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6	Title:
7	Integrative personality assessment in wild Assamese macaques (Macaca assamensis)
8	
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Abstract

In nonhuman animals, individuals of the same sex and age differ in their behavior patterns 41 consistently across time, comparable with human personality differences. To draw 42 conclusions about the adaptive value of behavior traits, it is essential to study them also in the 43 wild where animals are subject to the ecological pressures that promoted the evolution of 44 behavior strategies. This study was conducted in the Phu Khieo Wildlife Sanctuary, Thailand, 45 on four groups of habituated wild Assamese macaques by observers who had familiarized 46 themselves with the subjects over the course of an ongoing long-term study. We used a multi-47 48 method approach enabling the most comprehensive understanding of variation in stable interindividual differences in a species-typical ecological setting. We combined trait ratings (TR), 49 assessed with observer-report questionnaires (54 item HPQ) of 107 individuals of diverse 50 51 age-sex classes, with behavior codings (BC) of 24 adult males. We found male and female personality constructs to be congruent and examined reliability and construct validity. 52 Combining methods, we found two solutions with five factors to best describe the personality 53 structure of the males: one structure comprised the dimensions Gregariousness_{BC}, 54 Aggressiveness_{BC}, Sociability_{BC} and Vigilance_{BC}, complemented by a Confidence_{TR} domain 55 56 and the other structure Opportunism_{TR}, Confidence_{TR}, Friendliness_{TR}, Activity_{TR} complemented with Vigiance_{BC}. We discuss our findings with regard to the importance of 57 construct validity and reproducibility in the context of method development and 58 59 standardization in nonhuman animal personality research.

60

61 *Keywords*: personality, wild, macaques, behavior coding, trait rating, integrative assessment

Introduction

"Personality in the broadest sense is the internal organisation of behaviour that is stable over 63 considerable time periods in the individual vet varies among the individuals of a population 64 on latent dimensions" (Uher 2008 p. 476). Personality has a moderately heritable component 65 and is systematically associated with differences in fitness parameters, like survival, 66 reproductive success, and health in both animals and humans (Deary, Weiss, & Batty, 2010; 67 Penke & Jokela, 2016; Wolf & Weissing, 2012). Animal personality became an expanding 68 field of behavior ecology as well as comparative psychology in the last two decades (Carere 69 & Maestripieri, 2013; Dingemanse, Kazem, Réale, & Wright, 2010; Mehta & Gosling, 2008; 70 Uher, 2008). Yet, there are still no consistent definitions for personality dimensions, or 71 standardized assessment methods, and differences in species-specific behavior repertoires 72 73 make cross-species comparisons challenging (Gosling, 2001; Lilley, Kuczaj, & Yeater, 2017). 74

The two most common assessment methods in animal personality research are trait ratings 75 and behavior coding from naturalistic observations or experimental data (Réale, Reader, Sol, 76 McDonald, & Dingemanse 2007; Vazire, Gosling, Dickey, & Schapiro, 2007). In human 77 psychology, personality is mainly assessed via self-reported statement ratings on personality 78 inventories (Koski, 2011a; Uher, 2011) and expressed in broad bipolar or monopolar 79 dimensions, often referred to as the so-called "Big Five" Extraversion, Agreeableness, 80 81 Conscientiousness, Neuroticism, and Openness to Experience (Digman, 1990; John & Srivastava, 1999). In a top-down approach personality questionnaires have been modified for 82 animals to allow trait ratings by human observers familiar with the individuals (e.g., 83 Hominoid Personality Questionnaire; Freeman & Gosling, 2010; Weiss et al., 2009). To 84

avoid issues with validity possible anthropomorphic projections in trait ratings (Freeman et
al., 2013; Uher, 2018) or naturalistic observational approaches use previously established
ethograms defining behaviors and situations at the species level to quantify single behaviors
or behaviors in a behavioral situation (Uher, 2015, Massen et al. 2013). Experimental
observational approaches create situations to tap into one (Dammhahn, 2012) or several
personality dimensions at a time (Carter et al., 2012b; Koski & Burkart, 2015; Massen et al.,
2013; Réale et al., 2007; Vazire et al., 2007).

The choice of method typically depends on time and feasibility. Trait ratings by familiar 92 93 observers are less time-consuming and can cover a broader range of individual traits compared to behavior codings in experimental or natural settings. However, trait ratings 94 require that several raters are familiar with the individuals, because different observers know 95 96 an individual from different situations and may have unique observer biases (Freeman, Gosling, & Schapiro, 2011). Experimentation is better able to assess non-social personality 97 dimensions, such as boldness and exploration because relevant situations occur rarely and 98 unpredictable in naturalistic observations (Massen, Antonides, Arnold, Bionda, & Koski, 99 2013), but is not always feasible, especially in wild populations (but see: Neumann, Agil, 100 101 Widdig, Engelhardt, & Kalueff, 2013; Tkaczynski et al., 2018). When several methods have been applied to assess personality of the same subjects, convergent validity across methods 102 was often low (Freeman et al., 2011; John & Soto, 2007; Uher & Visalberghi, 2016). 103

Such disparity may result from the disadvantages of behavior codings, which may struggle with reliably detecting individual differences in behaviors that occur at low frequencies (Freeman et al., 2013) and behaviors that change from day to day, across seasons, or with changing social and physical environment (Brommer & Class, 2017; Uher, 2011). 108 Aggregation may overcome these shortcomings in behavior measurements, since a higher aggregation level inevitably leads to higher reliability scores (for discussion about the 109 Principle of Aggregation see Uher, 2011). In trait ratings, however, variability in behavior 110 due to random variance is partly cancelled out, because observers implicitly aggregate an 111 animal's behavior over time when they form an image of a subject's personality and subject it 112 to their own memory. This aggregation comes at a cost though, because such images may be 113 biased towards specific, more memorable events, and the assessment of subjects further may 114 be influenced by discussions among raters, and may be modified through recalled memories 115 (which are reshaped every time they are recalled). The advantage of behavior coding studies 116 is that behaviors are directly perceivable and measurable. Hence they are not susceptible to 117 most of the biases that can influence trait ratings (Freeman et al., 2011; van Aken & 118 119 Asendorpf, 2018). The above mentioned problems can be overcome by repeated experimentation and long-term observations, when even rare behaviors occur often enough to 120 reliably assess individual variation and all individuals are assessed across a variety of social 121 and ecological contexts. 122

The strengths and weaknesses of trait rating and behavior coding have been repeatedly 123 discussed (Freeman et al. 2011; Koski 2014; Uher et al. 2013; Uher & Visalberghi 2016; 124 Uher 2018; Weiss 2017). It has been argued that the most comprehensive understanding of 125 variation in stable inter-individual differences may come from studies combining approaches 126 127 to compensate for the weaknesses that each technique individually has (Koski 2014). Multimethod approaches in field and lab work use item selection based on reliability measures 128 (e.g., test-retest) and analyses of construct validity (Eckardt et al., 2015; Garai, Weiss, 129 130 Arnaud, & Furuichi, 2016), and may generate integrative/complemented personality structures to provide a more complete picture (e.g., behavior codings and experiments: 131

132 Massen & Koski, 2014; Neumann et al., 2013; Uher, Addessi, & Visalberghi, 2013; behavior codings and trait ratings: Iwanicki & Lehmann, 2015; Uher, Werner, & Gosselt, 2013; all 133 three methods: Tkaczynski et al., 2018). As can be expected from the differences in strength 134 and weaknesses of the methods, personality structures derived from trait ratings and behavior 135 codings do not always clearly correspond to each other. Aggressiveness related trait rating 136 dimensions are mainly well supported with aggressive behavior (Pritchard et al., 2014; Uher, 137 Werner, et al., 2013; Vazire et al., 2007), yet aggressive behavior may also correlate with a 138 Dominance dimension (Freeman et al., 2013; Uher, Werner, et al., 2013; Uher & Visalberghi, 139 2016) or Excitability (Tkaczynski et al., 2018). Sociability mostly displays sociable or 140 affiliative facets of behavior, yet grooming also correlates with Confident (Capitanio et al., 141 1999) or Irritability (Garai et al., 2016). The behaviors active and playful are often correlated 142 143 (Uher & Visalberghi, 2016; Vazire et al., 2007), but playful also correlates with anxious and scratch (Iwanicki & Lehmann, 2015). Further, being physically active (i.e. not resting) does 144 not always correlate with social activity (Koski, 2011). Thus, multi-method approaches may 145 146 reveal more subtle and complete personality structures because each method captures aspects of personality that are not fully grasped by the other (Garai et al., 2016; Uher & Visalberghi; 147 2016; Tkaczynski et al., 2018). 148

