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# The influence of phylogeny, social style, and sociodemographic factors on macaque social network structure

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American Journal of Primatology

WILEY

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32    **Abstract:**

33         Among nonhuman primates, the evolutionary underpinnings of variation in social

34    structure remain debated, with both ancestral relationships and adaptation to current

35    conditions hypothesized to play determining roles. Here we assess whether interspecific

36    variation in higher-order aspects of female macaque (genus: *Macaca*) dominance and

37    grooming social structure show phylogenetic signals, i.e. greater similarity among more

38    closely-related species. We use a social network approach to describe higher-order

39    characteristics of social structure, based on both direct interactions and secondary pathways

40    that connect group members. We also ask whether network traits covary with each other,

41    with species-typical social style grades, and/or with sociodemographic characteristics,

42    specifically group size, sex-ratio, and current living condition (captive vs. free-living). We

43    assembled 34-38 datasets of female-female dyadic aggression and allogrooming among

44    captive and free-living macaques representing 10 species. We calculated dominance

45    (transitivity, certainty), and grooming (centrality coefficient, Newman's modularity,

46    clustering coefficient) network traits as aspects of social structure. Computations of K

47    statistics and randomization tests on multiple phylogenies revealed moderate-strong

48    phylogenetic signals in dominance traits, but moderate-weak signals in grooming traits.

49    GLMMs showed that grooming traits did not covary with dominance traits and/or social

50    style grade. Rather, modularity and clustering coefficient, but not centrality coefficient,

51    were strongly predicted by group size and current living condition. Specifically, larger

52    groups showed more modular networks with sparsely-connected clusters than smaller

53    groups. Further, this effect was independent of variation in living condition, and/or

54    sampling effort. In summary, our results reveal that female dominance networks were more

55 phylogenetically conserved across macaque species than grooming networks, which were

56 more labile to sociodemographic factors. Such findings narrow down the processes that

57 influence interspecific variation in two core aspects of macaque social structure. Future

58 directions should include using phylogeographic approaches, and addressing challenges in

59 examining the effects of socioecological factors on primate social structure.

60 **Key words:**

61 Social networks, phylogenetic signals, social style, group size, macaques

62 **Introduction:**

63     In group-living animals, diversity in sociality may be characterized by variation in

64 social structure, i.e. the patterning and distribution of different types of interactions (e.g.

65 competitive, affiliative, cooperative) and relationships among group members (Hinde,

66 1976; Kappeler & Van Schaik, 2002). Several factors have been found to govern social

67 structure, including but not restricted to kinship, age similarity, sex and dominance status

68 (Hinde, 1976; Kappeler & Van Schaik, 2002). However, our understanding of the

69 evolutionary and ecological factors that produce diverse social structures remains limited.

70 Specifically, the extent to which such social structure has been influenced by species'

71 ancestral relationships versus variation in current conditions remains debated (Clutton-

72 Brock & Janson, 2012; Kasper & Voelkl, 2009; Koenig et al., 2013; Thierry, 2004). Here,

73 we use Social Network Analysis to assess whether variation in aspects of social structure

74 across multiple species of macaques (genus: *Macaca*) is related to species' phylogenetic

75 relatedness (Blomberg et al., 2003; Thierry, 2004), and hypothesized tendencies for social

76 traits to co-evolve with each other in suites or packages (de Waal & Luttrell, 1989; Thierry,

77 2007). We also investigate the extent to which such covariation may be influenced by

78    group-specific sociodemographic characteristics (Kasper & Voelkl, 2009; Sterck et al.,

79    1997; Sueur et al., 2011b)

80         A major explanatory framework for the evolution of variation in primate social

81    structure is related to species' ancestry or phylogenetic closeness (Blomberg et al., 2003).

