	0.309	0.424*
Affiliative behavior	Perform- grooming	−0.300	0.270	0.060	0.408*
	Receive- grooming	−0.008	0.318	0.003	0.045
	Embracing	0.517*	−0.195	−0.429*	−0.241
	Holding	0.497*	0.037	−0.263	−0.275
Aggressive behavior	Supplanting	0.274	0.144	−0.183	−0.153
	Threat	0.368*	−0.092	−0.611**	0.052
	Chasing	0.365*	−0.091	−0.454*	−0.289
	Fighting	0.293	0.046	−0.461*	−0.111
Submissive behavior	Avoiding	−0.319	0.196	0.647**	0.057
	Retreating	−0.142	0.289	0.624**	−0.010

n=39. *: Significant at P<0.05 after correction; **: Significant at P<0.01 after false discovery rate (FDR) correction.

behavioral variable.

Female transfer status: To evaluate the role of personality in long-term social cohesion, personality scores were compared between females that transferred and those that remained within their natal OMUs. During the observation period, 11 females transferred between OMUs. Comparisons between transferred (n=11) and non-transferred (n=21) females revealed no significant differences in personality scores. However, Sociability (Cohen's d=−0.79, t=−1.96, P=0.06) and Openness (Cohen's d=0.73, t=1.80, P=0.08) showed comparable but opposing effects in relation to female transfer (Figure 3).

Behavioral experiment: To assess short-term social cohesion and individual responses to transient disruptions in collective movement, the influence of personality traits on the likelihood of temporary separation from the OMU was tested by fitting a set of generalized linear mixed models and comparing them using AICc values (Supplementary Table S5). The best-fitting model only included Openness, which showed a significant effect (Estimate=2.89, Z=2.59, SE=1.12, P<0.01) on the likelihood of successful separation and accounted for a moderate proportion of variance (marginal R^2=0.52; conditional R^2=0.86). Individuals with higher Openness scores displayed a greater tendency to disengage temporarily from collective movement (Figure 4).

DISCUSSION

This investigation elucidated the personality architecture of golden snub-nosed monkeys through the integration of HPQ assessments with quantitative behavioral analyses, thereby advancing understanding of individual variation in social cohesion. Factor analysis yielded a robust four-factor structure, comprising Assertiveness, Openness, Neuroticism, and Sociability. These dimensions showed clear associations with affiliative interactions: Assertiveness and Sociability were positively correlated with affiliative behaviors, Openness predicted a higher likelihood of temporary separation from the OMU, and Neuroticism was negatively associated with unit dominance rank derived from conflict outcomes. While

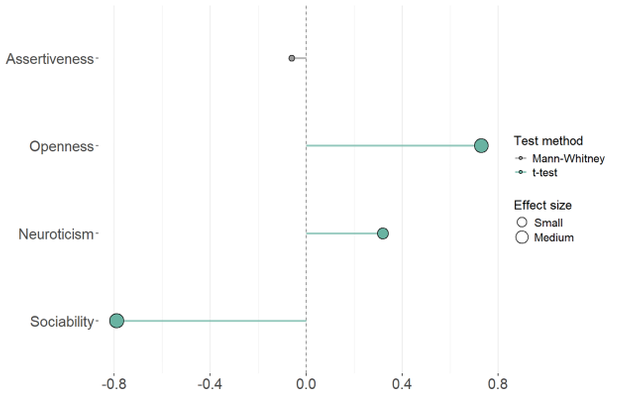

Figure 3 Effect sizes of personality traits in relation to female transfer

X-axis represents effect size, with bar color indicating test method. For Mann-Whitney *U* test, effect size was calculated as rank-biserial correlation coefficient, whereas for the *t*-test, effect size was calculated using Cohen's d.

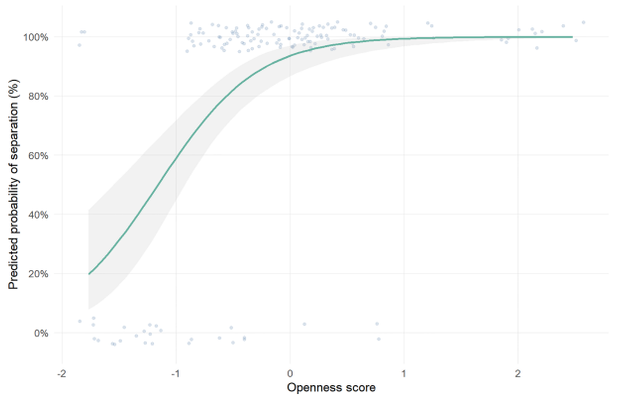

Figure 4 Predicted probability of temporary separation from the OMU as a function of Openness factor scores, based on a binomial GLMM

Solid blue line represents fitted values of the model, with the shaded area indicating 95% confidence intervals. Blue dots represent observed outcomes across four experimental trials per individual (n=4 trials, 39 individuals).

personality differences between transferred and non-transferred females were not statistically significant, Sociability and Openness demonstrated comparable but opposing effect sizes, indicating a potential influence on female dispersal.