Different species of the macaque genus vary in their social style, i.e. in aspects of affiliation, aggression, dominance, nepotism, maternal behavior and socialization (Thierry, Singh, & Kaumanns, 2004). Adams and colleagues (2015) showed that similarities in personality dimensions capturing aggression and social competence are related to similarities in social styles (ranging from despotic via intermediate to egalitarian), and that the personality structure of the intermediately tolerant Assamese macaques (*Macaca assamensis*) studied here clustered with that of egalitarian crested macaques (*Macaca nigra*). In contrast to many

other male primates, male Assamese macaques form differentiated non-kin social
relationships with other males (Schülke, Bhagavatula, Vigilant, & Ostner, 2010) with females
(Haunhorst, Schülke, & Ostner, 2016), and with immatures (Minge, Berghänel, Schülke, &
Ostner, 2016) and engage in frequent coalition formation and different affiliative behaviors,
like grooming, gentle touch, and male–infant–male interactions (Kalbitz, Schülke, & Ostner,
2017; Ostner & Schülke, 2014).

The aim of this study was to explore the personality structure of male Assamese macaques in 162 their natural habitat to provide the baseline for future studies on the socioecology of inter-163 individual differences. We employed behavior coding to emphasize prosocial personality 164 traits that received less attention in previous studies (Koski, 2014), but may influence social 165 partner choice (Massen & Koski, 2014) and individual fitness (Seyfarth & Cheney, 2013). 166 167 The behavior coding was combined with trait rating to develop a more comprehensive personality model that integrates the strengths of both methods. Our discussion will 168 contribute to the ongoing debate about personality assessment in nonhuman animals (e.g., 169 Iwanicki & Lehmann, 2015; Tkaczynski et al., 2018; Uher & Visalberghi, 2016). 170

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Methods

173 Study Site and Subjects

Fieldwork took place in the Phu Khieo Wildlife Sanctuary (PKWS: 16°5' – 35'N, 101°20' –
55'E) which is part of the ca. 6,500 km² interconnected and well-protected Western Isaan
Forest Complex in north-eastern Thailand (Borries, Larney, Kreetiyutanont, & Koenig,
2002). The study area is covered by hill evergreen forest and harbors a diverse community of
large mammals and predators (Borries et al., 2002). Data for this study were collected on four

multimale-multifemale groups from April 2014 (ASM and AOM groups) or October 2014
(ASS and AOS groups) to March 2016. Group sizes at the beginning of behavior data
collection are shown in Table S1.

182

183 Data collection

184 *1)* Trait ratings

All adult females and males of the four groups were rated with the 54 item Hominoid 185 186 Personality Questionnaire (HPQ; King & Figueredo, 1997; Weiss et al., 2009), which had previously been successfully used to assess personality in different macaque species, 187 including Assamese macaques (Adams et al., 2015). Each adjective item is defined within the 188 context of general behaviors common to primates. For example, 'fearful' is defined as 189 "Subject reacts excessively to real or imagined threats by displaying behaviors such as 190 screaming, grimacing, running away or other signs of anxiety or distress." Adjective items 191 are rated on a 7-point scale with 1 defined as "Displays either total absence or negligible 192 193 amounts of the trait" and 7 defined as "Displays extremely large amounts of the trait." (Weiss et al., 2009). Ratings were done in an office away from the animals, and observers were 194 instructed to base their ratings on overall impressions of the individual's behavior, and not to 195 discuss the questionnaires with each other. The Thai project members used a Thai language 196 version of the questionnaire that was back-translated to ensure accuracy. Within the study 197 period from April 2014 to March 2016, four Thai field assistants, AE and another PhD 198 student, all familiar with the subjects for 6 months to 7 years in April 2014, rated the animals 199 twice. Eighty-one individuals were rated in the first year, all adult males in March 2015, and 200 all adult females and sub-adult males in September 2015. Of these 81, 74 individuals were 201

rated again in March 2016. Animals were rated by the same observers who collected thebehavior data within the study period.

One of the groups (ASM) had been rated earlier (2009) by eight observers (2 of them rated again in this study) familiar with the animals from focal animal data collection (60 adult and juvenile males and females) (Adams et al., 2015). Of these 60 individuals, 26 had emigrated into a non-study group or died by the beginning of this study and were included here to extend our data set to ensure a higher observations-to-variables ratio.

209

210 2) Behavior codings

We collected 4,628 hours of focal animal observations (Altmann, 1974) from 24 adult males 211 (mean per subject = 193h; range = 86h-284h) of the four study groups. Focal animals were 212 included in the study if they were present longer than three months within one year of the 213 two-year study period. Individuals were followed for 40 minutes with continuous recording 214 of all approaches and departures within 1.5m of the focal animal and all affiliative and 215 216 agonistic social interactions with directionality and the identities of interaction partners, and several solitary behaviors (e.g., scratching, yawning, display; supplement Table S2). Activity 217 of the focal animal was recorded instantaneously at 2-minutes intervals. Every 10min, we 218 recorded the identities of all individuals within a 5m sphere around the focal animal. An 219 effort was made to equally distribute observation time across individuals and time of the day. 220 This study includes an extended data set of socially motivated behaviors, such as affiliative 221 triadic male-infant-male interactions (Kalbitz et al., 2017; Paul, Kuester, & Arnemann, 1996). 222 223

224 Data analysis

All statistical analyses were run with R (version 3.4.2; R Core Team, 2017).

226 1) Trait ratings

We reduced the data to only those raters who used the entire 7-point scale, and those items that were rated by more than half of the remaining reliable observers, and those items that showed normal distribution. We calculated interrater-reliability, a measure of consistency across raters, and test-retest reliability, examining consistency over time, to assess reliable adjective items that would then be included in a factor analysis.

For each year (2009, 2015, 2016), data were visually inspected via scatterplots, histograms 232 and Q-Q plots to examine the rating performance of observers and the distribution of each 233 adjective item. Three observers had to be excluded from further analyses due to incorrect use 234 of the coding protocol. Specifically, in 2009 three of eight observers and in 2015 and 2016 235 one of six observers (one of the two, who rated in all 3 years) did not use the complete 7-236 point scale, and used "1" ("Displays either total absence or negligible amounts of the trait") 237 instead of "4" as mean rating value. The item "autistic" was excluded since 8 of the 238 remaining reliable 9 observers did not rate it, leaving 53 items for further analysis. 239

Interrater-reliability was measured as Intraclass Correlation Coefficients (ICC; Shrout & 240 Fleiss, 1979). *ICCs* assess reliability by comparing item variability across all observers. *ICC* 241 quantifies the similarity of single trait ratings of each adjective for every individual among all 242 observers (3,1), or mean trait ratings of each adjective for every individual among all 243 observers (3,k). A good level of agreement for primate studies has been set at ICC(3,k) =244 0.48 (Freeman & Gosling, 2010). A meaningful item selection is based on positive values 245 when confidence intervals do not include zero, and often a cut-off criterion of ICC(3,k) > 0.4246 is applied (Cicchetti, 1994). 247

Temporal stability of trait ratings was assessed with Pearson correlations (corrected for 248 multiple testing by the false discovery rate, hereafter fdr) of mean adjective items, averaged 249 across observers, for each individual from one rating to the next. High retest reliability 250 measures for the trait ratings of 74 individuals present in 2015 and 2016 ($N_{adjective items} = 53$; M 251 = 0.66; range: 0.3–0.92) support data aggregation. Thus, we assessed the overall personality 252 structure from trait ratings of 107 subjects, a combination of mean ratings of 74 individuals 253 present in 2016, plus seven individuals present in 2015 (which emigrated or died later), and 254 additional 26 individuals that were present in the study group only in 2009. Only temporally 255 256 stable adjective items, i.e. significant positive correlations > 0, were subjected to a factor analysis. 257

