Social status predicts self-directed behaviors, contingent on broader social dynamics

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Abstract

Emotional states like anxiety are adaptive, preparing individuals to respond to (socially-)aversive situations. Humans can self-report anxiety, but assessing comparable states in animals requires objective measures. Self-directed behaviors (SDBs)—including self-scratch, autogroom, and yawn—are indicators of anxiety across species, particularly in nonhuman primates. Prevailing hypotheses suggest that social status modulates SDBs, as they offer predictability. Yet, it remains untested how broader social dynamics influence SDBs, given that they influence the quality of life of individuals. We studied 13 macaque groups across six species spanning four social styles (*despotic–egalitarian*). Our findings revealed partial correlational consistency among the elemental behaviors constituting composite SDB measures, highlighting their differential functions. Age and sex were associated with self-scratch and yawn. Individuals receiving more aggression self-scratched more frequently. While the most despotic species tended to exhibit least amounts of SDBs, within species' rank effects were non-linear. High-ranking individuals self-scratched less but yawned more, and alpha status was linked to increased yawning. This suggests (un)certainty in social interactions—mediated by individual rank and societal structure—influence anxiety. Thus, SDBs are not byproducts of subordination, instead reflect partially overlapping emotional responses. We provide insights into how social structure and complexity shape the evolution of emotion regulation.

Keywords

Affective states, Despotism, Emotional arousal, *Macaca*, Social anxiety, Social complexity, Social unpredictability, Stress

Introduction

Individual emotional states are mediated by physiological and behavioral changes across species, offering benefits that range from welfare to survival [1,2]. In social contexts, a common emotional state is anxiety – an individual's response to aversive situations or threats [3,4]. While adult humans can self-report their experience of anxiety, assessing this psychosocial or affective state in animals requires objective methodological approaches. Self-directed behaviors (SDBs), defined by behaviors directed toward the self, such as self-scratch, autogroom, and yawn [5], are powerful proxies to capture anxiety-related emotional states in animals [6]. Several hypotheses have been proposed to explain the functional mechanisms of SDBs, including social, environmental, and hygienic [6–10]. In particular, the social or anxiety hypothesis has received support from empirical research based on several species. By testing the discriminant validity of SDBs, previous research has found their positive correlations with physiological measures of anxiety and broadly 'stress'. For instance, post-conflict SDBs positively correlated with maximum heart rate in greylag geese (*Anser anser*) [11]. In European starlings (*Sturnus vulgaris*), acute crowding led to elevated SDBs, heart rates, and corticosterone concentrations [12]. SDBs increased when long-tailed macaques (*Macaca fascicularis*) were given anxiety-inducing drugs [13,14]. However, a lack of positive correlation between SDBs and those physiological measures was also reported (see [15–17]). Nonetheless, research on various social contexts, such as during allogrooming and conflict, has found systematic fluctuations in SDBs [18–21], establishing their mediating roles in anxiety. Thus, the consensus is that SDBs are displacement behaviors that do not necessarily reflect chronic stress (but see [22]) and are instead associated with transient or short-term emotional states with *coping* benefits [5,6,11,17,23–27], for example, helping individuals overcome challenges associated with stressful situations (e.g., during intragroup conflicts). Yet, considerable between-individual variation in the expression of SDBs is prevalent, and comprehensive evidence about their underlying proximate mechanisms is still poorly understood.

Demographic factors such as age and sex, as well as social factors like aggression, are known to be associated with SDBs and their variations. A decline in physical conditions with ageing can be associated with higher negative affective states [28]. Consequently, older individuals may use SDBs as a functional means of coping, or they may increase reliance on frequent hygienic activities [8,29]. By contrast, general life experience with ageing may lead to better emotional regulation [30], where individuals become more certain about their relationships with group members, potentially leading to a decrease in SDBs. Sex-level differences have been reported too, with males often showing higher SDBs than females [31]. For instance, yawning in males can lead to the exposure of large canines, carrying social information on dominance and promoting group stability. Inter-sex competition, including aggression [32], can also potentially lead to variations in SDBs. Thus, sex-level differences can be explained by the anatomical (*sensu* sexual dimorphism), physiological (such as concentration of androgens), as well as social (such as competition and aggression) factors [32–34]. However, sex-based variations in SDBs are not conclusive as comparable rates between females and males have also been reported (see [35,36]). Moreover, aggression can influence SDBs, irrespective of sex differences [8,37–39], with a positive association between receiving frequent aggression and exhibiting higher rates of SDBs. It is also noteworthy that SDBs are often represented as a composite measure in existing studies (e.g., see [17,29,40,41]), based on the assumption that the elemental

behaviors (i.e., self-scratch, autogroom, and yawn) exhibit correlational consistency, or simply due to limited sampling effort, rendering too little data on each behavior separately. Overall, while there is still a critical knowledge gap regarding how age, sex, and aggression are associated with specific elemental anxiety-related behaviors, the existing inconclusive evidence also points to the need to investigate other social factors.

In stable social hierarchies, social status or dominance rank influences SDBs. Particularly, the broad mechanisms – (un-)certainty in within-group social relationships and differential energetic constraints – can be grouped under two non-mutually exclusive hypotheses. The uncertainty hypothesis suggests that individuals lower in rank show more frequent SDBs than those higher in rank, potentially due to the associated uncertainty in subordinates regarding outcomes in social interactions, rendering emotional costs but potential coping benefits [38,41–45]. In subordinates, such 'reactive' coping benefits may come from heightened SDBs and 'flight' responses, helping them to avoid higher-ranking group members and potential conflicts, or to seek support from closely affiliated group members [6,38,46–48]. The energetic constraint hypothesis suggests that different ranks in a stable hierarchy are associated with unique costs and benefits and that stress-related responses are contingent on them [49]. In line with this hypothesis, the top ranks, such as the 'alpha status', are linked to elevated energetic demands (*sensu* 'executive stress syndrome') [49], potentially due to the heightened physiological costs of mating, functional needs for vigilance (e.g., against outgroup threats, but also intragroup competitors/challengers), and group maintenance. Yet, the directional associations between social status and physiological indicators of stress-related behaviors are not always consistent [50]. For instance, in despotic societies in which hierarchies are maintained through frequent physical reassertion of dominance, high-ranking individuals experience the most stress. By contrast, low-ranking individuals are susceptible to elevated stress in despotic societies when hierarchies are maintained through intimidation. Furthermore, in egalitarian societies, rank-related influences on stress are not apparent. This necessitates considering both inter- and intra-specific (i.e., between groups) variations, the stability of dominance hierarchies, and most importantly, the broader social dynamics such as social styles, while evaluating the mechanisms of SDBs [50,51].

The genus *Macaca* represents ~22 species of group-living primates, with similar social organizations yet strikingly different social tolerance levels or social styles [52–54], providing an excellent opportunity to comparatively investigate SDBs and their proximate mechanisms. The broader social styles (interchangeably used with tolerance grades) in macaques are shaped by socio-ecologically and phylogenetically co-varying structural traits [52–55], reflected mainly by how individuals tolerate each other within a group. These co-varying traits include hierarchical steepness of dominance, coalitionary tendencies, and nepotistic and kin biases. While robust comparative empirical evidence is still rare, some studies show that these traits indeed covary, and macaque species or societies can be categorized under four distinct grades along a despotic–egalitarian gradient [56–58]. Despotic societies are primarily associated with steeper dominance hierarchies and also more frequent aggressive interactions than egalitarian ones [56,59]. From grade one (or despotic end) to four (or egalitarian end), social tolerance is considered to increase (but see [60]). Accordingly, primatologists use these grades to distinguish the different macaque species and to test various ecological, social, and cognitive hypotheses. As varying social styles can influence the lives of individuals at the physiological [61], behavioral [62], and cognitive [63] levels,

SDBs can potentially be shaped by them too. Furthermore, rank-related uncertainties are higher in more egalitarian than despotic societies, claiming egalitarian societies as “complex” with regard to within-group communication and interaction [64,65]. Yet, how social styles drive SDBs through rank-related influences and whether SDBs generally vary across social styles remains rarely investigated. Therefore, a comparative assessment of SDBs across macaque societies representing the four social styles can provide critical insights into their functions and, broadly, evolution.

Here we comparatively investigated three different SDBs (self-scratch, autogroom, and yawn) across six macaque species – Japanese (*Macaca fuscata*), rhesus (*M. mulatta*), long-tailed (*M. fascicularis*), lion-tailed (*M. silenus*), barbary (*M. sylvanus*), and crested (*M. nigra*) macaques. These species represented all four social styles (Grade 1: *M. fuscata* and *M. mulatta*; Grade 2: *M. fascicularis*; Grade 3: *M. silenus* and *M. sylvanus*; Grade 4: *M. nigra*, cf. [52–54]). In our comprehensive dataset including 113 individuals (>4 years of age) and 524 hours of observation (mean = 4.6 hours/individual), we investigated (i) whether the three SDBs show correlational consistency, (ii) the associations of SDBs with two demographic factors: age and sex, (iii) the influence of aggression on SDBs, (iv) the influence of social styles on SDBs, i.e., whether SDBs varied across social styles, and finally (v) the effects of social ranks on SDBs within each social style, i.e., the predictions of the uncertainty and energetic constraint hypotheses. Notably, while our decision to analyze SDBs at the composite methodological construct- or the elemental behavior-level was contingent on checking the correlational consistency or the first part of analysis (cf. point 1), we made the predictions at the composite SDB level.