Personality structure of golden snub-nosed monkeys

Golden snub-nosed monkeys exhibited a multidimensional personality structure consistent with the predicted four-factor model. The emergence of Openness, Sociability, and Neuroticism corresponded to expectations based on ecological and social conditions. Specifically, Sociability and Openness reflected the importance of affiliative interactions and exploratory behavior in an MLS, while Neuroticism captured sensitivity to environmental uncertainty and heightened resource competition. In contrast, no distinct Dominance dimension was identified, consistent with the prediction that dominance-related traits would be less central in a system with infrequent intra-unit conflict. The absence of this dimension may also be attributable to the negative correlation between Assertiveness and Neuroticism, indicating that emotional stability and aspects of competitive behavior are integrated within a composite dimension rather than expressed as an independent Dominance factor. Notably, the number of factors aligned with findings in captive populations, suggesting that the underlying structure is not substantially altered by differences in living environments (Jin et al., 2013). Instead, divergence from other primates lies primarily in the distribution of trait loadings within each factor. Comparative studies suggest that sociability may not consistently exhibit the same degree of adaptive flexibility as other dimensions, indicating that social orientation in this species may be evolutionarily conserved, whereas other traits more directly respond to environmental pressures (Gartland et al., 2022).

Assertiveness represents a composite personality dimension for golden snub-nosed monkeys encompassing emotional reactivity, affiliative orientation, and competitive drive. Across primate species, loading items such as excitable, impulsive, unemotional, and irritable are often aligned with Neuroticism (Goldberg, 1990; King & Figueredo, 1997; Weiss et al., 2006), whereas gentle and friendly are more typically linked to Agreeableness or Sociability (Adams et al., 2015; Wilson et al., 2018). Other items such as defiant, bullying, and aggressive tend to cluster within Dominance, as observed in bonobos and captive golden snub-nosed monkeys (Garai et al., 2016; Jin et al., 2013). In the present study, these varied behavioral tendencies converged within a single Assertiveness factor, capturing variation in emotional reactivity, affiliative tendencies, and competitive behaviors along a single continuum. Its lack of correlation with dominance rank supports the use of the term Assertiveness in this context and aligns with patterns described in baboons and macaques (Morton et al., 2013; Pritchard & Palombit, 2022). This dimension highlights individual variability that may be shaped by the demands of balancing affiliation, emotional arousal, and social competition in a multilevel social system. This interpretation is reinforced by behavioral evidence of ritualized conflict management and post-conflict reconciliation, such as embracing and holding in this species (Zhang et al., 2008a, 2010).

Openness in golden snub-nosed monkeys represented a composite of exploratory drive, activity, and vitality—an evolutionarily flexible trait that has arisen independently in multiple primate lineages (Robinson et al., 2016). In this study, loadings combined items typically associated with both Openness and Extraversion in the human Five-Factor Model (Goldberg, 1990). Items such as active, playful, lazy, and solitary, characteristic of Extraversion in chimpanzees, orangutans (*Pongo pygmaeus* and *Pongo abelii*), and langurs (King & Figueredo, 1997; Konečná et al., 2008; Weiss et al., 2006), were integrated with innovative, curious, and inventive, which align with Openness (Adams et al., 2015). Previous work suggests that high Openness may be favored under ecological conditions requiring exploratory foraging and learning (Konečná et al., 2012) and in socially complex systems with fission-fusion dynamics, where high activity levels influence interaction patterns (Eckardt et al., 2015). In golden snub-nosed monkeys, which inhabit high-altitude temperate forests and reside within complex MLSs, Openness may support adaptive behavioral flexibility and responsiveness to shifting ecological and social contexts.

Neuroticism, as defined here, encompasses threat sensitivity, withdrawal, and social avoidance, traits linked to conflict management style and competitive strategies (Eckardt et al., 2015; Konečná et al., 2012). Core loadings include

fearful, timid, vulnerable, anxious, and autistic, which have consistently been classified under Neuroticism in humans, orangutans, and other primates (Goldberg, 1990; Pritchard & Palombit, 2022; Weiss et al., 2006). Additional items such as submissive, manipulative, and dominant often align with Dominance in other primates (Eckardt et al., 2015; Weiss et al., 2006, 2021). However, in golden snub-nosed monkeys, the predominance of anxiety and fear-related loadings supports classification as Neuroticism, with aggressive traits contributing minimally. The observed negative correlation between Neuroticism and unit dominance rank may reflect anxiety-induced behavioral inhibition, particularly in natural contexts where avoidance is favored over direct conflict and where behavior is shaped by ecological pressures (Guo et al., 2020).