After data reduction based on reliability analyses, two measures of sampling adequacy were 258 259 applied to check for moderate inter-correlations and hence factorability of variables. The Kaiser-Mayer-Olkin-(KMO) index compares values of correlations between items and those 260 of partial correlations to check if at least two or three variables correlate with each other 261 ("KMO" function in "psych" package; Revelle, 2018). The Bartlett's test of sphericity 262 compares the observed correlation matrix to the identity matrix with no correlation and is 263 significant when it deviates from identity ("bartlett.test" function in "REdaS" package; 264 Maier, 2015). 265

The number of factors to be retained for factor analysis was determined using the "fa.parallel" function ("psych" package) and the "paran" function ("paran" package; Dinno, 2012) to perform a scree test (Cattell, 1966) with parallel analysis (Horn, 1965). Exploratory factor analysis was done with the "fa" function of the "psych" package. Principle axis factoring with promax rotation was applied to attain an optimal simple structure that 271 maximize high loadings on one factor for each variable. Oblique factor rotation allows for inter-correlations of factors, which is more adequate for trait ratings by observers as well as 272 behavior codings (Uher & Visalberghi, 2016). For interpretation, salient factor loadings were 273 274 considered to be $\geq |0.4|$, and items with salient cross loadings were included in the factor on which they had the highest loading (Field, Miles, & Field, 2012). A clean factor structure is 275 achieved by item loadings above |0.30| with preferably no cross loadings, and no factors with 276 less than three items (Costello & Osborne, 2005; Freeman et al., 2013). Behavioral 277 personality research, however, does often accept dimensions with less than three salient items 278 (Koski, 2011b; Manson & Perry, 2013; Pritchard, Sheeran, Gabriel, Li, & Wagner, 2014; 279 Seyfarth, Silk, & Cheney, 2012; Sussman, Ha, Bentson, & Crockett, 2013). Internal 280 consistency for each retained personality dimension was calculated as Cronbach's Alpha on 281 282 mean ratings of adjective items across raters for all 107 subjects ("alpha" function in "psych" package). Alpha ranges from zero to one, with higher values indicating greater internal 283 consistency. 284

For further analyses, factor scores for each dimension were extracted with the "factor.scores" 285 function ("psych" package) using the regression ("Thurstone") method. Rank order stability 286 of the personality structures from one year to the next (March 2015 and 2016) was assessed 287 with the "factor.congruence" function ("psych" package), comparing the factor loadings of 288 respective dimensions. Confidence intervals (CI) were calculated with the "boot.data" 289 function, we applied 1000 iterations and sampled 60 out of 74 individuals with no 290 replacement. Further, to demonstrate that the convergent structure relies on individual 291 stability, individual factor scores were correlated for every dimension applying fdr 292 293 corrections for multiple testing. Due to a rather small sample size, which exaggerates the

effect of single individuals on the analysis output, the same variables and individuals weresubmitted to factor analysis for both years.

The data sets for trait rating and behavior coding were imbalanced. TR was conducted for 296 297 male and female infants, juveniles and adults to increase the number of observations above that of items in the factor analysis. Observational data for behavior coding were collected 298 only on adult males though. To assess whether this imbalance affected comparisons of 299 constructs derived from both methods we used a parceling approach for item reduction in the 300 TR data set (Little, Cunnigham, Shahar, Widaman, 2002). We ran separate factor analyses for 301 302 males and females, and compared the resulting constructs (further details in SEM). The resulting separate four factor solutions for males (n=59) and females (n=48) had high factor 303 congruence of factor loadings (M=0.93, range: 0.90-0.98) suggesting they were similar or 304 305 equal (Lorenzo-Seva & ten Berge, 2006). We ran further tests to assess whether the trait-rated factors from the males only (n=24) structure differed from the structure derived from the full 306 data set on males and females (n=107) and found high factor congruence in factor loadings 307 again (M=0.98, range: 0.96-0.99). All further analyses were run on the TR construct built 308 from the full data set. 309

310 2) Behavior codings

Variables for behavioral coding were derived from a long ethogram provided in the supplement (Table S2). To arrive at our final set of variables for behavioral coding, we first omitted variables that could not be measured reliably either because the behavior was shown very rarely by the adult male subjects ('yawning'; 'treeshake'; 'submission'; 'reconciliation'; 'rejection'; 'dominance'; 'interference'; 'ignorance'; 'playface') or because of problems with data collection; the variable 'fidgeting' which should have captured how often an individual 317 changed between different activities, was omitted because we were unable to record these changes in the continuous protocol and our instantaneous recording interval was too long to 318 capture its effects. In an effort to reduce the overall number of variables, we collapsed those 319 320 variables that had been defined per age-sex class into just one variable for all partners. We then assessed for each study period separately whether those behaviors that comprised an 321 aggregated variable were positively correlated amongst each other and retained only those 322 that were. For 'friendly behavior' this meant that 'MIMI' was added, but 'peer', 'play', 323 'kiss', 'genital touch', 'mount', 'present' were omitted from the aggregate. We had planned 324 to aggregate aggressive behaviors into 'threats' and 'aggression'; we tested the validity of 325 these constructs by PCA and found three instead of two principle components that we named 326 327 'mild aggression', 'overt aggression' and 'physical aggression'. The aggressive behaviors 328 'open mouth', 'point', 'pretend grab', 'bite', and 'chase' were omitted, because they were not consistently across years correlated to behaviors from one of the three aggregated aggression 329 variables. New aggregated variables were built from correlated behaviors that individually 330 occurred at rather low rates; 'auto-grooming' and 'scratching' into 'self-directed'; 'body-331 contact' and 'grooming' into 'contact time' and 'contact diversity'; 'involvement', 'policing' 332 and 'agonistic support' aggregated into 'agonistic involvement'; the low frequency variables 333 mentioned above were omitted because they did not fit into any aggregate variable. The 334 aggregate variable 'vocalization' was dropped, because components were moved into other 335 aggregates; 'growl' was included in 'overt aggression'. One variable 'being left' was omitted 336 to further reduce the number of variables. 337

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339 After this first data reduction, 20 behavior variables were defined and extracted from the focal animal observations (supplement Table S7). Most of the behavior variables were 340 calculated as rate per hour, corrected by the individual observation time. Other variables were 341 342 calculated as proportions, across all partners in social measures. To assess the personality construct, variables were aggregated from the overall data collection period to maximize 343 construct stability, which is compromised by low frequencies (Freeman et al., 2013). 344 Reliability was assessed with Pearson correlations of mean values from one year to the next, 345 and only the 18 stable out of the 20 variables were used (Table S7). The two years of data 346 collection were split in half, to have one year of behavior codings before the trait ratings in 347 March 2015 and 2016, respectively. In the first period, continuous data collection started half 348 a year later for six adult males due to age-class change in October 2014. All behavior 349 350 variables were visually inspected via histograms and Q-Q plots to examine their distribution pattern. "Display" was log transformed for the single years and square root transformed for 351 the both years together. Variables were z-transformed before submitted to further analyses. 352

After data reduction, behavior variables were treated as described for the trait ratings (see 353 above) to evaluate their suitability for factor analysis, except that further methods were 354 considered to determine the number of factors to retain for factor analysis (besides scree test 355 with parallel analysis using "fa.parallel" and "paran" function), to search for similar results 356 across several criteria to overcome data insecurities (Freeman et al., 2013; Preacher & 357 358 MacCallum, 2003). Additional methods were the Very Simple Structure Criterion (VSS; Revelle & Rocklin, 1979) and Velicer's Minimum Average Partial test (MAP; Velicer, 359 1976), both using the "vss" function ("psych" package), as well as Kaiser's rule (Kaiser, 360 361 1960) and scree tests with parallel analysis using the "nScree" function ("nFactors" package; Raiche, 2010). 362

Exploratory factor analysis and further steps were implemented as described above for the rating analysis, except that maximum likelihood method with oblimin rotation was applied, and that the CI's for factor congruence were calculated based on a sample of 19 out of 22 individuals (bootstrapping required subsampling).