We made a two-tailed prediction for age: older individuals would exhibit either higher (due to the general decline of physical conditions leading to increased hygienic requirements) or lower (due to better emotion regulation and more certainty of social relationships) amounts of SDBs. Furthermore, aligning with the dimorphism hypothesis, we expected that SDBs would vary between females and males, with males showing higher SDBs than females [33,34]. Finally, we expected a relationship between aggression and SDBs, specifically with individuals receiving more frequent aggression exhibiting higher amounts of SDBs.

We further hypothesized that SDBs would vary with the broader social styles of the species as well as with an individual’s social rank within those social styles. For social styles, we had two alternative predictions. If despotism intensifies social stress through frequent aggressive interactions and intimidation (cf. [52,59]), then individuals in more despotic societies are expected to exhibit higher rates of SDBs than those in more egalitarian societies. Alternatively, if egalitarian societies are characterized by more fluid and less predictable (i.e., more complex) social relationships (cf. [41,63]), individuals in these societies would experience higher social uncertainty than those in despotic societies, subsequently leading to increased SDBs. Since the influence of broader social dynamics or hierarchy on individuals cannot be disregarded (cf. [50]), our predictions for social ranks driving SDBs were not generalized. The effects of ranks were not checked overall; instead, they were checked separately within each social style. Moreover, due to the non-mutually exclusive nature of the uncertainty and energetic constraint hypotheses, we expected complex non-linear relationships between ranks and SDBs (cf. [49]) within the social styles. In particular, if despotic societies are managed by intimidation, we predicted that lower-ranking individuals would display higher amounts of SDBs than their higher-ranking group members due to

uncertainty in the outcomes of social interactions. Such rank-related influences would potentially not exist in more egalitarian societies (cf. [50,51]) due to the lack of intimidation. If higher ranks are associated with unique costs, such as elevated energy demands (cf. [49]), then the highest ranks or the alpha status, irrespective of social style and species, would be associated with higher amounts of SDBs than the rest of the group members.

Materials and Methods

Ethical permissions

We received ethical approval from the Animal Experiments Committee and the Animal Welfare Organisation at the Biomedical Primate Research Centre (BPRC) (approval no. 019E). At each participating zoo, internal ethical committees further approved and carefully monitored the research procedures. Observations were carried out from considerable distance without deliberately influencing the behavior of animals. The entire study was strictly non-invasive in accordance with European Directive 2010/63, and we followed the guidelines set forth by the American Society of Primatologists regarding the appropriate treatment and inclusion of animals.

Study subjects

We observed 13 captive macaque groups across six species—*Macaca fuscata*, *M. mulatta*, *M. fascicularis*, *M. silenus*, *M. sylvanus*, and *M. nigra*—in their existing social environments. See **Table S1** for details on the subjects, and housing and husbandry protocols. Only individuals ≥ 4 years – considered sexually mature [66,67] – at the time of testing (n = 113) were included in the study and analyses (see **Table S1**). All groups had unrestricted access to fresh drinking water. No alterations were made to feeding protocols for the purposes of this research. Behavioral observations were conducted in a randomized sequence to minimize bias. The animals were well habituated to the presence of the observers and exhibited no signs of stress during data collection.

Behavioral data collection using continuous focal sampling

Behavioral observations were carried out using the continuous focal sampling method between late 2020 and early 2023. We conducted these observations from 0800 to 1830 hours. Each focal observation lasted 20 minutes without periods when the individual was out of sight. The order in which focal animals were observed was randomized. From the 113 individuals (≥ 4 years, range: 4 – 29 years; female = 92, male = 21), we obtained a total of 31,480 minutes of behavioral data (**Table S1**). The mean (± SD) observation minutes per individual was 278.58 ± 75.23 (range = 160 – 460 min). The number of observation minutes differed across groups, largely due to the varying group sizes. Focal data were used to assess SDBs, dominance ranks, as well as aggressive behaviors.

Self-directed behaviors

We investigated three widely recognized SDBs – self-scratch, autogroom, and yawn [5,6,13,16,23,41,68]. Self-scratch was defined by the events when an individual used their

finger, hand, or foot to rake across their own skin. Autogroom was defined by an individual grooming themselves by closely inspecting the skin, hands, nails, toes, or other body parts. Finally, we used the widely accepted definition of yawn (cf. [68]) – an involuntary and powerful gaping of the jaw with deep inspiration, followed by a temporary period of peak muscle contraction and a passive closure of the jaw with shorter expiration. We calculated the rates of self-scratch and yawn (frequency per minute) separately to control for the varying observation minutes across groups and species. For autogroom, we quantified the duration and controlled for the observation variation by calculating seconds per minute. A new autogroom bout was considered if it was resumed after an interval of at least 5 seconds to account for data independence.

Aggression initiated and received

We extracted data on five behavioral variables (*lunge, open-mouth threat, physical attack/hit*, *bite,* and *chase*, see [69] for definitions) that represented both contact- and non-contact aggression. For each individual, we calculated the rates (frequency per minute) of aggression initiated (toward others) and aggression received (from others). By calculating rates, we controlled for the varying observation minutes across groups and species.

Dominance rank and social style

Based on five variables that represent unprovoked submissive behaviors (*avoid*, *be displaced*, *silent-bared teeth*, *flee*, and *social presence*, see [69] for definitions), we assessed individual dominance (or social) ranks as well as the steepness of the within-group dominance hierarchies using a Bayesian Elo-rating method. For all groups, except the *M. fuscata*, we used previously published data to obtain these values [60]. Individual dominance ranks were obtained as ordinal ranks at the group level. For *M. fuscata*, the limited number of dyadic unprovoked submissive interactions could not be used to reliably calculate the ordinal ranks. Therefore, we used previously published results on the matrilines to which those individuals belong [70]. Since the sampled individuals were adult females only in the *M. fuscata* group (cf. **Table S1**), matrilineal rank inheritance can be assumed [71], and these alternative measures can be useful to determine ordinal ranks of the individuals. Nonetheless, we took caution while performing statistical analyses using this group in some cases. Due to the relatively long-term data collection (i.e., across ~8 months per group), hierarchies were assumed to be stable, and no rank reversals could be seen during observations.

The steepness of hierarchies followed the assumption of the co-variation framework (cf. [52–54]) that more despotic societies show higher steepness than more egalitarian ones [60]. Previously published data on our study groups found a moderate to strong correlation between macaque tolerance grades (or social styles) and hierarchy steepness (with all individuals: r = -0.33; with only adult females: r = -0.61) [60]. The fulfillment of this assumption, based on empirical data, validated our assignment of social styles to the species we investigated.

Data coding

Video-recorded data were coded using BORIS (version 7.13.6) or in a frame-by-frame manner using PotPlayer (version 240618). Due to data coding by multiple trained coders (by

D.B., E.S.J.vD., R.E.M.dV., C.E.K., M.V., and A.N.Z., with assistance from 14 more coders), we comprehensively checked for inter-rater reliability. The agreement check was performed after all the coders became fully trained to code behavioral data. Overall, the agreement was high (Intraclass correlation coefficient or ICC(3,k) = 0.88, including SDBs, dominance rank, and aggression). Particularly, for the SDBs, the ICC(3,k) value was 0.94, suggesting excellent agreement among all coders.

Statistical models and packages

Statistical analyses were conducted in R (version 4.1.1) [72]. We used Spearman's rank correlation tests to investigate how the three SDBs were associated with each other, i.e., whether they showed strong correlational consistency. Furthermore, Spearman's rank correlation tests were used to investigate the associations of the three SDBs with age and rates of aggression (initiated and received). To assess sex-level associations with SDBs, Wilcoxon rank-sum tests were performed.

We conducted Bayesian mixed modeling analyses to evaluate whether SDBs varied across macaque tolerance grades. We specifically built three models (*first set of models*) for each of the three SDBs modeled as a function of categorical tolerance grade (Grades 1 to 4). Given the right-skewed distribution of the SDBs, we specified skew-normal distribution, which allowed for modeling asymmetry in the response distribution via an additional shape parameter. We used weakly informative priors: a normal prior with a mean (m) of 0 and a standard deviation (SD) of 5 for the intercept term, a normal prior for the fixed-effect coefficient with m = 0 and SD = 1, and an exponential prior with a rate parameter of 1 to the SD of the random effects. Due to the hierarchical structure of our data, we included random effects of groups nested within species. Additionally, to account for the varying group sizes, log-transformed offset terms were added to the models.