82    According to this framework, aspects of sociality are expected to show phylogenetic

83    signals, i.e. to exhibit greater similarity in social structure among more closely-related than

84    distantly-related species (Blomberg et al., 2003). Ecological adaptation is not ruled out but

85    rather hypothesized to occur minimally, or in response to novel, drastic environmental

86    changes (Blomberg et al., 2003; Chan, 1996; Matsumura, 1999). In the past, proponents of

87    phylogenetic signals often referred to them as outcomes of phylogenetic constraints or

88    phylogenetic inertia (Blomberg et al., 2003). However, more recent theory recognizes that

89    phylogenetic signal refers to the observed patterns of trait similarity, rather than one or

90    more evolutionary processes – e.g. random genetic drift, stabilizing selection, pleiotropy, or

91    low rates of evolution -- by which such patterns may arise (reviewed in Kamilar & Cooper,

92    2015). Rather than attempt to distinguish between possible processes or the rates at which

93    they occur, here we simply aim to identify strong and weak phylogenetic signals in order to

94    determine the extent to which social network structure covaries with macaques'

95    phylogenetic closeness.

96         Across animal societies, behavioral traits are more labile to evolutionary change in

97    comparison to morphological and/or physiological characteristics (Blomberg et al., 2003).

98    Primates are no exception, with traits like brain size, body mass and canine dimorphism

99    exhibiting stronger phylogenetic signals than those related to social organization and

100    activity budgets (Kamilar & Cooper, 2015). As such, phylogenetic signals for aspects of

101 primate social network traits have been hard to identify. For instance, Kasper and Voelkl

102 (2009) established that several aspects of affiliative social networks – e.g. community sub-

103 group formation or modularity, mean centrality in the connectedness of individuals, and the

104 density of network connections (see Methods for precise definitions) -- all showed greater

105 variation between closely related than between distantly related species, i.e. weak

106 phylogenetic signals and a substantial effect of socioecological or demographic factors on

107 network structure. Similarly, Pasquaretta et al. (2014) found no effect of phylogenetic

108 signals on the efficiency of information flow through affiliative social networks of

109 primates, including humans. Tests for phylogenetic signals in aspects of sociality within

110 specific primate families and genera have also revealed inconsistencies. In the genus

111 *Eulemur*, group size and sex-ratio both strongly correlated with phylogenetic distances

112 (Ossi & Kamilar, 2006). Yet among both baboons (genus: *Papio*) and squirrel monkeys

113 (genus: *Saimiri*), interspecific variation in multiple forms of social organization seem to be

114 strongly linked to ecological factors like food distribution, predation pressure, and

115 intergroup feeding competition (Barton et al., 1996; Boinski, 1999; Henzi & Barrett, 2003).

116 Nevertheless, among all primate genera, phylogenetic signals in social traits have

117 been most consistently detected within the genus *Macaca*. Macaques constitute 23 species

118 of Old World primates, with wide-spread geographic distributions in nature (Cords, 2013).

119 Although all species show a predominantly similar social organization (multi-male, multi-

120 female social groups, female philopatry and male dispersal), they show broad inter- and

121 intraspecific variation in several aspects of female social structure (Thierry, 2007).

122 Specifically, post-conflict affiliation, rates of affiliative contact (Thierry et al., 2008), the

123 steepness of dominance hierarchies (Balasubramaniam et al., 2012a), and asymmetry in

124  aggression (Balasubramaniam et al., 2012a; Thierry et al., 2008) all show phylogenetic

125  signals, whereas grooming kin bias shows a weak signal (Thierry et al., 2008). These

126  findings have led some proponents of phylogenetic explanations to posit that core aspects

127  of macaque social structure may also be structurally linked, covarying with each other at

128  the species level (Petit et al., 1997; Thierry et al., 2008). Thierry (2007) has characterized

129  this tendency to covary by assigning macaque species to positions on a four-grade 'social

130  style' scale that is broadly consistent with phylogenetic lineage splits (Thierry, 2007). At

131  one extreme, 'grade-1' species (e.g. rhesus macaques (*Macaca mulatta*), Japanese

132  macaques (*M. fuscata*)) of the Fascicularis lineage are hypothesized to show 'despotic'

133  social structure, characterized by steep and asymmetric dominance hierarchies, low levels

134  of post-conflict affiliation, intense affiliative kin-bias, and highly modular or sub-structured

135  social networks in which grooming is both centralized among dominant individuals and is

136  concentrated among more preferred partners. At the other extreme, 'grade-4' species (e.g.