Sociability in the golden snub-nosed monkey represented a single composite dimension integrating social affiliation and individual autonomy. In frameworks where these aspects were separated into distinct personality dimensions, traits such as affectionate, sympathetic, and protective loaded on Agreeableness or Friendliness, while independent, individualistic, and depressed loaded on Neuroticism or Extraversion (Adams et al., 2015; Goldberg, 1990; Konečná et al., 2008). In species with stable and cohesive social structures, like gorillas and marmosets (*Callithrix jacchus*), a unified Sociability dimension has been reported (Eckardt et al., 2015; Weiss et al., 2021), reflecting enduring social roles and the capacity to maintain close bonds (De la Fuente et al., 2022; Robbins & Robbins, 2018). Social complexity may determine whether affiliation and autonomy emerge as distinct dimensions. In golden snub-nosed monkeys, although group membership occurs within an MLS structure, OMUs are internally egalitarian and lack a pronounced female dominance hierarchy. Such conditions may promote the emergence of a single Sociability dimension, consistent with the observed positive association between Sociability and grooming frequency, linking this trait to mechanisms of social cohesion.

Personality effects on social cohesion maintenance

A behavioral experiment was conducted to assess short-term individual contributions to unit cohesion, complemented by analysis of 12 behavioral variables and female transfer records as indicators of long-term social stability in breeding bands of golden snub-nosed monkeys. Integrating personality trait scores into this framework provided new insights into the mechanisms through which complex societies maintain social cohesion over varying temporal scales. In this species, multilevel social organization generates two distinct social contexts: the tightly integrated structure of the OMU and the more diffuse network spanning multiple OMUs. Our second hypothesis—that these contrasting contexts exert differential selective pressures on personality, fostering strategies that promote both intra-unit cohesion and inter-unit coexistence—was partially supported.

Within-unit cohesion was influenced by sex-specific personality profiles in golden snub-nosed monkeys. Resident males exhibited markedly higher Assertiveness scores than females, a pattern accompanied by elevated rates of aggressive behaviors alongside select affiliative behaviors, such as embracing and holding, and reduced engagement in self-directed behaviors. This combination mirrors patterns observed in other obligately social species inhabiting complex societies, where aggression and affiliation function as complementary elements of a unified social strategy rather than opposing tendencies (Grueter et al., 2012). In such systems, assertive interactions can consolidate social bonds and reinforce group structure, facilitating reconciliation processes and stabilizing group dynamics (de Waal, 1986). The conflict-cohesion hypothesis posits that groups exposed to external threats tend to intensify internal cohesion through heightened affiliative behavior (Thompson et al., 2020). As principal participants in intergroup confrontations, males may benefit from female alliance and post-conflict consolatory behaviors, thereby strengthening OMU stability (Zhang et al., 2010; Zhao et al., 2016). In contrast, females scored higher on Sociability, with elevated grooming rates—a core affiliative behavior fundamental to the establishment and maintenance of unit cohesion (Arlet et al., 2015; Nishikawa et al., 2014). Sociability is widely recognized as a key trait in cohesive social systems, underpinning enduring affiliative networks, reducing conflict, and fostering cooperative interactions (Gartland et al., 2022; Patzelt et al., 2014). Conversely, individuals with high Neuroticism engaged less frequently in affiliative behaviors, reflecting a strategy to minimize exposure to social stressors (Chapman et al., 2011). Neuroticism may not actively contribute to cohesion maintenance but instead may represent an adaptive response to the dominance hierarchy, favoring a passive role in social integration.

At the breeding band level, affiliative exchanges between OMUs were rare, with coordinated interactions among resident males occurring primarily during exceptional events such as bachelor incursions (Qi et al., 2017; Xiang et al., 2014). Consequently, inter-OMU coexistence and broader breeding band stability depended largely on female transfers (Fang et al., 2022). Such transfers likely reinforce kinship networks across units, promoting wider social integration through mechanisms such as female kin selection (Grueter et al., 2020). Although no significant personality differences emerged between transferring and non-transferring females in our study, Sociability and Openness demonstrated opposing effects of similar magnitude, suggesting potential trends that warrant further investigation despite not reaching conventional significance. Notably, weak evidence suggested that females transferring out of their natal units tended to have lower Sociability scores, while higher Openness scores were significantly associated with an increased likelihood of temporarily leaving the OMU. These tendencies may regulate inter-unit fluidity, facilitate reproductive opportunities, and reduce inbreeding probability in spatially structured populations (Guo et al., 2015).

This study was constrained by a modest sample size and the absence of repeatability measures for personality and behavior. Nonetheless, our results provide empirical evidence that personality structure contributes to the maintenance of cohesion and adaptability in complex societies, thereby expanding comparative models of primate personality. Longitudinal studies, particularly those incorporating all-male units, will be critical for elucidating the role of personality in cohesion dynamics. Comparative analyses across primate taxa and social systems are also warranted to integrate personality into models of social evolution and to clarify the evolutionary and proximate mechanisms driving personality variation and the emergence of complex sociality.

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

N.L.L. and B.G.L. conceived the ideas and designed the methodology; N.L.L. collected the data; R.H. designed and conducted behavioral experiments; C.L.W. and K.H. designed the statistical analysis methods; N.L.L. and K.H. analyzed the data; H.T.Z. and X.W.W. assisted with all fieldwork; N.L.L. and H.T.Z. led the writing of the manuscript. All authors read and approved the final version of the manuscript.

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