To investigate whether social ranks predicted self-scratch, autogroom, and yawn at the tolerance grade level, we again took a Bayesian approach. We built 12 Bayesian mixed models (*second set of models*) for the three SDBs for each grade. For all these 12 models, rank was modeled using a natural spline with three degrees of freedom to capture potential nonlinear effects. Unlike the first set of Bayesian models, here we used Gaussian distributions. To achieve normality, square-root transformations of the response variables were performed in relevant models. All priors were similar to that of the first set of models, except we used a SD of 2 or 5 for the normal prior of the intercept term. The random intercepts and offset term were also identical to that of the first set of models. For sufficient convergence, Bayesian models were subjected to 5500 iterations with 1000 warmup sessions. We reported median estimate coefficients (*Est*), 95% credible interval (*crl*), containing 95% of the posterior probability density function, and probability of direction (*pd*) that indicated certainty of an effect. We established model convergence by following Bayesian statistics guidelines [73]. Furthermore, we checked trace and autocorrelation plots, Gelman-Rubin convergence estimations, and density histograms of posterior distributions. The posterior distributions were sampled using 10,000 iterations and 2000 warmups. We used the "*DHARMa.helpers*" package [74] and investigated model fits by examining the residual distributions (i.e., deviation, dispersion, and outliers). Finally, Wilcoxon rank-sum tests were carried out to compare SDBs between alpha individuals and the rest of the individuals.

Results

Self-directed behaviors in macaques show partial correlational consistency

Our results revealed only partial correlational consistency in these behaviors (**Figure 1**). Individuals exhibiting more frequent self-scratch also engaged in more prolonged autogrooming (Spearman's rank correlation test: *rho* = 0.35, *n* = 113, 95% CI [0.17 – 0.50], *p* < 0.001, **Figure 1a**). Individuals who self-scratched more frequently also yawned more often (*rho* = 0.26, *n* = 113, 95% CI [0.07 – 0.42], *p* < 0.001, **Figure 1b**). However, autogroom and yawn were not correlated (*rho* = 0.16, *n* = 113, 95% CI [-0.03 – 0.34], *p* = 0.09, **Figure 1c**). The low to moderately strong correlation coefficients of the significant relationships and the non-significant pattern for autogroom and yawn indicate that these behaviors may have varying underlying drivers and that they only serve partially overlapping functions. Therefore, we analyzed the three SDBs separately in all subsequent analyses, rather than combining them into one composite measure.

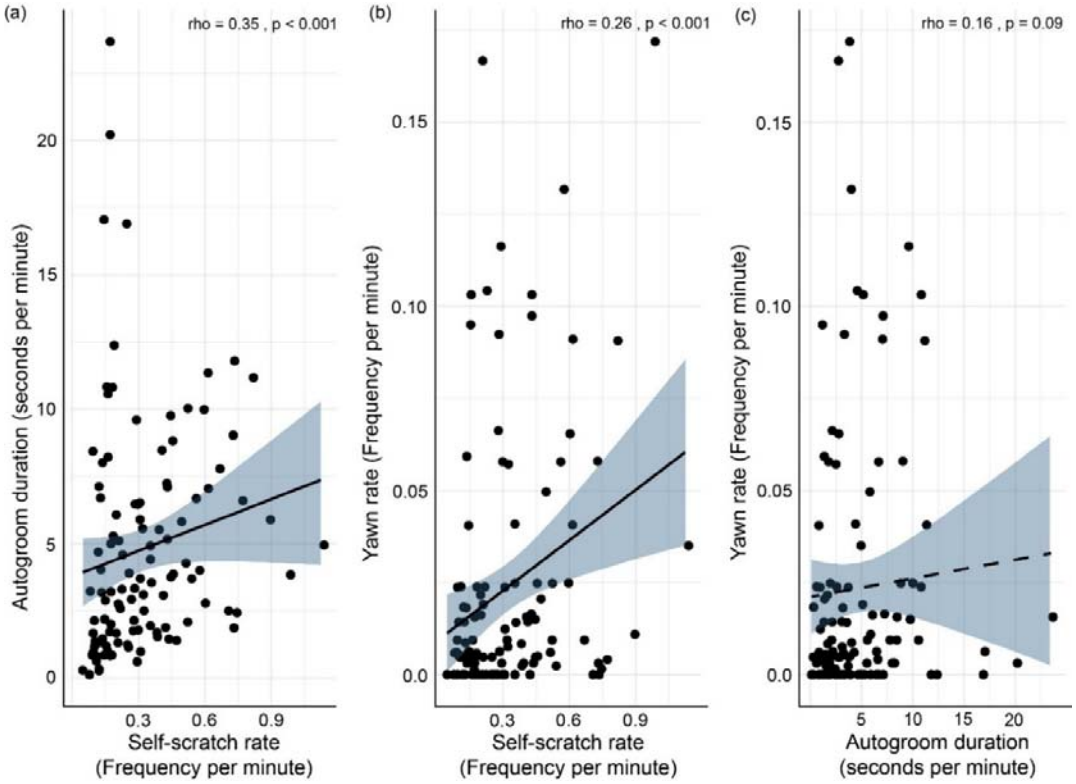

Figure 1. Self-directed behaviors partially correlate with each other. (a) Correlation between the duration of autogroom and self-scratch rate (*rho* = 0.35, *p* < 0.001). (b) Correlation between the rates of yawn and self-scratch (*rho* = 0.26, *p* < 0.001). (c) Correlation between the duration of autogroom and yawn rate (*rho* = 0.16, *p* = 0.09). Spearman's rank correlation coefficients are represented by *rho,* and significance by *p*-values. The shaded areas represent 95% confidence intervals. Solid black dots show the distribution of data.

Age- and sex-level associations in self-directed behaviors

Older individuals exhibited lower rates of self-scratch behavior (Spearman's rank correlation test: *rho* = -0.26, *n* = 113, 95% CI [0.08 – 0.43], *p* = 0.004, **Figure 2a**). No significant relationship was found between age and autogroom (*rho* = -0.08, *n* = 113, 95% CI [-0.26 – 0.11], *p* = 0.40, **Figure 2b**). Similarly, age and yawn were not correlated (*rho* = -0.03, *n* = 113, 95% CI [-0.22 – 0.15], *p* = 0.71, **Figure 2c**).

The mean (±SD) rates of female and male self-scratching were 0.29 ± 0.20 and 0.45 ± 0.23, respectively. Males displayed more frequent self-scratch than females (Wilcoxon rank-sum test: *z* = -3.08, Cohen's d = 0.58, *p* = 0.002, **Figure 2d**). The mean durations of autogroom in females and males were 4.57 ± 4.35 and 5.62 ± 3.57 seconds per minute, which was comparable (*z* = -1.70, Cohen's d = 0.32, *p* = 0.08, **Figure 2e**). The yawn rates were 0.012 ± 0.018 and 0.075 ± 0.047 in females and males, respectively. We found that males yawned more frequently than females (*z* = -5.97, Cohen's d = 1.12, *p* < 0.001, **Figure 2f**).