137  Tonkean macaques (*M. tonkeana*), crested macaques (*M. nigra*)) belonging to the Sulawesi

138  lineage are hypothesized to be more 'tolerant' or 'egalitarian', showing shallower

139  dominance hierarchies with more frequent counter-aggression from subordinates towards

140  dominants, high proportions of post-conflict affiliation, less grooming kin bias, and denser,

141  less centralized or modular grooming social networks (Balasubramaniam et al., 2012a;

142  Berman & Thierry, 2010; de Waal & Luttrell, 1989; Sueur et al., 2011b; Thierry, 2007;

143  Thierry et al., 2008). Some versions of the covariation hypothesis posit that a species that

144  shows a single behavioral trait associated with a particular social style will display all other

145  traits (Castles et al., 1996; Petit et al., 1997). However, this extent of covariation has not

146  always been found. Rather, most studies (but see Thierry et al. 2008) thus far have revealed

147 marked differences between species at the extreme ends of the social style scale (grade-1

148 and grade-4 macaques, e.g. Sueur et al., 2011b), but found inconsistencies among macaques

149 in intermediate grades (reviewed in Balasubramaniam et al., 2012b).

150    In the present study, we expand on the above findings by assessing phylogenetic

151 signals and covariation in dominance and grooming social network traits across 10 species

152 of macaques representing all four social style grades, and groups from both captive and

153 free-living conditions. In accordance with the predictions of socioecological models, we

154 also examine whether sociodemographic factors, specifically group size and current living

155 condition (Kasper & Voelkl, 2009; Pasquaretta et al., 2014), influence social network traits

156 in addition to, or instead of, social style or phylogenetic closeness. Broadly, socioecological

157 models differ from phylogenetic explanations by positing that social structure is relatively

158 more labile to changes in current conditions, and that such changes are independent of

159 phylogenetic relatedness (Koenig et al., 2013; Sterck et al., 1997; van Schaik, 1989).

160 Specifically, some versions of the model predict that among free-living primates, larger

161 group size should lead to the evolution of more despotic social network structures,

162 characterized by steeper, asymmetric dominance hierarchies, and highly centralized,

163 modular grooming networks with less dense connections/ redundant ties. This may be

164 because larger groups are likely to display heightened levels of contest competition for

165 resources (Koenig et al., 2013; Sterck et al., 1997; van Schaik, 1989) and/or increased

166 temporal constraints (Berman & Thierry, 2010; Dunbar, 1992; Korstjens et al., 2010). On

167 the other hand, smaller groups may be expected to show greater within-group social

168 tolerance characterized by more reversals in dominance interactions, and de-centralized

169 grooming networks that show greater density/ redundancy of ties. Such effects may also be

170   influenced by the spatial constraints imposed by captive housing that may result in more

171   frequent social interactions among individuals with a potentially wider range of partners

172   (Duboscq et al., 2013; McCowan et al., 2008).

173         Following the pioneering applications of social network analysis on macaque social

174   structure by Sade (1972), comparative studies of nonhuman primate social structure have

175   increasingly used social network approaches to compare various types of societies (Griffin

176   & Nunn, 2012; Kasper & Voelkl, 2009; Pasquaretta et al., 2014; Sueur et al., 2011b). SNA

177   tools improve on earlier methods by constructing aspects of higher-order group structure

178   from a combination of both direct interactions and indirect or secondary connections among

179   group members, and by identifying consistent patterns of interaction among sub-sets of

180   individuals (Brent et al., 2011; Croft et al., 2008; Farine & Whitehead, 2015; Kasper &

181   Voelkl, 2009; Krause et al., 2007; Lusseau & Newman, 2004; McCowan et al., 2008;

182   Newman, 2004; Sueur et al., 2011a; Wey et al., 2008). Yet in comparison to applied animal

183   behavioral research (e.g. infectious disease transmission (reviewed in Drewe & Perkins, 2015),

184   quantifying group social stability (reviewed in McCowan et al., 2008)), SNA has been used less

185   extensively to examine the evolutionary bases for variation in primate social structure (see Kasper

186   & Voelkl, 2009; Griffin & Nunn, 2012; Sueur et al., 2011b).