367 *3)* Construct validity

Convergent construct validity examines the correlation between different measures of the 368 same construct (John & Soto, 2007). Convergent construct validity between personality 369 constructs, derived from trait ratings and behavior codings, was assessed in two ways. First, 370 individual factor scores of 24 adult males were correlated (Pearson's r) for every dimension 371 (Freeman et al., 2013; Garai, Weiss, Arnaud, & Furuichi, 2016b). Second, percentage bend 372 correlation (Wilcox, 1994) was used to measure the relation between the behavior data from 373 24 adult males and the overall personality scores from questionnaire ratings from 107 374 individuals (Iwanicki & Lehmann, 2015; Morton et al., 2013; Tkaczynski et al., 2018). Z-375 transformed behavior variables were correlated via the "pbcor" function ("WRS2" package; 376 Mair, Schoenbrodt, & Wilcox, 2017) with factor scores of every trait rating personality 377 dimension. 378

379

380

Results

381 *Trait ratings (TR)*

Eight adjective items were excluded because of low interrater reliability, leaving 45 items with $ICC_{mean} = 0.6$; range: 0.4–0.87 (Table S8). The remaining 45 adjective items were submitted to measures of sampling adequacy and met the criteria. The overall KMO – index was higher than 0.5 (KMO = 0.87; range: 0.57–0.92) and the Bartlett's test for homogeneity of variances was significant (Bartlett's K-squared (44) = 360.17; p < 2.2e-16).

The visual inspection of the scree plot with parallel analysis suggested retaining four factors 387 to explain most of the variability in the data. Two items (thoughtless and unperceptive) had 388 loadings < |0.4| on all factors and were excluded. Factor analysis with the remaining 43 items 389 yielded a similar construct. Four dimensions were extracted: Opportunism_{TR}, Confidence_{TR}, 390 Activity_{TR} and Friendliness_{TR} (Table 1). Opportunism_{TR} comprises items such as aggressive, 391 bullying, irritable, impulsive, not gentle and not stable. Confidence_{TR} includes dominant, not 392 a follower, not vulnerable, not timid and not submissive. Activity_{TR} is described by being 393 curious, active, playful, not depressed and not lazy. Friendliness_{TR} is characterized with 394 affectionate, sociable, friendly and not solitary. All four factors together explain 72% of the 395 396 item variance (Table 1). The communalities are the sum of the squared factor loadings for a given variable and may be interpreted as a reliability indicator (Field, 2000). No item 397 loadings were below |0.4|, there were relatively few cross loadings, and mean item 398 communality h^2 was rather high (M = 0.72; range: 0.39–0.93), with only three items below 399 0.5 (clumsy, individualistic and intelligent), indicating robust personality dimensions 400 401 (Costello & Osborne, 2005; de Winter, Dodou, & Wieringa, 2009).

402

403

Insert Table 1 about here

404

405 Correlations among personality dimensions, as computed with the "fa" function (M = |0.16|; 406 range: |0.01-0.44|), were generally weak, apart from a moderate correlation between 407 Opportunism_{TR} and Activity_{TR}. Internal consistencies for the factor scores (*Cronbach's* 408 $alpha_{mean} = 0.92$; range: 0.88–0.98) were high..

409	Rank order stability of personality dimensions from March 2015 to March 2016 was
410	confirmed, with similar results for the congruence of factor loadings Φ (M = 0.95; range:
411	0.91–0.98) and the correlations of factor scores r (M = 0.81; range: 0.72–0.87; Table 2).
412	
413	Insert Table 2

414

415 *Behavior codings (BC)*

416 Test-retest reliabilities *r* of behavior variables were rather low (N_{behavior variables} = 20; M = 0.39; 417 range: -0.16–0.69; Table S7). Two variables, grooming symmetry and overt aggression, did 418 not meet the criteria for temporal stability, i.e. positive correlations > 0, and were excluded 419 from further analyses.

The remaining 18 behavior variables were submitted to measures of sampling adequacy. The overall KMO – index for the total observation period was slightly lower than 0.5 (KMO = 0.46; range: 0.20–0.76) and the Bartlett's test for homogeneity of variances was significant (Bartlett's K-squared(17) = 1014.8; p < 2.2e-16). Low KMO values might result from the rather small observations-to-variables ratio and these variables were not rejected.

The visual inspection of the scree plot and parallel analysis ("psych" and "paran" package) suggested to retain three factors to explain most of the variability in the data. The VSS suggested four and the MAP test five factors to retain ("psych" package). The "nFactors" 434

Due to these inconsistencies, we ran two factor analyses, extracting three and four factors, 435 respectively. The 4-factor solution, with the dimensions Gregariousness_{BC}, Aggressiveness_{BC}, 436 Sociabiliy_{BC} and Vigilance_{BC}, (Table 3) yielded more robust factors as described below 437 (Costello & Osborne, 2005), though less robust than in the trait rating analysis, with seven of 438 18 variables showing item communalities below 0.5. The 4-factor solution had higher mean 439 440 communality values (4-factor solution: $M(h^2) = 0.62$; range: 0.3–1 and 3-factor solution: 441 $M(h^2) = 0.55$; range: 0.2–0.95), as well as a higher proportion of variance explained (4-factor solution: 62% and 3-factor solution: 55%). The variable "display" had no reliable loading (< 442 |0.4|) in the 4-factor solution and cross loadings of |0.4| (in two dimensions) in the 3-factor 443 solution, reflecting its instability. In addition, the fourth factor was mainly marked by the 444 variable "vigilant", with a very high factor loading (0.99) and communality ($h^2 = 1$), but the 445 lowest communality ($h^2 = 0.2$) and a weak factor loading (-0.43) in the 3-factor solution. This 446 emphasizes that "vigilant" represents a separate factor, though it is rather unstable, with only 447 one additional variable "not active" loading on it, probably, due to the lack of more non-448 social variables in the data. In other personality studies, vigilance also groups with negatively 449

loaded activity behaviors, and positively with other behaviors, not captured in our analysis,
e.g., provisioning (Iwanicki & Lehmann, 2015).

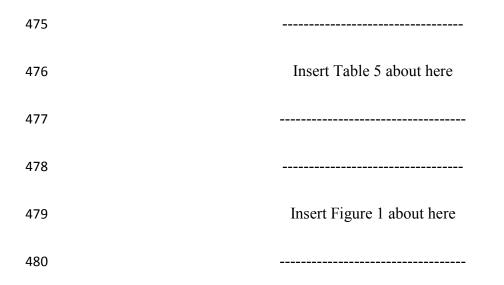
As with the rating analysis, there were also moderate intercorrelations *r* among dimensions (M = |0.16|; range: |0.02-0.35|), speaking against varimax factor rotation. Internal consistency of the personality dimensions was fair to excellent (M(*Cronbach's alpha*) = 0.77; range: 0.62-0.92).. Alpha for Vigilance_{BC} was rather low at 0.62, but comparable with other studies where personality dimensions include less than three variables (e.g., Manson & Perry, 2013). To assess rank order stability, the three factor solution was applied for the single years, even though there was a Heywood case (i.e. factor loading > 1.0) for "quitting" in the second year.

There was no clear result for factor determination, considering different methods and the criteria for construct robustness, as mentioned above. This ambiguity underlines the need to aggregate the data (two-year observation period) to overcome the shortcoming of low frequencies in behavior codings, in order to enable interpretation of the personality structure.

Rank order stability of personality dimensions from one year to the next was moderate, and revealed some differences between the congruence of factor loadings Φ (M = 0.69; range: 0.37–0.92) and the correlations of factor scores r (M = 0.40; range: 0.24 – 0.57; Table 4).

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467	Insert Table 4 about here
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470	Construct validity TR with BC

471 Significant positive correlations of individual factor scores were found between personality 472 dimensions Friendliness_{TR} and Gregariousness_{BC} (r = 0.69; p < 0.001), as well as between 473 Sociability_{BC} and Activity_{TR} (r = 0.63; p = 0.001), and a low negative correlation between 474 Friendliness_{TR} and Sociability_{BC} (r = -0.41; p = 0.046) (Table 5.; Figure 1).