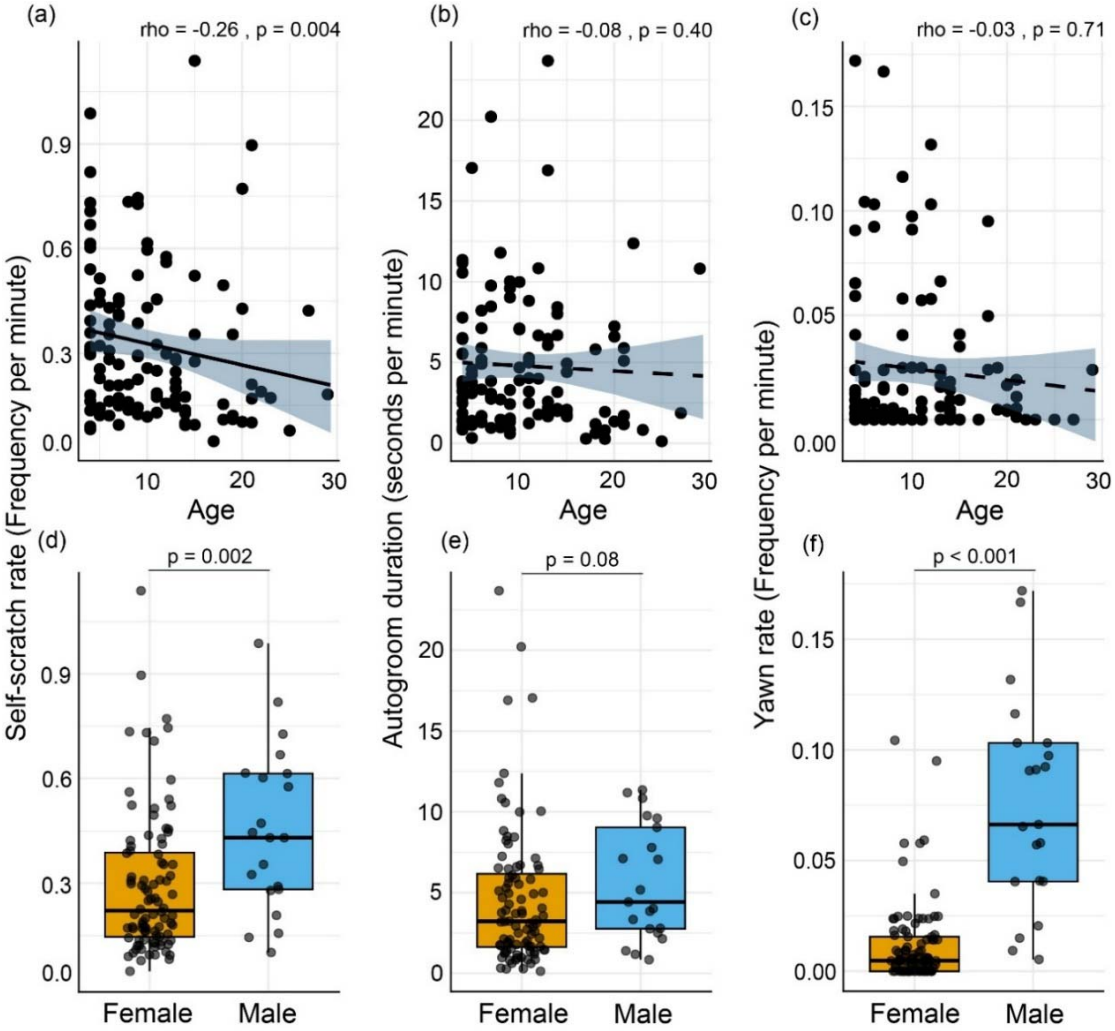

Figure 2. Associations of age and sex with self-directed behaviors independent of species and social styles. (a) Correlation between age and self-scratch rate (*rho* = -0.26, *p* = 0.004). (b) Correlation between age and duration of autogroom (*rho* = -0.08, *p* = 0.40). (c) Correlation between

age and yawn rate (*rho* = -0.03, *p* = 0.71). (d) Rate of self-scratch between females and males (*p* = 0.002), (e) Duration of autogroom between females and males (*p* = 0.08), (f) Rate of yawn between females and males (*p* < 0.002). In a–c, Spearman's rank correlation coefficients are represented by *rho,* the shaded areas represent 95% confidence intervals, and solid black dots show the distribution of data. In d–e, boxes represent interquartile ranges, and whiskers represent the upper and lower limits of the data; the horizontal bars within the boxes represent median values, and solid black dots show data distribution.

More frequently receiving aggression corresponds to elevated self-scratch behavior

Aggressive interactions among group members are often considered influential factors shaping SDBs [8,38]. We tested whether SDBs were associated with the rates of *aggression initiated* (towards group members) and *received* (from group members). Notably, group- and species-level variations were not accounted for, as our primary interest lay in the general relationship dynamics between aggression and SDBs. We found no significant associations between aggression initiated and the three SDBs (Spearman's rank correlation test: self-scratch - *rho* = -0.02, *n* = 113, 95% CI [-0.20 – 0.16], *p* = 0.81; autogroom - *rho* = -0.10, *n* = 113, 95% CI [-0.28 – 0.08], *p* = 0.26; yawn - *rho* = 0.15, *n* = 113, 95% CI [-0.04 – 0.32], *p* = 0.11). However, unlike aggression initiated, individuals who received aggression more frequently also self-scratched more often (*rho* = 0.31, *n* = 113, 95% CI [0.13 – 0.47], *p* < 0.001). No significant associations were found between aggression received and either autogroom or yawn (autogroom: *rho* = 0.02, *n* = 113, 95% CI [-0.16 – 0.21], *p* = 0.76; yawn: *rho* = 0.10, *n* = 113, 95% CI [-0.08 – 0.28], *p* = 0.27). The only significant relationship of aggression with self-scratch, and not autogroom or yawn, further suggests that the elemental behaviors have varying underlying mechanisms.

Self-directed behaviors are comparable across macaque social styles

Based on empirical data [60], we found that the steepness of hierarchies of our study groups aligned with the assumption of the co-variation framework (cf. [52–54], also see **Methods**). In other words, more despotic societies indeed had steeper hierarchies than more egalitarian ones [60], validating the assignment of tolerance grades or social styles to the different species within our sample, and warranting tests of the uncertainty hypothesis across our study groups.

The mean (±SD) rates (frequency/min) of self-scratch were 0.18 ± 0.08, 0.36 ± 0.25, 0.46 ± 0.21, and 0.41 ± 0.22 for Grades 1, 2, 3, and 4, respectively (**Figure 3a**), whereas the mean durations (seconds/min) of autogroom bouts were 3.14 ± 2.98, 8.61 ± 5.70, 5.12 ± 3.34, and 3.13 ± 2.52 (**Figure 3b**). Likewise, the mean rates of yawn were 0.01 ± 0.02, 0.02 ± 0.04, 0.03 ± 0.04, and 0.03 ± 0.04 for the four tolerance grades (**Figure 3c**). After controlling for varying group sizes in the models (see **Methods**), we found no strong evidence that any of the three SDBs varied significantly across tolerance grades (**Table S2–S4**). However, there was a clear trend for species in Grade 1 to exhibit the lowest levels of SDBs, and particularly self-scratching, compared to species in other grades (cf. **Figure 3**). While tolerance grade

level differences in SDBs were not that apparent, we next tested whether individual social ranks within each grade predicted SDBs.

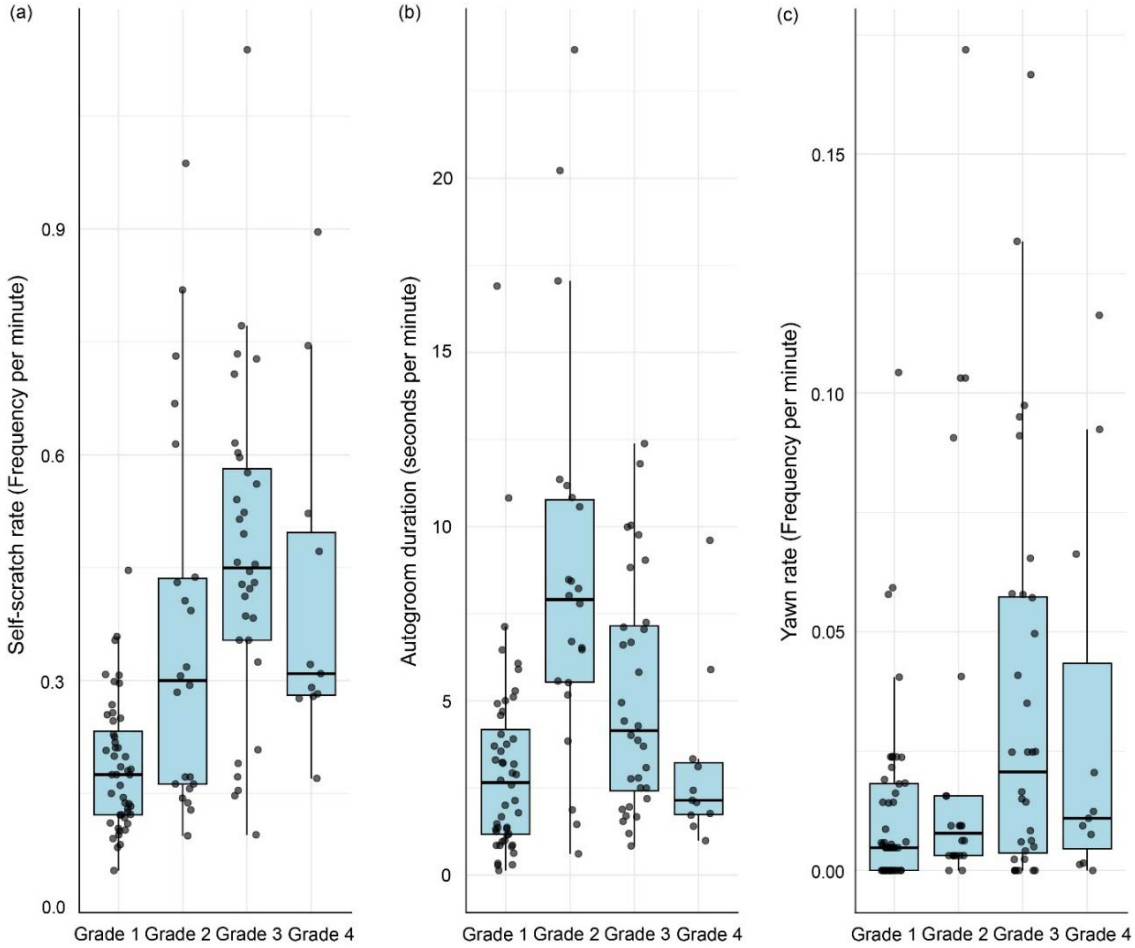

Figure 3. Self-directed behaviors across macaque tolerance grades. (a) Rate of self-scratch behavior, **(b)** Duration of autogroom, and **(c)** Rate of yawn behavior. Boxes represent interquartile ranges, and whiskers represent the upper and lower limits of the data. The horizontal bars within the boxes represent median values. Solid black dots show the distribution of data.