187         We first ask whether aspects of female dominance and grooming networks show

188   strong phylogenetic signals (Q1) and whether grooming networks covary with dominance

189   networks (Q2) and/or hypothesized social style grades across macaques (Q3). In

190   accordance with the covariation and social style hypotheses, we predict that macaque

191   species that have the most transitive, decided and/or certain dominance relationships will

192   also show (a) the greatest tendencies for high-ranking individuals to occupy more central

193   positions in more modular grooming networks, and (b) networks that are more modular

194    with sparser, less redundant ties. In comparison, those with the least transitive and/or

195    uncertain dominance relationships are expected to show the opposite characteristics.

196    Further, we predict that transitions from more despotic to more tolerant social styles will be

197    correlated with systematic decreases in the centralization of grooming among dominants

198    and modularity, and increases in network density or redundancy of ties. Finally, we also

199    examine (Q4) the potential impact of sociodemographic factors on networks and patterns of

200    covariation. Specifically, we predict that group size will be positively associated with the

201    centralization of grooming among dominants and with grooming modularity, and

202    negatively associated with the density/ redundancy of ties in grooming network clusters.

203    We also explore the effects of living condition on such relationships, and the impact of a

204    third sociodemographic characteristic -- female-to-male sex ratio -- on such covariation.

205    **Methods:**

206        This research adhered to the American Society of Primatologists principles for the

207    ethical treatment of primates. We first assembled behavioral and phylogenetic datasets from

208    various sources – published literature, our own unpublished data, and personal donations

209    from other researchers (Table 1). Below we describe these data, the computation of social

210    network measures, and statistical analyses.

211    *Datasets – macaque social behaviors and phylogenetic trees:*

212        To compute dominance network measures, we assembled a total of 38 behavioral

213    datasets on dyadic aggressive interactions among adult female macaques (individuals $\geq$ 3.5

214    - 5 years of age, depending on species-typical ages of maturity) from groups living in

215    captive and free-living (free-ranging and wild) conditions (Table 1). These encompassed 20

216    populations representing 10 macaque species from all four social style grades. Except for

Balasubramaniam et al. 10

217　stumptailed macaques (*M. arctoides*) and bonnet macaques (*M. radiata*), we acquired at

218　least two datasets for each species; these were either from different social groups or from

219　the same social group during different stable study-periods. To compute grooming network

220　measures, we obtained data from 34 (out of the 38) datasets from nine species (Table 1).

221　　　　The datasets had been collected using different types of sampling approaches, and

222　varied in sampling effort per subject (Table 1). The majority (aggression: 33/ 38, or 87%;

223　grooming: 25/34, or 74%) had been collected using focal-animal and/or all-occurrences

224　sampling methods (Altmann, 1974; see citations provided in Table 1). For these datasets,

225　all subjects within a dataset had been observed for roughly equal amounts of time (see

226　corresponding citations; information available on request). A minority used either scan

227　sampling (aggression: 2/38, or 5%; grooming: 7/34, or 20%) or *ad-libitum* sampling along

228　with focal animal sampling (aggression: 3/38, or 8%; grooming: 2/34, or 6%). The scan

229　sampling datasets were included based on a previous study on Japanese macaques revealing

230　that for a given number of scans, this approach yields identical amounts of behavioral data

231　to focal sampling for the same duration (in minutes) as the number of scans (Romano et al.,

232　2016). Datasets that used *ad libitum* sampling were included after ensuring that they had

233　been (a) used in previous comparative studies (Balasubramaniam et al., 2012a; Schino &

234　Aureli, 2008), and (b) conducted for overall durations that were comparable to those of the

235　focal- or all-occurrences sampled datasets (6 – 12 months).

236　　　　All datasets included had been collected as part of long-term studies, and during

237　periods when the groups were socially stable in terms of group composition, size,

238　dominance relationships, age-class and/or sex ratios. Out of 38 datasets, the majority (27, or

239　71%) was from free-living groups of macaques. We found significant differences in group

240  size (captive = 28.4 ± 19.1; free-living = 48.3 ± 23.9; ANOVA: $F_{1, 32} = 6.04, p = 0.02$) and

241  sex ratios (captive = 0.50 ± 0.21; free-living = 0.33 ± 0.09; ANOVA: $F_{1, 32} = 12.07, p <$

242  $0.01$) between captive vs. free-living macaques. Hence, we either conducted separate

243  assessments for only free-living groups (Q1), or directly examined the effect of living

244  condition in our analyses (Q2 - Q4).