Regarding the relations between behavior variables many of which were integrated and 481 personality dimensions based on trait ratings (Table 6), "mild aggression" correlated with 482 Opportunism_{TR} (ρ percentage bent, hereafter $\rho_{pb} = 0.41$; p = 0.049). "Display" ($\rho_{pb} = 0.59$; p =483 0.003), "vigilant" ($\rho_{pb} = -0.43$; p = 0.035) and "self-directed" ($\rho_{pb} = -0.56$; p = 0.005) 484 correlated with Confidence_{TR}. "Friendly behavior" ($\rho_{pb} = 0.55$; p = 0.006) and "peripheral" 485 ($\rho_{pb} = 0.43$; p = 0.037) correlated with Activity_{TR}. Nine out of 18 variables correlated with 486 Friendliness_{TR}: "active" ($\rho_{pb} = -0.44$; p = 0.031), "alone" ($\rho_{pb} = -0.66$; p = 0.001), "display" 487 $(\rho_{pb} = 0.44; p = 0.033)$, "friendly approach" ($\rho_{pb} = 0.60; p = 0.002$), "leaving" ($\rho_{pb} = 0.63; p = 0.63$ 488 0.001), "neighbor diversity" ($\rho_{pb} = 0.65$; p = 0.001), "physical aggression" ($\rho_{pb} = 0.50$; p =489 0.012), "peripheral" ($\rho_{pb} = -0.45$; p = 0.026) and "tolerance" ($\rho_{pb} = 0.60$; p = 0.002). 490

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Discussion

This study was not designed as a validation study comparing personality structures derived 496 with different methods or with the goal to compare results with the published literature. An 497 elaborate method comparison is hampered by the imbalance in our data sets for the two 498 499 methods and also would have required deriving a priori predictions about which factors from each method would be congruent (Koski et al., 2017; Tkaczynski et al., 2018). A method 500 comparison would also have benefitted from including rating of adjectives that had been 501 derived from the species' behavior repertoire instead of applying constructs derived from 502 lexical accounts in humans (Uher et al., 2008). A validation study would assess which 503 constructs derived by one method are congruent with a construct derived by the second 504 method and thereby arrive at a possibly reduced set of constructs that have been validated. 505 506 Accepting that to some extent each method will grasp slightly different aspects of personality, 507 the aim of this study was to build a comprehensive personality structure by also retaining dimensions that were not congruent across methods and thereby extending the structure space 508 beyond what could be achieved by a single method. Before we describe this structure, we will 509 relate the personality structures and dimensions developed here with published work on the 510 same and other macaque species and other nonhuman primates to establish how robust and 511 reproducible they are across studies using slightly or vastly different methods. 512

513 Reproducibility of trait ratings and construct validity

514 A previous study on Assamese macaque personality (Adams et al., 2015) did not employ item selection and extracted five personality dimensions from HPQ ratings (labelled as 515 Confidence_{TR}, Activity_{TR}, Openness_{TR}, Friendliness_{TR} and Opportunism_{TR}) whereas our 516 rating analysis revealed four dimensions: Opportunism_{TR}, Confidence_{TR}, Activity_{TR} and 517 Friendliness_{TR} which we named the same when replicated. Our Opportunism_{TR} domain 518 comprised all adjectives representing Opportunism_{TR}, as well as 4 out of 10 items of 519 Openness_{TR} in Adams et al. Behavior codings from adult males also resulted in a four-factor 520 structure, with Gregariousness_{BC}, Aggressiveness_{BC}, Sociability_{BC} and Vigilance_{BC}, that has 521 522 considerable overlap with the personality structure from trait rating and does reflect previous findings in other macaque studies (Neumann et al., 2013). Friendliness_{TR} was convergent 523 with Gregariousness_{BC} and inverse Sociability_{BC}, whereas Activity_{TR} correlated with 524 525 Sociability_{BC}. In addition, Opportunism_{TR} was weakly associated with Aggressiveness_{BC}. Confidence_{TR} replicated very well, but showed no association with the behavior personality 526 dimensions. 527

The trait rating dimension Friendliness_{TR} confirmed previous findings (Adams et al., 2015; 528 Konečná et al., 2008; Sussman et al., 2013; Weiss, Adams, Widdig, & Gerald, 2011): the 529 rather strong link between Friendliness_{TR} and Gregariousness_{BC} is explained by all behavior 530 variables belonging to Gregariousness_{BC} having significant correlations with Friendliness_{TR}. 531 More specifically, adjectives, like "sympathetic" (kind towards others), "sociable" (seeks and 532 enjoys company) and "not solitary" (spends considerable time alone) correlate with behaviors 533 like "friendly approach" or "tolerance", "neighbor diversity" and "not alone". 534 Gregariousness_{BC} represents spatial proximity aspects that have been suggested to measure 535 536 social integration, i.e., close proximity to and higher rates of affiliation with diverse partners. The evidence for a Gregariousness_{BC} dimension is mixed for macaques. There are similar 537

domains with the focus on close and distant proximity in Barbary, crested, and Rhesus macaques (Capitanio, 1999; Neumann et al., 2013; Tkaczynski et al., 2018), or domains with a mixture of behaviors belonging to our Gregariousness_{BC} and Sociability_{BC} in Barbary, longtailed, lion-tail, and Tibetan macaques (Pritchard et al., 2014; Rouff, Sussman, & Strube, 2005; Tkaczynski et al., 2018; Uher, Werner, et al., 2013).

543 The negative correlation between Friendliness_{TR} and Sociability_{BC}, while being weak, still seems unexpected. Friendliness_{TR} does not seem to cover the behavior personality dimension 544 Sociability_{BC}, since four out of the five variables with positive factor loadings on 545 Sociability_{BC} correlated negatively with Friendliness_{TR}. Sociability_{BC} seems to have two 546 facets: first, it was primarily described by high rates of short-term affiliation (such as 547 "embrace"), with a factor loading of 0.99 (mean loadings of other variables < 0.5) and a 548 549 negative correlation with Friendliness_{TR}, and thus may reflect an aspect of social integration, not included in Friendliness_{TR}. Second, Sociability_{BC} seems to express variation in social 550 bonding, i.e. the tendency to focus affiliation on a few close partners (Ostner & Schülke, 551 2014). Individuals with stronger bonds have a higher "contact time" (time in body contact 552 and grooming) with less social partners leading to a negative correlation of "contact 553 diversity" with Friendliness_{TR}. Also, "contact time", as a measure for "affectionate" 554 (closeness and frequent grooming with others), was not correlated with Friendliness_{TR}, as 555 high scores may result from a few long or from many short periods of contact. In addition, 556 rates of "friendly behavior" do not need to be high for strongly bonded individuals, since they 557 might engage in prolonged but less frequent social interactions with their bonded partners. 558 Crested and Rhesus macaques exhibit a similar behavior Sociability_{BC} dimension with high 559 560 grooming and affiliation rates as well as diverse grooming and affiliation (Neumann et al., 2013; von Borell, Kulik, & Widdig, 2016). Interestingly, "peripheral" (staying outside the 561

group center) included in Sociability_{BC} underlines that there is no need for individuals to stay close to the core of the group to be socially integrated. In Barbary and Crested macaques being "central" loads on a dimension most similar to this study's Gregariousness_{BC} (Neumann et al., 2013; Tkaczynski et al., 2018).