Dominance ranks have complex non-linear relationships with self-scratch and yawn

In Grade 1, we found a non-linear effect of rank predicting self-scratch behavior. Specifically, the second spline component was associated, indicating less frequent self-scratching among the highest- and lowest-ranked individuals than the intermediate-ranked ones (Estimate or *Est* = 0.21, 95% critical interval or *crl* [0.03 – 0.38], probability of direction or *pd* = 0.99; **Figure 4a and 4i**, **Table S5**). No effect of rank on self-scratch was found in Grades 2, 3, and 4 (**Figure 4c, 4e, 4g**, **Table S6–S8**). We did not find any effect of rank on autogroom for the four tolerance grades (**Table S9–S12**). For yawn behavior, we found strong effects of rank in all grades except Grade 4 (**Figure 4g**, **Table S13**). In Grade 1, a non-linear relationship was found (third spline component), indicating higher yawn rates in highest- and lower-ranked individuals than intermediate ones (*Est* = 0.11, 95% *crl* [0.05 – 0.18], *pd* = 0.99; **Figure 4b**

and **4j**, **Table S14**). Strong non-linear relationships, but for the second splines, were found in Grades 2 and 3, indicating lower rates of yawn behavior in intermediated-ranked individuals than their higher- and lower-ranked counterparts (Grade 2: *Est* = -0.27, 95% *crl* [0.11 – 0.44], *pd* = 0.99; **Figure 4d** and **4k**, **Table S15**; Grade 3: (*Est* = -0.25, 95% *crl* [0.04 – 0.46], *pd* = 0.99; **Figure 4f** and **4l**, **Table S16**).

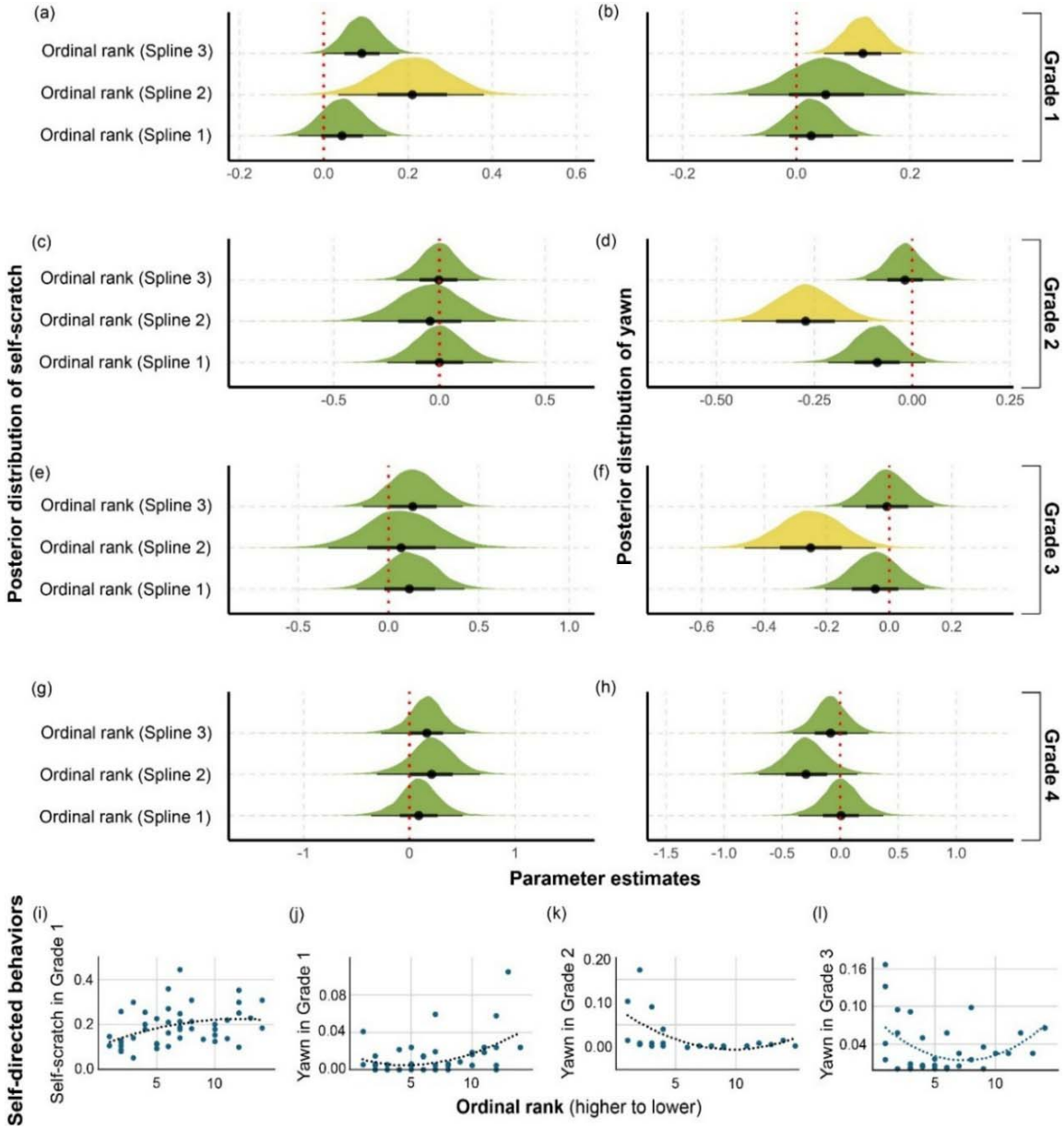

Figure 4. Effects of dominance ranks on self-scratch and yawn in macaque species belonging to four tolerance grades. (a-b) The posterior predictive effects of ordinal ranks on self-scratch and yawn in Grade 1 species. (c-d) The posterior predictive effects of ordinal ranks on self-scratch and yawn in Grade 2 species. (e-f) The posterior predictive effects of ordinal ranks on self-scratch and yawn in Grade 3 species. (g-h) The posterior predictive effects of ordinal ranks on self-scratch and yawn in Grade 4 species. (i) Non-linear relationship between rank and self-scratch in Grade 1 species. (j) Non-linear relationship between rank and yawn in Grade 1 species. (k) Non-linear relationship between rank and yawn in Grade 2 species. (l) Non-linear relationship between rank and yawn in Grade 3 species. In a-h, the width of the 'half-eye' represents data distribution (95% *crl*), and

solid black points on the horizontal bars indicate median values. The vertical red dashed lines indicate a parameter estimate of zero, i.e., the overlap of the credible interval with this line suggests no effect of the corresponding predictor. The yellow color highlights strong effects. In i-l, the black dashed lines indicate the non-linear trendlines, and the solid dots show data distribution.

Yawn under pressure? Alpha status is linked to increased rates of yawn

The alpha status may come at an elevated energetic cost in comparison to immediate or more subordinate group members [49]. Since the non-linear effects of dominance rank on SDBs indicated similarly complex patterns, we additionally compared each SDB between alpha (n = 12) individuals and the rest (n = 75), independent of species or social styles. We used the SDB values from the respective alpha individuals and the rest of the group members from all study groups. However, we discarded the data on *M. fuscata* particularly for these comparisons for two reasons: males were not included in the sample, and dominance rank relationships were assessed through matrilineal ranks. The mean (±SD) rates of self-scratch for alpha and the rest were 0.326 ± 0.154 and 0.362 ± 0.244, respectively. We found no significant difference in self-scratch rates between the two categories (Wilcoxon rank-sum test: z = -0.05, p = 0.95, **Figure 5a**). The mean (±SD) durations of autogroom bouts for alpha and the rest were 5.105 ± 3.628 and 4.984 ± 4.533, respectively. Like self-scratch, we did not find any significant difference in the duration of autogroom (z = 0.47, p = 0.63, **Figure 5b**). Finally, the mean (±SD) rates of yawn for alpha and the rest were 0.068 ± 0.054 and 0.022 ± 0.032, respectively. Unlike self-scratch and autogroom, we found that alpha individuals yawned more frequently than those of other ranks (z = 3.23, p = 0.001, **Figure 5c**).