245      In order to assess and control for the effects of phylogenetic signals, we extracted a

246  Bayesian consensus tree (Supplementary Figure 1) and a tree-block of 10 trees from

247  *10Ktrees*, an online resource for primate phylogeny based on mitochondrial and nuclear

248  genetic datasets (Arnold et al., 2010). All 11 phylogenies showed proportional branch-

249  lengths, and identical topologies that were also consistent with previously constructed

250  macaque topologies using parametric approaches (e.g. Chatterjee et al., 2009; Tosi et al.,

251  2003). We hence report the results of tests performed using the consensus phylogeny, with

252  those from the tree-block submitted as supplementary material (Supplementary Table 4).

253  *SNA – Dominance and Grooming Measures:*
254
255      Table 2 provides the definitions and details of the dominance and grooming network

256  traits that we computed. We computed dominance network measures from winner-loser

257  dominance matrices in which non-diagonal cells contained data on the frequencies of

258  dyadic contact and non-contact aggression from animals in the rows to animals in the

259  columns. Acts of bi-directional or counter-aggression were scored twice, once on either

260  side of the diagonal for each interactant. Bidirectional and counter-aggression were

261  included to produce representative measures of dominance network traits, particularly for

262  grade-3 and grade-4 macaque species that typically experience high proportions of such

263  interactions (Balasubramaniam et al., 2012a; Thierry et al., 2008). From each dominance

264   matrix, we computed two traits – triangle transitivity (Shizuka & Mcdonald, 2012) and

265   dominance certainty (Fujii et al., 2013; Fushing et al., 2011) – that have not been used in

266   previous comparative studies of primate social networks (see Table 2 for definitions).

267   Whereas most methods for describing group level dominance hierarchies consider only

268   dyadic wins and losses from agonistic encounters (e.g., dominance gradient (hierarchical

269   steepness: de Vries et al., 2006), and dominance asymmetry (Directional Consistency

270   Index: de Vries, 1998)), the computation of network-based measures, particularly

271   dominance certainty, uses both direct dominance interactions and indirect pathways of

272   imputed wins and losses (Fujii et al., 2013; Fushing et al., 2011). Thus, they capture more

273   global aspects of a dominance hierarchy than steepness or DCI, and are less susceptible

274   than steepness to error due to the numbers of non-interacting dyads present in the dataset.

275   Specifically, dominance certainty incorporates the presence of non-interacting dyads in its

276   calculation (Table 2) by weighting both the total number of direct wins by an individual 'A'

277   against an individual 'D' (A→D), as well as imputed wins incurred via the likelihood of

278   traversing longer paths (e.g. A→B→C→D) through the dominance network. In doing so,

279   the certainty measure characterizes the network-level flow-structure of dominance

280   information, thereby accounting for hidden elements in dominance structure such as

281   avoidance between individuals (Fujii et al., 2013; Fushing et al., 2011) (Table 2).

282        We constructed grooming networks (Figure 1) from weighted, undirected networks,

283   i.e. where individuals represented by *nodes* were connected by *edges* that represent the

284   normalized values of grooming given and received for each pair of nodes. Weighted

285   networks were used to account for the potential impact of differences in observation times

286   across comparative datasets (Griffin & Nunn, 2012; Newman, 2004). Specifically, we

287    calculated three measures – centrality coefficient, Newman's modularity, and global

288    clustering coefficient -- that were all (a) not collinear (see below), (b) captured biologically

289    different aspects of network structure, and (c) mathematically independent of the number of

290    nodes (or group size: Nunn et al., 2015). First, we calculated *centrality coefficient* as the

291    correlation coefficient between individuals' dominance statuses (computed using

292    normalized David's scores computed from dominance matrices: Gammell et al., 2003) see

293    below) and their centralities within grooming networks (as in Sueur et al., 2011b; see Table

294    2 for definitions). For the latter, we used standardized *eigenvector centrality*, i.e. the

295    number and strength of an individuals' direct and indirect grooming connections indicating