Opportunism_{TR} completely comprises adjectives referring to Adam's and colleagues 566 Opportunism_{TR}, as well as four out of ten adjectives belonging to their Openness_{TR} 567 dimension, i.e. "excitable", "impulsive", "erratic", "distractible" (Adams et al., 2015). The 568 remaining five 'Openness_{TR} adjectives' (e.g., "thoughtless", "innovative") were excluded 569 from our analysis and "individualistic" loaded on Confidence_{TR}. It was unexpected that 570 Opportunism_{TR} and Aggressiveness_{BC} were not strongly correlated. This weak relationship 571 was likely driven by the behaviors "mild aggression" and "quitting", because observers may 572 573 have perceived more frequent behaviors as more important ("mild aggression" was 5 times more frequent than "physical aggression"). Similarly, in chimpanzees, aggression related trait 574 ratings converged strongly with "threat", but only weakly with the lower frequency "attack" 575 behavior measures (Vazire et al., 2007). "Physical aggression" and "leaving" correlated 576 positively with Friendliness_{TR}, which is similar to a positive association of "contact 577 aggression" and the socio-positive Extraversion_{TR} found in chimpanzees (Freeman et al., 578 2013). As "physical aggression" is often expressed in more serious conflicts which in 579 chimpanzees and Assamese macaques often turn polyadic, an individual acting aggressively 580 may at the same time be supportive and helpful in a coalitionary context. "Helpful" is 581 included in Friendliness_{TR}, possibly causing the positive correlation between "physical 582 aggression" and Friendliness_{TR}. In addition, there is a general link between affiliative and 583 584 aggressive interactions among partners due to the increasing probability of conflict with increasing time spent in close proximity to others (Silk et al., 2010; Widdig, Nürnberg, 585

586 Krawczak, Streich, & Bercovitch, 2002). In line with this, in macaque personality studies affiliative and aggressive behaviors are frequently correlated as are social behavior and 587 aggressiveness-related rating dimensions (Capitanio, 1999; Rouff et al., 2005; Tkaczynski et 588 al., 2018; Uher, Werner, et al., 2013). So far, rating Opportunism_{TR} domains are described for 589 Assamese (this study), crested (Adams et al., 2015), pigtail and longtailed (Sussman et al. 590 2013, Uher, Werner, et al., 2013) as well as Tibetan macaques (Pritchard et al., 2014), 591 whereas Confidence_{TR} or Dominance_{TR} dimensions are found in Rhesus (Adams et al., 2015; 592 Capitanio, 1999, Weiss et al., 2011) and Confidence_{TR} and Opportunism_{TR} or Excitability_{TR} 593 594 in Barbary macaques (Adams et al. 2015; Konečná et al., 2012; Tkaczynski et al., 2018).

Confidence_{TR} is almost equivalent to the dimension found previously (Adams et al., 2015). 595 Confidence_{TR} was weakly related to Vigilance_{BC} as a statistical trend, given the negative 596 597 correlation of "vigilant" behavior with Confidence_{TR}. However, the two dimensions seem not convergent, since other candidate behaviors for Confidence_{TR} did not correlate with 598 "vigilant". For instance, "display", presumably a dominance behavior (Freemann et al., 2013; 599 Uher, Werner, et al., 2013; Tkaczynski et al., 2018), showed no reliable loading on any 600 behavior personality dimension, but a prominent positive correlation with Confidence_{TR}. In 601 602 addition, "self-directed" behavior correlated negatively with Confidence_{TR}, suggesting it is a measure of anxiety (Brent et al., 2014; Koski, 2011b; Neumann et al., 2013; Iwanicki & 603 Lehmann, 2015; Tkaczynski et al., 2018), but here it only loaded negatively, although 604 605 weakly, on Sociability_{BC}. There was a lack of behavior variables supporting Confidence_{TR} adjectives like "dominant" and "submissive", because adult Assamese macaques rarely show 606 unprovoked submissive behavior towards other individuals. Similarly, a study on wild 607 608 Barbary macaques did not find behavior variables to be correlated with their Confidence_{TR} dimension, which is a mixture of items belonging to our Confidence_{TR} and Opportunism_{TR} 609

610 (Tkaczynski et al., 2018). Confidence_{TR} was correlated with dominance rank though in 611 Hanuman langurs and with rank stability in Barbary macaques (Konečná et al., 2008; 612 Konečná, Weiss, Lhota, & Wallner, 2012). Taken together, a fifth behavior dimension 613 replicating Confidence_{TR} may be possible.

In contrast to the reverse correlation of "vigilant" and "active" in this study, a positive 614 correlation of "vigilance" with "playfulness" and "physical activity" was found in longtailed 615 macaques (Uher et al., 2013) and play behavior in brown capuchins (Morton et al., 2013). In 616 these studies, vigilance was measured as social attentiveness, monitoring the activities of 617 other group members. Further, "vigilant" loaded on the Anxiety dimension derived from 618 playback experiments in wild Barbary macaques (Tkaczynski et al., 2018). However, it was 619 only used as playback reaction measure and not as a neutral variable in the every-day 620 621 behavior coding. A behavior study with free-ranging Rhesus macaques (von Borell et al., 2016) described a Fearfulness_{BC} dimension, resembling some of the behavior variables of this 622 study loading on Gregariousness_{BC} (i.e. friendly approach, proximity, resting) grouped 623 together with "submissive". If our "vigilance" represented an anxiety measure, it would most 624 likely group with other potential anxiety behaviors, but instead it represented its own 625 626 dimension. Thus, the "vigilance" variable in this study reflected a general attentiveness to the surrounding environment, social or ecological. 627

Activity_{TR} shared the most descriptive adjectives with highest loadings, e.g., "active" (considerable time moving or engaging in energetic behavior) and "not lazy" and "playful", with earlier findings (Adams et al., 2015). Additionally, our Activity_{TR} included "curious", like in other macaque studies (Barbary, Konecná et al., 2012; longtailed, Uher, Werner, et al, 2013; Tibetan macaques, Pritchard et al., 2014), but the Activity_{TR} dimension was not found 633 across all macaque rating studies. Activity_{TR} was not correlated with "active" behavior, but with "friendly behavior" and "peripheral" instead, leading to a strong correlation between 634 Activity_{TR} and Sociability_{BC}. Activity_{TR} may thus be mainly perceived as socially active and 635 636 spending a greater amount of time outside the group center, yet not necessarily alone. However, there was no convergence between $Activity_{TR}$ and $Sociability_{BC}$, because the 637 correlation was only driven by one social behavior (out of six behaviors loading on 638 Sociability_{BC}); it was not correlated with "active" behavior, despite the high loadings of 639 "active" and "not lazy" on Activity_{TR}. Generally, rating and behavior Activity dimensions are 640 641 related to social behaviors in primates (Konečná et al., 2008; Tkaczynski et al., 2018; Uher, Werner, et al., 2013; Vazire et al., 2007), but further analyses are needed to better understand 642 these links. 643

644 The inconsistencies identified in this descriptive comparison between our and previous findings for Assamese macaques (Adams et al., 2015) could be due to sensitivity of the 645 personality structure to rather small sample sizes, leading to small observations-to-variables 646 ratios for the factor analyses (trait ratings with 107 individuals and 43 adjective items). If we 647 assume moderately plastic personality, the construct might change due to new animals being 648 649 rated in 2015 and 2016, and 19 of the 34 animals already rated in 2009 having matured into adulthood (Dingemanse & Wolf, 2013). Inconsistencies may additionally be due to 650 differences in method; the original study (Adams et al., 2015) neither exclude unreliable 651 652 raters, nor items with low interrater reliability, while we exclude half of the items included in the original Openness_{TR} dimension which was found in four out of five species studied. Some 653 studies found similar Openness dimensions as well (e.g., Konečná et al. 2012; Uher, Werner, 654 655 et al., 2013), but others did not (e.g., Capitanio, 1999; Tkaczynski et al., 2018). Differences in method may thus explain the main discrepancies between ours and the previous study on the 656

same population. Another replication study, using the same trait rating method on different
populations of common marmosets also revealed to some extent differences in the personality
structures, even adding a fifth dimension (Koski et al., 2017).

660 Comparison with other multi-method primate studies

In the following we provide a brief review of seven macaque and eleven other primate studies 661 that employed a multi-method approaches (macaques: Capitanio 1999; Pritchard et al., 2014; 662 Rouff et al., 2005; Sussman et al., 2013; Tkaczynski et al., 2018; Uher, Werner, et al., 2013; 663 this study; other nonhuman primates: Carter, Marshall, Heinsohn, & Cowlishaw, 2012; 664 Eckardt et al., 2015; Freeman et al., 2013; Garai et al., 2016; Iwanicki & Lehmann, 2015; 665 Konečná et al., 2008; Morton et al., 2013; Pederson, King, & Landau, 2005; Uher & 666 Asendorpf, 2008; Uher & Visalberghi, 2016; Vazire et al., 2007). To date, trait rating studies 667 668 identified a unique macaque Friendliness_{TR} dimension described with the same adjectives in all species, whereas other primate studies often define two discriminant social domains, 669 mostly named Extraversion_{TR} and Agreeableness_{TR}. In nearly all of the reviewed multi-670 method studies social rating domains were best validated, revealing positive correlations with 671 social behaviors or behavior domains, generally resembling a mixed pattern of behaviors 672 reflecting social integration (e.g., proximity) and bonding (e.g., grooming skew). 673 Opportunism_{TR} and Dominance_{TR} related dimensions (or Confidence_{TR} as in most macaques) 674 were validated in half of the studies. Dominance_{TR} and Opportunism_{TR} are not seen as 675 interchangeable, because Dominance_{TR}, described with dominant and confident adjectives, is 676 indeed often correlated with dominant and aggressive behaviors. In contrast, Opportunism_{TR} 677 is correlated with dominance behavior only, if the two aspects are integrated in one 678 Dominant-Competitive-Aggressive dimension. Most studies describe either Opportunism_{TR} 679

(macaques) or Dominance_{TR} (other species) and one third made both domains part of the personality profile. Other dimensions, as Excitability_{TR+BC}, Emotionality_{TR+BC} or Boldness_{TR+BC} are less reliably measured and validated. Half of the studies in non-macaque species, and one in macaques, define an Openness_{TR+BC} domain, consistently loaded with "curious", which in all cases correlated with "playful" behavior.