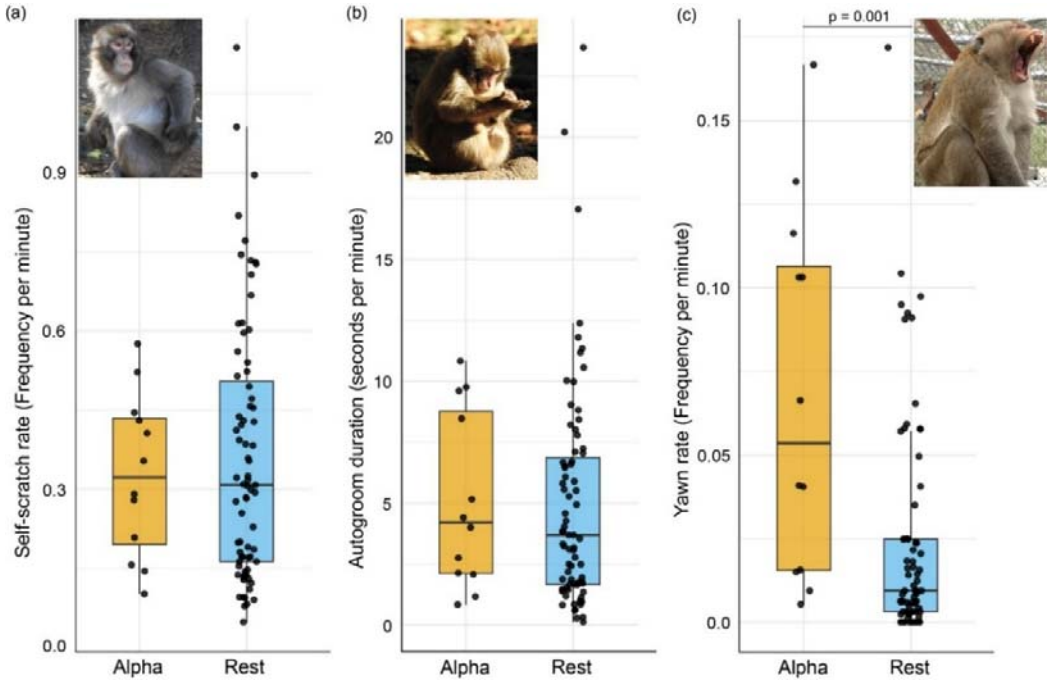

Figure 5. Self-directed behavior between alpha individuals and the rest. (a) Self-scratch rates between the highest-ranked individuals and the rest. (b) The duration of autogroom bouts between

the highest-ranked individuals and the rest. (c) Yawn rates between the highest-ranked individuals and the rest. Boxes represent interquartile ranges, and whiskers represent the upper and lower limits of the data. The horizontal bars within the boxes represent the median values. Solid black dots show the distribution of data. The *p*-value shows significance. Macaque photo credits: Jana Jäckels (a & b), Monkey Reality project from Animal Behaviour & Cognition group, Utrecht University (c).

Discussion

SDBs are displacement behaviors that mediate anxiety-like emotional states and serve crucial functions, like assisting individuals to avoid potential conflicts or seek support from closely affiliated group members through visual means [6,13,22,41]. Yet conclusive evidence on the proximate drivers underlying variations in SDBs is lacking. We conducted extensive behavioral observations on macaques from six different species that varied along a despotic–egalitarian gradient, and investigated three widely recognized SDBs: self-scratch, autogroom, and yawn. Our results show that these elemental behaviors only partially correlate with each other. Overall, we found support for self-scratch as a reliable behavioral indicator of anxiety-like emotional states. Also, importantly, we provide compelling evidence that both broader social dynamics and individual social status within them shape the elemental behaviors (cf. [50,51]), and that they together explain the functional mechanisms of certain behaviors better.

Partially overlapping social functions of self-scratch, autogroom, and yawn

To broadly explain the functions of SDBs, several hypotheses have been proposed, ranging from social and environmental to hygienic [6–10]. A study comparing the explanatory power of these three hypotheses found stronger support for the parasitic or hygienic model over the other two (cf. [8]). However, they also found support for social status (dominance rank) and the uncertainty (presence of nearby group members) of social interactions predicting SDBs. In the current study investigating the social or emotional aspects of SDBs, we found that not all three elemental behaviors (i.e., self-scratch, autogroom, and yawn) positively correlated. This is clearly indicative of partially overlapping social functions and underlying mechanisms attributed to the elemental behaviors constituting the typical composite SDB measures. This is further corroborated by the fact that each of these elemental behavior was differentially influenced by some of the demographic and social factors we looked at. Consequently, our findings call for the re-evaluation of several previous studies using composite SDB measures as proxies for anxiety, and we thus strongly advocate for treating these measures separately in future research.

Demographic factors and aggression predict self-scratch and yawn but not autogroom

We found that older individuals engaged in less frequent self-scratch behavior than their younger counterparts. This finding is line with the hypothesis that established social status of relatively older individuals in a group and/or their general life experiences may lead to better emotional regulation [75]. It could potentially also suggest a role of successful social ageing in driving anxiety-related behaviors and in general, emotional states [76]. That is, with ageing, individuals may limit their social connections but can maintain or even increase the strengths of such connections, subsequently leading to lower exhibition of anxiety-like

behaviors. In humans, greater social contacts have been found to alleviate ageing anxiety, too [77], indicating the evolutionary parallels of emotion regulation between human and nonhuman primates. However, autogroom and yawn were not dependent on age. This lack of association of age with autogroom and yawn corroborated the findings of some previous research (see [78,79]).

Unlike age, sex, was strongly associated with self-scratch and yawn, but not with autogroom. Males displayed higher rates of both self-scratch and yawn than females. For autogroom, there was a trend in the similar direction. More frequent self-scratching by males than females could be attributed to the lack of sufficient social buffering for males, as strong social bonds are often restricted to females, which is the philopatric sex in macaques [80]. By contrast, sex-specific bias in yawning can be explained by sexual dimorphism (cf. [33,34]). Since males are more dominant than females in macaque societies, males may exert dominance and signal threats by yawning more as they possess larger canines than females.

As per our prediction, we found that individuals who received more frequent aggression from group members also self-scratched at higher rates. This finding aligns with previous research [8,37–39,81], and clearly points towards the fact that self-scratch indeed mediates negative emotional states. However, the non-significant relationships of autogroom and yawn indicate that direct social interactions in the form of aggression may not be a prerequisite to elicit anxiety-related emotional states (but see [37–39]). Nonetheless, these results further underline the differential mechanisms and functions of the three behaviors.

Despotic societies tend to show the least amounts of SDBs

Our results revealed no strong social style level variations in self-scratch, autogroom, and yawn. However, individuals belonging to the most despotic social style (i.e., Grade 1) showed a tendency to exhibit lower levels of these behaviors than others. These patterns are contradictory to the prediction that despotism inflicts pressure on individuals in the form of power asymmetries and frequent aggressive interactions, and that individuals are highly susceptible to negative emotions like anxiety [52,54,59,82]. In line with our findings, a comparative study between despotic long-tailed and egalitarian Tonkean macaques (*Macaca tonkeana*) showed that long-term cortisol concentrations (used as an indicator of stress) were higher among individuals of Tonkean than those of long-tailed macaques [61]. While harsh leadership (such as in despotic societies) can induce stress among humans [83], macaques belonging to the despotic social styles can rely on alternative mechanisms to alleviate and cope with anxiety, such as forming and maintaining selectively strong bonds [84–86] as a social buffer [87] (*sensu* social buffering hypothesis [47]) and engaging in discriminate cooperative and prosocial interactions [60,88–91]. By contrast, in egalitarian societies, such inter-individual bonds are not necessarily predictable, strong, and stable [59–61,92], potentially dampening the positive effects of tolerance [48]. Moreover, a recent study using the same groups (except the Japanese macaques) as the current, experimentally showed that co-feeding tolerance levels were higher in more despotic societies (cf. [60]). Therefore, the strong selective bonds in despotic societies might have been translated into higher tolerance, which in turn resulted in less frequent exhibition of SDBs.

The alternative prediction, i.e., higher social uncertainty in more egalitarian than despotic societies, was partially supported, at least based on the trend in the most despotic society. Due to the predictable nature of social relationships in despotic societies, individuals are certain about the possible outcomes of social interactions, subsequently exhibiting lower levels of SDBs. By contrast, higher uncertainty in less despotic or more egalitarian societies can lead to individuals showing greater levels of SDBs. Notably, social uncertainty is considered a critical measure of social complexity [64,65]. Thus, in other words, we can assume that social complexity can play a role in driving anxiety-like behaviors, which should be tested in future studies.

Individual social status predicts self-scratch and yawn, but only within certain social styles

Individual social status or dominance ranks within certain social styles were intricately associated with self-scratch and yawn, reflected by their complex non-linear relationships. Moreover, these rank-related effects and their directions were not consistent for self-scratch and yawn, and also greatly varied across social styles, further stressing the potential differential mechanisms governing the different SDBs and emphasizing the role of broader social dynamics in driving them. Notably, the lack of an effect of dominance rank on autogroom has also been reported previously (see [81]).

Our findings partially support the predictions of both uncertainty and energetic constraint hypotheses. Self-scratch was predicted by dominance rank only in the most despotic social style. The rate of self-scratch gradually increased from higher to lower ranks, but started to decline again among individuals with lowest-ranks. Such a pattern could be attributed to both certainty and the unique costs and benefits of social ranks in despotic societies (cf. [38,41,44]). The relatively higher self-scratch rates among intermediate-ranking individuals could potentially be due to the high probabilities of rank mobility, whereas, the highest and lowest ends of the spectrum remain somewhat reserved [93].

Yawning was predicted by rank in Grades 1 to 3. The consistently elevated rates of yawning among higher-ranking individuals indicate the heightened physiological demands of mating, vigilance, and group maintenance. This was even further strongly supported by the finding of increased yawning among alpha individuals in comparison to the rest (cf. [49]). In particular, frequent yawning by alpha individuals can convey social signals of dominance (i.e., by exposing canines) to other group members [94,95], which can help maintain the stability of social groups. Alternatively, although not mutually exclusive, yawns are known to function as a brain cooling mechanism and may become more frequent in alpha individuals due to their high loads of vigilance [96]. While elevated rates of yawning in higher-ranking individuals can reflect on certain energy demands, it might be indicative of different emotional costs in lower-ranking individuals. Thus, it is possible that the lower-ranking individuals are probably ‘certain that they are uncertain’ in predicting the outcomes of social interactions (also see [97]), subsequently leading to elevated rates of yawning. These results may also suggest the probable mechanisms of vigilance and social tension at play for lower-ranked individuals. Nonetheless, the functions of yawning are multifaceted, and more interdisciplinary research is required to assess its role with regard to social dynamics.