Disparities between methods measuring the same construct, as found in the majority of 685 studies, demand multi-method approaches to check for validity in every species under study 686 to further ensure reproducibility. We should not assume validity if only shown once, since 687 688 most personality dimensions have not been reliably validated in the nonhuman literature (but see discussion for nun-human primates in Koski et al., 2017). Particularly studies on wild 689 primates with low sample sizes and limited observational data (partly due to lower behavior 690 691 frequencies compared to captivity) need to be replicated. Replication studies on the same subjects, groups and populations could build up on each other enabling longer observation 692 periods, and hence larger sample sizes, which may allow including behaviors with low 693 frequencies. Eventually, male, female and juvenile behavior data could be integrated. 694 Subsequent studies could focus on a single dimension, which might require experimental 695 696 settings (e.g., boldness) which are difficult to conduct in the wild (e.g., playback experiments in demanding habitats). Altogether, this may lead to more complex and fine grained 697 personality structures of nonhuman animals. In addition, mixed findings in personality 698 699 profiles between species also call for replication studies to understand the socio-ecological 700 relevance of similar behaviors in different species.

701 A comprehensive personality structure for male Assamese macaques

702 We propose two solutions for how to combine the 8 dimensions from trait rating and behavior coding. Congruence between $Friendliness_{TR}$ and $Gregariousness_{BC}$ as well as 703 between Activity_{TR} and Sociability_{BC} make them largely redundant. Based on the 704 705 considerations laid out above about the role of behavior frequency we also consider Opportunism_{TR} and Aggressiveness_{BC} to reflect a similar dimension of inter-individual 706 variation in behavior. Despite the correlation between factor loadings on Confidence_{TR} and 707 Vigilance_{BC} being the same as between Opportunism_{TR} and Aggressiveness_{BC} dimensions, we 708 considered congruence to be low between the former. It follows that the full 5-factor structure 709 710 is either built from all trait rating dimensions plus Vigilance_{BC} or from all behavior coding dimensions plus Confidence_{TR}. Both solutions have their strengths and weaknesses. 711

We demonstrated the importance of the examination of rating performances of observers, as 712 713 well as reliability analyses for item selection. However, even if a strong agreement among observers can ensure that trait ratings are not purely idiosyncratic interpretations, all 714 observers may be biased in the same way (Freeman et al. 2011; Koski et al 2011a; Uher 715 2008, Uher & Asendorpf 2008). This aspect of trait ratings deserves continued attention. For 716 instance, an individual which is mainly staying in the periphery of the group and spotted less 717 718 often will more likely be rated as unsocial, although it is extremely social when joining the group. In statistical terms trait ratings have to be preferred over behavior coding results here 719 720 because the former were much more robust.

Advantages of behavior coding include that behaviors are directly perceivable and measurable and therefore more objective (Freeman et al., 2011) so that more subtle variation in sociability can be detected. So far, trait rating studies in macaques identified a single Friendliness dimension (Adams et al., 2015), whereas behavior coding studies frequently found two distinct prosocial personality domains (Capitanio, 1999; Neumann et al., 2013; Tkaczynski et al., 2018; this study). Researchers in animal and human personality studies stress that social personality dimensions can only be identified in the context of social relationships especially in species with complex societies (Cooper, 2002; Koski, 2011b; Reis, Collins, & Berscheid, 2000). This is highlighted by the fact that affinitive behavior loaded on a different factor than actual affiliative interaction variables because individuals may tolerate and be tolerated sometimes without implications for friendly contact behaviors.

One disadvantage of the behavior coding data is that measurement reliability for individual differences may be low for rare behaviors that may, however, bebut biologically very important such as support in agonistic conflicts. Observers may be better able to represent variation in rare behaviors in their ratings.

We conclude that two solutions with five factors best describe the personality structure of the male Assamese macaques studied here. One 5-factor structure is built from all trait rating dimensions plus Vigilance_{BC} and the other from all behavior coding dimensions plus Confidence_{TR}. Both solutions have their strengths and weaknesses. We encourage the use of integrative approaches including trait ratings, behavioral codings, and experiments embracing the Transdisciplinary philosophy-of-science paradigm (Uher, 2018), which aims to broaden the horizon in personality research in a transdisciplinary way.

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Item	Opportunism _{TR}	Confidence _{TR}	Activity _{TR}	Friendliness _{TR}	h^2
bullying	0.96	0.21	-0.12	-0.02	0.92
aggressive	0.93	0.28	-0.1	-0.01	0.92
irritable	0.93	0	0.01	-0.09	0.88
greedy	0.92	0.21	-0.38	0.15	0.77
jealous	0.92	0.01	-0.14	0.10	0.75
manipulative	0.87	0.24	-0.17	0.09	0.77
defiant	0.81	0.09	0.12	0.02	0.81
excitable	0.78	-0.31	0.15	-0.05	0.77
impulsive	0.72	0.12	0.27	-0.01	0.82
erratic	0.71	-0.17	0.25	-0.21	0.76
distractable	0.55	(-0.49)	0.16	-0.05	0.58
persistent	0.49	(0.44)	0.20	0	0.63
cool	-0.46	(0.42)	-0.36	0.13	0.63
unemotional	-0.62	0.12	-0.39	-0.03	0.76
stable	-0.66	0.16	-0.36	0.15	0.79
gentle	-0.77	-0.17	-0.06	0.41	0.80
dominant	0.30	0.82	-0.19	0.05	0.81
decisive	0.20	0.79	-0.16	0.03	0.70
independent	-0.07	0.68	-0.32	(-0.42)	0.65
protective	0.17	0.61	-0.21	(0.47)	0.75
intelligent	0.10	0.60	-0.13	0.05	0.39
individualistic	0	0.53	-0.08	(-0.49)	0.41
clumsy	0.36	-0.53	-0.52	0.22	0.44
quitting	0.18	-0.71	-0.37	0.01	0.60
anxious	0.18	-0.74	0.05	-0.21	0.66
timid	-0.24	-0.78	0.11	-0.15	0.77
fearful	0.25	-0.83	-0.04	0.01	0.68
submissive	-0.23	-0.86	-0.04	0.10	0.82

communalities (h^2) *derived from trait ratings (TR).*

vulnerable	-0.11	-0.88	-0.1	0.03	0.83
follower	0.03	-0.91	0.01	0.30	0.78
playful	-0.17	-0.17	0.84	0.09	0.65
active	0.09	0.01	0.79	-0.06	0.68
curious	0.32	-0.06	0.61	0.15	0.73
inquisitive	0.31	-0.04	0.61	0.08	0.68
depressed	-0.07	(-0.44)	-0.48	-0.29	0.71
cautious	0.19	(-0.42)	-0.58	-0.09	0.50
lazy	-0.16	0.13	-0.73	-0.03	0.68
affectionate	-0.10	-0.10	0.01	0.91	0.81
sympathetic	-0.31	-0.11	-0.02	0.81	0.71
friendly	(-0.46)	-0.14	-0.05	0.77	0.77
sociable	0.22	0.11	0.14	0.76	0.79
helpful	0.12	0.30	0.16	0.66	0.74
solitary	-0.15	-0.24	-0.22	-0.64	0.72
Variance	27%	22%	11%	12%	
explained					

Note. Salient factor loadings $\geq |0.4|$ are shown in bold.

- 1019 Table 2: Rank-order stability of personality dimensions from trait ratings (TR) in 2015 and
- 1020 2016 with factor congruence of factor loadings (first number in cell) and Pearson

correlations of extracted factor scores (second number in cell).

	2016			
2015	Opportunism _{TR}	Confidence _{TR}	Friendliness _{TR}	Activity _{TR}
Opportunism _{TR}	0.97 / 0.87	-0.04 / -0.20	-0.03 / -0.04	-0.18 / -0.39
Confidence _{TR}	-0.03 / -0.12	0.98 / 0.79	-0.17 / -0.29	0.05 / 0.07
Friendliness _{TR}	-0.02 / -0.07	-0.11 / -0.17	0.94 / 0.72	-0.02 / -0.29
Activity _{TR}	-0.20 / -0.46	0.01 / 0.14	-0.01 / -0.13	0.91 / 0.84

Note. $N_{adjectives} = 41$. Values with 90% confidence intervals excluding zero, shown in bold.

 $N_{individuals} = 74$. Significant values after correcting for fdr shown in bold.

Variable	Gregariousness _{BC}	Aggressiveness _{BC}	Sociability _{BC}	Vigilance _{BC}	h^2
neighbor diversity	0.91	0.08	-0.14	-0.06	0.95
tolerance	0.88	0.02	0.13	0.12	0.78
friendly approach	0.84	0.10	-0.10	0.01	0.80
active	-0.52	0.08	-0.04	(-0.46)	0.46
alone	-0.99	0.06	-0.05	0.06	0.94
quitting	0.04	0.85	0.10	-0.12	0.77
mild aggression	-0.14	0.73	0.13	0.16	0.49
agonistic involvement	-0.02	0.67	0.03	-0.08	0.45
physical aggression	0.27	0.60	-0.14	0.16	0.61
leaving	0.21	0.48	-0.24	0.01	0.43
friendly behavior	-0.01	0.14	0.99	-0.02	1.00
contact diversity	0.03	-0.21	0.56	0.11	0.34
peripheral	-0.34	-0.24	0.49	-0.06	0.55
initiation	-0.17	-0.05	0.42	-0.28	0.38
contact time	0.38	-0.19	0.42	-0.10	0.30
self-directed	-0.35	0.01	-0.44	0.24	0.38
vigilant	-0.03	0.00	-0.03	0.99	1.00
display	0.39	0.38	-0.06	-0.24	0.46
Variance explained	25%	15%	13%	9%	

Table 3: Personality structure derived from behavior codings (BC) after oblimin rotation with

1026 factor loadings and item communalities (h^2) .

- 1029 Table 4: Rank-order stability of personality dimensions from behavior codings (BC) in
- 1030 04/14–03/15 and 04/15–03/16 with factor congruence of loadings (first number in cell) and
- 1031 *Pearson correlation of extracted factor scores (second number in cell).*

	2015–2016					
2014–2015	Gregariousness _{BC}	Sociability _{BC}	Quitting _{BC} ^a			
Gregariousness _{BC}	0.92 / 0.57	0.01 / -0.27	0.38 / 0.04			
Sociability _{BC}	-0.01 / 0.01	0.78 / 0.40	0.02 / 0.25			
Mild aggression _{BC} ^a	0.18 / -0.01	-0.25 / -0.24	0.37 / 0.24			

1032 *Note*. $N_{behaviors} = 18$. Significant value, i.e. 95% confidence interval excluding zero, shown in 1033 bold. $N_{individuals} = 22$. Significant values after controlling for fdr shown in bold and trends in

1034 italics.

^a3rd factor named after behavior variables with highest loading on that factor, resembling, but not equivalent to, Aggressiveness_{BC} in the 4-factor solution of the aggregated data.

1037

1039 Table 5: Construct validity as Pearson correlations of individual factor scores derived from

	Behavior Coding			
Trait Rating	Gregariousness _{BC}	Aggressiveness _{BC}	Sociability _{BC}	Vigilance _{BC}
Opportunism _{TR}	-0.26	0.36	0.06	-0.08
Confidence _{TR}	0.30	0.29	0.07	-0.36
Friendliness _{TR}	0.69	0.35	-0.41	0.20
Activity _{TR}	-0.13	0.14	0.63	-0.05

trait ratings (TR) and behavior codings (BC).

Note. Bold type significant after controlling for fdr, italic type statistical trend.

	Personality dimension _{TR}							
Behavior variable	Opportunism _{TR}	р	Confidence _{TR}	р	Activity _{TR}	р	Friendliness _{TR}	р
active	0.34	0.11	0.02	0.92	0.13	0.06	-0.44	0.03
agonistic involvement	0.07	0.75	0.32	0.13	-0.15	0.48	0.14	0.52
alone	0.32	0.13	-0.34	0.10	0.24	0.27	-0.66	0.00
contact diversity	-0.21	0.32	0.01	0.96	0.10	0.63	-0.40	0.05
contact time	-0.40	0.06	0.29	0.17	-0.01	0.95	-0.03	0.88
display	-0.23	0.28	0.59	0.00	-0.18	0.40	0.44	0.03
friendly approach	-0.02	0.92	0.08	0.71	-0.25	0.24	0.60	0.00
friendly behavior	0.06	0.79	0.01	0.96	0.55	0.01	-0.34	0.11
initiation	0.27	0.21	-0.24	0.25	0.19	0.37	-0.34	0.11
leaving	0.15	0.49	0.22	0.31	0.14	0.52	0.63	0.00
mild aggression	0.41	0.05	-0.11	0.61	0.08	0.72	0.10	0.64
neighbor diversity	-0.20	0.35	0.22	0.29	-0.33	0.12	0.65	0.00
physical aggression	0.05	0.82	0.17	0.43	-0.19	0.39	0.50	0.01
quitting	0.34	0.10	0.23	0.28	0.17	0.42	0.32	0.13
self-directed	0.09	0.68	-0.56	0.01	-0.20	0.36	-0.04	0.85
peripheral	0.15	0.48	-0.10	0.66	0.43	0.04	-0.45	0.03

1043 Table 6: Correlation coefficients (ρ_{pb}) of behavior variables with personality factor scores from trait ratings (TR).

tolerance	-0.34	0.11	0.15	0.49	-0.32	0.13	0.60	0.00
vigilant	-0.04	0.85	-0.43	0.04	-0.13	0.55	0.06	0.79

Note. Significant values after fdr correction shown in bold.

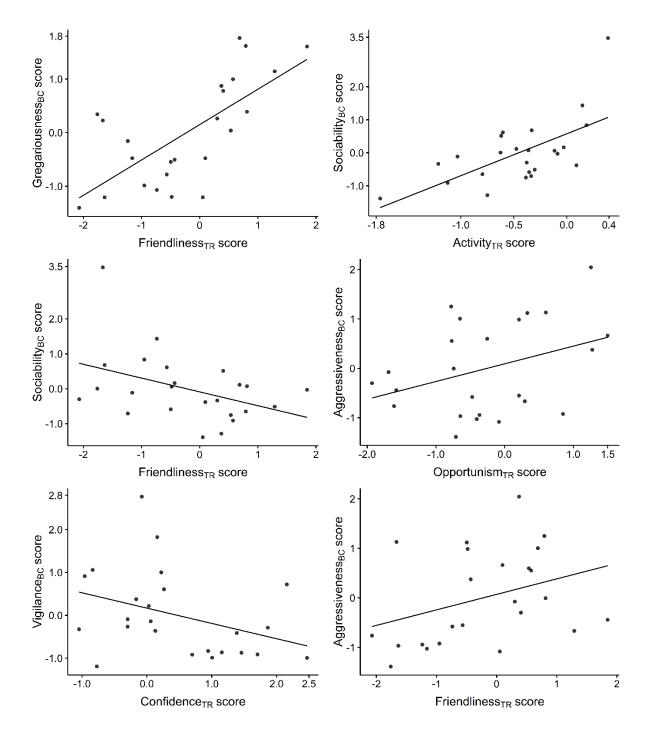




Figure 1. Congruence in factor scores of 24 males between constructs from behavior coding

1048 BC and trait rating TR. For statistics see table 5.