Conclusion

Research on anxiety-like emotional states in animals predominantly includes specific social contexts, like affiliative interactions and conflicts, and often uses social variables like proximity to neighbors (to assess dominance and indirect social influence of group members on others). However, complex emotional states like anxiety are shaped by the continuous and multifaceted processes of social interactions, including broader social dynamics. We show that a composite behavioral construct is not appropriate in assessing anxiety-like states in macaques, recommending for the use of single yet reliable measures, like self-scratch. Furthermore, our comparative findings underscore the complex roles of broader social styles and individual social status within social styles in shaping macaque emotional states through the exhibition of certain self-directed behaviors. We also emphasize the role of social complexity in driving these behaviors through an underlying process of social uncertainty. We highlight the unique costs and benefits associated with social ranks, leading to varying expressions in self-scratch and yawn. To conclude, our findings provide critical insights into the proximate drivers of a common emotional state (at the behavioral level) by highlighting the potential functional mechanisms in nonhuman primate societies.

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Author contributions

Conceptualization: D.B. and J.J.M.M.; methodology: D.B. and J.J.M.M.; investigation: D.B., E.S.J.vD., R.E.M.dV., C.E.K., M.V., and A.N.Z.; Formal analysis – D.B. and J.J.M.M.; writing – original draft: D.B.; writing – review and editing: D.B. and J.J.M.M.; visualization: D.B.; supervision: D.B. and J.J.M.M.; project administration: D.B. and J.J.M.M.; funding acquisition: D.B. and J.J.M.M.

Declaration of interests

The authors declare no competing interests.

Data and code availability

All data and code will be made publicly available upon publication.

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Supplementary information to

Social status predicts self-directed behaviors, contingent on broader social dynamics

Table S1. Summary of study species and groups with sampling and demographic information.

Species	Group ID	Focal sampled	Age (years)	Sex
Macaca fuscata (Japanese)	Affenberg	N = 26; 280 min/focal	4 – 29 (median age = 10)	Female = 26; Male = 0
Macaca mulatta (Rhesus)	R3G2	N = 12; 160 min/focal	4 – 14 (median age = 5)	Female = 11; Male = 1
	R3G7	N = 10; 210 min/focal	4 – 25 (median age = 13)	Female = 9; Male = 1
Macaca fascicularis (Long-tailed)	J1G4	N = 8; 320 min/focal	4 – 9 (median age = 4)	Female = 7; Male = 1
	J1G7	N = 10; 320 min/focal	4 – 14 (median age = 12.5)	Female = 9; Male = 1
	NWR	N = 4; 320 min/focal	4 – 6 (median age = 4)	Female = 0; Male = 4
Macaca silenus (Lion-tailed)	Blijdorp	N = 3; 240 min/focal	6 – 18 (median age = 7)	Female = 2; Male = 1
	Apenheul	N = 6; 340 min/focal	7 – 27 (median age = 18.5)	Female = 5; Male = 1
Macaca sylvanus (Barbary)	Gaia	N = 14; 240 min/focal	4 – 20 (median age = 10.5)	Female = 8; Male = 6
	Apenheul	N = 9; 420 min/focal	4 – 20 (median age = 7)	Female = 8; Male = 1
Macaca nigra (Crested)	Blijdorp	N = 3; 460 min/focal	5 – 21 (median age = 13)	Female = 2; Male = 1
	Artis	N = 3; 320 min/focal	9 – 21 (median age = 15)	Female = 3; Male = 0
	Planckendael	N = 5; 180 min/focal	4 – 15 (median age = 6)	Female = 2; Male = 3

The *M. fuscata* group was located at Affenberg Landskron Park in Villach, Austria, within a large 40,000 m² enclosure characterized by native mixed woodlands typical of Southern Austria. This group comprised approximately 170 individuals. Two *M. mulatta* groups (R3G2 and R3G7), with 30 and 25 members respectively, were housed at the BPRC in Rijswijk, the Netherlands. Both groups lived in facilities featuring identical enclosure sizes: 74 m² indoors and 250 m² outdoors. At the same facility (BPRC), we also studied three *M. fascicularis* groups: J1G4 (15 individuals), J1G7 (18 individuals), and NWR (4 individuals). J1G4 and J1G7 had access to the same enclosure sizes (49 m² indoor and 183 m² outdoor), while the smaller NWR group was housed in smaller enclosures measuring 3.55 m² indoors and 3.88 m² outdoors. The two groups of *M. Silenus* were housed at Blijdorp Zoo and Apenheul Primate Park in the Netherlands. The Blijdorp group comprised 3 individuals and had 100 m² indoor and 106 m² outdoor spaces, whereas the Apenheul group included 8 individuals, with access to an 80 m² indoor enclosure and a significantly larger 768 m² outdoor area. Two *M. sylvanus* groups were included: one at Gaia Zoo in the Netherlands and the other at Apenheul Primate Park. The Gaia Zoo group consisted of 14 individuals and had access to a large 3522 m² outdoor area and a 108 m² indoor space. The Apenheul group, with 13 individuals, lived exclusively in a 3829 m² outdoor enclosure featuring natural elements such as vegetation, rocks, and a creek. Finally, the three *M. nigra* groups were housed at Blijdorp

Zoo, Artis Zoo (both in the Netherlands), and Planckendael Zoo in Belgium. Group sizes were 5, 4, and 6 individuals, respectively. The Blijdorp group was kept in a 70 m² indoor and a 160 m² outdoor enclosure. At Artis Zoo, the enclosures measured 65 m² indoors and 761 m² outdoors, while the Planckendael group had access only to an 82 m² indoor enclosure.

In all cases where both indoor and outdoor spaces were provided, macaques could freely move between them via connecting tunnels. An exception was the Apenheul *M. sylvanus* group, where only the outdoor space was available during observations. Group sizes include all members, including infants under one year of age.

Although husbandry practices varied slightly between groups—reflecting differences in species-specific needs and institutional protocols—all followed the standards set by the European Association of Zoos and Aquaria for animal housing and care. Enclosures were equipped with various enrichment items, including climbing structures, ropes, tree trunks, wooden elements, and slides. With the exception of the *M. fuscata* and Apenheul *M. sylvanus* groups, which were kept exclusively in outdoor habitats, indoor housing areas were climate-controlled and featured concrete floors layered with sawdust bedding. Feeding schedules differed across groups to meet specific dietary requirements but remained consistent with their usual routines during our observations. Standard diets included commercial monkey pellets, a variety of fruits and vegetables, and seed mixes such as sunflower and corn.

Table S2. Bayesian mixed model investigating the effects of macaque tolerance grades on self-scratch rates.

Family: skew normal
Links: mu = identity; sigma = identity; alpha = identity
Formula: self-scratch ~ grade + offset(log(groupsize)) + (1 | species/group)
Draws: 4 chains, each with iter = 5500; warmup = 1000; thin = 1;
total post-warmup draws = 18000

	Estimate	95% critical interval	Probability of direction
Intercept	-2.48	-3.68, -1.10	0.99
Grade [2]	0.36	-1.24, 1.83	0.69
Grade [3]	0.57	-0.98, 1.96	0.78
Grade [4]	0.68	-1.08, 2.20	0.79

Table S3. Bayesian mixed model investigating the effects of macaque tolerance grades on autogroom durations.

Family: skew normal
Links: mu = identity; sigma = identity; alpha = identity
Formula: autogroom ~ grade + offset(log(groupsize)) + (1 | species/group)
Draws: 4 chains, each with iter = 5500; warmup = 1000; thin = 1;
total post-warmup draws = 18000

	Estimate	95% critical interval	Probability of direction
Intercept	1.85	0.09, 3.68	0.97
Grade [2]	0.95	-0.96, 2.79	0.83
Grade [3]	0.29	-1.41, 1.96	0.63
Grade [4]	0.05	-1.68, 1.78	0.52

Table S4. Bayesian mixed model investigating the effects of macaque tolerance grades on yawn rates.

Family: skew normal
Links: mu = identity; sigma = identity; alpha = identity
Formula: yawn ~ grade + offset(log(groupsize)) + (1 | species/group)
Draws: 4 chains, each with iter = 5500; warmup = 1000; thin = 1;
total post-warmup draws = 18000

	Estimate	95% critical interval	Probability of direction
Intercept	-2.79	-4.01, -1.42	0.99
Grade [2]	0.32	-1.27, 1.80	0.66
Grade [3]	0.53	-1.03, 1.95	0.77
Grade [4]	0.61	-1.08, 2.11	0.78

Table S5. Bayesian mixed model investigating the effects of dominance ranks on self-scratch rates in Grade 1 species.

Family: gaussian
Links: mu = identity; sigma = identity
Formula: self-scratch ~ ns(ordinal rank, df = 3) + offset(log(groupsize)) + (1 | species/group)
Draws: 4 chains, each with iter = 5500; warmup = 1000; thin = 1;
total post-warmup draws = 18000

	Estimate	95% critical interval	Probability of direction
Intercept	-2.70	-4.67, 0.14	0.97
Ordinal rank [Spline 1]	0.04	-0.06, 0.15	0.79
Ordinal rank [Spline 2]	0.21	0.03, 0.38	0.98
Ordinal rank [Spline 3]	0.09	0.05, 0.00	0.97

Table S6. Bayesian mixed model investigating the effects of dominance ranks on self-scratch rates in Grade 2 species.

Family: gaussian
Links: mu = identity; sigma = identity
Formula: self-scratch ~ ns(ordinal rank, df = 3) + offset(log(groupsize)) + (1 | species/group)
Draws: 4 chains, each with iter = 5500; warmup = 1000; thin = 1;
total post-warmup draws = 18000

	Estimate	95% critical interval	Probability of direction
Intercept	-1.53	-3.04, 0.09	0.97
Ordinal rank [Spline 1]	0.00	-0.25, 0.25	0.51
Ordinal rank [Spline 2]	-0.04	-0.35, 0.27	0.60
Ordinal rank [Spline 3]	0.00	-0.19, 0.20	0.51

Table S7. Bayesian mixed model investigating the effects of dominance ranks on self-scratch rates in Grade 3 species.

Family: gaussian
Links: mu = identity; sigma = identity
Formula: self-scratch ~ ns(ordinal rank, df = 3) + offset(log(groupsize)) + (1 | species/group)
Draws: 4 chains, each with iter = 5500; warmup = 1000; thin = 1;
total post-warmup draws = 18000

	Estimate	95% critical interval	Probability of direction
Intercept	-1.55	-3.12, 0.13	0.97
Ordinal rank [Spline 1]	0.10	-0.21, 0.41	0.73
Ordinal rank [Spline 2]	0.06	-0.34, 0.48	0.62
Ordinal rank [Spline 3]	0.15	-0.14, 0.43	0.85

Table S8. Bayesian mixed model investigating the effects of dominance ranks on self-scratch rates in Grade 4 species.

Family: gaussian
Links: mu = identity; sigma = identity
Formula: self-scratch ~ ns(ordinal rank, df = 3) + offset(log(groupsize)) + (1 | species/group)
Draws: 4 chains, each with iter = 5500; warmup = 1000; thin = 1;
total post-warmup draws = 18000

	Estimate	95% critical interval	Probability of direction
Intercept	-1.17	-2.10, -0.28	0.98
Ordinal rank [Spline 1]	0.09	-0.35, 0.53	0.69
Ordinal rank [Spline 2]	0.21	-0.29, 0.68	0.84
Ordinal rank [Spline 3]	0.16	-0.24, 0.54	0.83

Table S9. Bayesian mixed model investigating the effects of dominance ranks on autogroom durations in Grade 1 species.

Family: gaussian
Links: mu = identity; sigma = identity
Formula: autogroom ~ ns(ordinal rank, df = 3) + offset(log(groupsize)) + (1 | species/group)
Draws: 4 chains, each with iter = 5500; warmup = 1000; thin = 1;
total post-warmup draws = 18000

	Estimate	95% critical interval	Probability of direction
Intercept	-0.83	-2.73, 1.23	0.83
Ordinal rank [Spline 1]	0.23	-1.50, 1.91	0.60
Ordinal rank [Spline 2]	0.16	-1.68, 2.01	0.56
Ordinal rank [Spline 3]	0.66	-0.95, 2.25	0.79

Table S10. Bayesian mixed model investigating the effects of dominance ranks on autogroom durations in Grade 2 species.

Family: gaussian
Links: mu = identity; sigma = identity
Formula: autogroom ~ ns(ordinal rank, df = 3) + offset(log(groupsize)) + (1 | species/group)
Draws: 4 chains, each with iter = 5500; warmup = 1000; thin = 1;
total post-warmup draws = 18000

	Estimate	95% critical interval	Probability of direction
Intercept	5.57	2.27, 8.53	0.99
Ordinal rank [Spline 1]	0.01	-1.90, 1.92	0.50
Ordinal rank [Spline 2]	0.01	-1.92, 1.92	0.50
Ordinal rank [Spline 3]	0.42	-1.45, 2.32	0.66

Table S11. Bayesian mixed model investigating the effects of dominance ranks on autogroom durations in Grade 3 species.

Family: gaussian
Links: mu = identity; sigma = identity
Formula: autogroom ~ ns(ordinal rank, df = 3) + offset(log(groupsize)) + (1 | species/group)
Draws: 4 chains, each with iter = 5500; warmup = 1000; thin = 1;
total post-warmup draws = 18000

	Estimate	95% critical interval	Probability of direction
Intercept	2.64	0.19, 4.76	0.98
Ordinal rank [Spline 1]	0.67	-1.17, 2.52	0.76
Ordinal rank [Spline 2]	-0.32	-2.21, 1.55	0.63
Ordinal rank [Spline 3]	0.18	-1.60, 1.97	0.57

Table S12. Bayesian mixed model investigating the effects of dominance ranks on autogroom durations in Grade 4 species.

Family: gaussian
Links: mu = identity; sigma = identity
Formula: autogroom ~ ns(ordinal rank, df = 3) + offset(log(groupsize)) + (1 | species/group)
Draws: 4 chains, each with iter = 5500; warmup = 1000; thin = 1;
total post-warmup draws = 18000

	Estimate	95% critical interval	Probability of direction
Intercept	1.60	-0.51, 3.62	0.94
Ordinal rank [Spline 1]	0.20	-1.68, 2.06	0.58
Ordinal rank [Spline 2]	-0.34	-2.21, 1.57	0.63
Ordinal rank [Spline 3]	-0.13	-1.96, 1.71	0.55

Table S13. Bayesian mixed model investigating the effects of dominance ranks on yawn rates in Grade 4 species.

Family: gaussian
Links: mu = identity; sigma = identity
Formula: sqrt(yawn) ~ ns(ordinal rank, df = 3) + offset(log(groupsize)) + (1 | species/group)
Draws: 4 chains, each with iter = 5500; warmup = 1000; thin = 1;
total post-warmup draws = 18000

	Estimate	95% critical interval	Probability of direction
Intercept	-1.31	-1.64, -0.98	0.99
Ordinal rank [Spline 1]	0.00	-0.36, 0.38	0.51
Ordinal rank [Spline 2]	-0.31	-0.73, 0.12	0.93
Ordinal rank [Spline 3]	-0.12	-0.44, 0.22	0.80

Table S14. Bayesian mixed model investigating the effects of dominance ranks on yawn rates in Grade 1 species.

Family: gaussian
Links: mu = identity; sigma = identity
Formula: sqrt(yawn) ~ ns(ordinal rank, df = 3) + offset(log(groupsize)) + (1 | species/group)
Draws: 4 chains, each with iter = 5500; warmup = 1000; thin = 1;
total post-warmup draws = 18000

	Estimate	95% critical interval	Probability of direction
Intercept	-3.52	-6.00, -0.65	0.98
Ordinal rank [Spline 1]	0.03	-0.06, 0.11	0.73
Ordinal rank [Spline 2]	0.05	-0.08, 0.19	0.77
Ordinal rank [Spline 3]	0.11	0.05, 0.18	0.99

Table S15. Bayesian mixed model investigating the effects of dominance ranks on yawn rates in Grade 2 species.

Family: gaussian
Links: mu = identity; sigma = identity
Formula: sqrt(yawn) ~ ns(ordinal rank, df = 3) + offset(log(groupsize)) + (1 | species/group)
Draws: 4 chains, each with iter = 5500; warmup = 1000; thin = 1;
total post-warmup draws = 18000

	Estimate	95% critical interval	Probability of direction
Intercept	0.25	-0.16, 0.63	0.94
Ordinal rank [Spline 1]	-0.09	-0.22, 0.03	0.92
Ordinal rank [Spline 2]	-0.27	-0.44, -0.11	0.99
Ordinal rank [Spline 3]	-0.02	-0.12, 0.08	0.67

Table S16. Bayesian mixed model investigating the effects of dominance ranks on yawn rates in Grade 3 species.

Family: gaussian
Links: mu = identity; sigma = identity
Formula: sqrt(yawn) ~ ns(ordinal rank, df = 3) + offset(log(groupsize)) + (1 | species/group)
Draws: 4 chains, each with iter = 5500; warmup = 1000; thin = 1;
total post-warmup draws = 18000

	Estimate	95% critical interval	Probability of direction
Intercept	-1.68	-3.38, 0.08	0.97
Ordinal rank [Spline 1]	-0.04	-0.20, 0.11	0.71
Ordinal rank [Spline 2]	-0.25	-0.46, -0.04	0.98
Ordinal rank [Spline 3]	-0.01	-0.16, 0.13	0.57