296    each individual's access to social capital or support (Farine & Whitehead, 2015; Newman,

297    2004; Whitehead, 2008). Eigenvector centrality is among the most biologically meaningful

298    of the centrality measures; it is more indicative of individuals' social status than measures

299    of *betweenness* and *closeness* centrality in taxa such as primates that have more complete

300    network graphs (Brent et al., 2010; Farine & Whitehead, 2015; Kasper & Voelkl, 2009;

301    McCowan et al., 2008; Sueur et al., 2011a). We also calculated Newman's eigenvector-

302    based modularity, which is a global measure of network sub-structuring into communities

303    (Newman, 2006; Nunn et al., 2015; see Table 2 for a detailed definition). Finally, as a

304    measure of the density/ redundancy of ties in the network, we calculated the *global*

305    *clustering coefficient*, which is an unweighted measure of how well-connected nodes are to

306    their immediate neighbors (Table 2). Clustering coefficient captures the underlying

307    redundancy of node connectivity at a more local level than alternative measures like

308    network density, making it mathematically independent of the number of nodes (Table 2;

309    Nunn et al., 2015). However, since increased localized clustering may also be a

310   characteristic of more modular networks (Nunn et al., 2015), we confirmed that clustering

311   coefficient was positively correlated with network density measures across our datasets (*n*

312   *= 34, r = 0.91, p < 0.01*). Grooming measures were calculated using the *statnet* (for

313   eigenvector centrality) and *igraph* (for Newman's modularity and global clustering

314   coefficient) R packages (Csardi & Nepusz, 2006; Handcock et al., 2006). Individuals'

315   dominance David's scores were calculated from the aggression matrices using the *steepness*

316   R package (de Vries et al., 2006; Leiva & de Vries, 2014).

317          Supplementary Table 1 shows the values of the various network measures computed

318   for each dataset. To avoid potentially pseudoreplicating our results owing to network

319   measures being collinear to each-other, we confirmed that collinearity diagnostics were met

320   for both dominance measures (Pearson's r correlation = 0.61; variance inflation factors

321   (VIF) < 2), and grooming measures (r < 0.78 for all pairs; generalized variance inflation

322   factors (GVIF) < 3) using the *car* package in R (Fox & Weisberg, 2011). Given the

323   susceptibility of network measures to variation in sampling effort (Croft et al., 2008; Croft

324   et al., 2011; Farine & Whitehead, 2015; Lusseau et al., 2008), we performed diagnostic

325   tests to ascertain that these did not impact our analyses. For each grooming dataset, we

326   generated 1000 permuted networks using a bootstrapping algorithm (Lusseau et al., 2008),

327   by randomly sampling increasingly smaller subsets (100%, 80%, 60%, 40%, and 20%) of

328   edges from the original network. Plots of percent sampling effort and mean grooming

329   network measure computed across 200 permuted networks under each category of sampling

330   effort revealed asymptotic relationships (Supplementary Figure 2). Further, Wilcoxon rank-

331   sum tests revealed that network measures computed from the original data were not

332   significantly different to those computed from the bootstrapped networks that used smaller

333    subsets of data (80% - 40% sampling effort; but see clustering coefficient at 20% sampling

334    effort: Supplementary Table 2). Finally, we confirmed that across datasets, sampling effort

335    calculated as the mean observation times spent per subject (Table 1) was unrelated to

336    group-level dominance and/or grooming network measures (Supplementary Table 3;

337    Supplementary Figure 3).

338    *Statistical Analyses:*

339        To examine evidence for phylogenetic signals (Q1) in dominance and grooming

340    network traits at the species level, we used the Phytools R package (Revell, 2012). For each

341    trait, we computed Blomberg's Kappa (K) coefficient (Blomberg et al., 2003) as the ratio

342    between the Mean-Squared Errors (or MSE) of the raw, species-means of behavioral traits

343    over the MSEs of traits that have been phylogenetically transformed using tree-specific

344    branch-length information. The K coefficient therefore indicates the strength of the

345    phylogenetic signal and further, is scaled by a similar ratio of MSEs calculated assuming a

346    Brownian motion model of evolution where trait change is hypothesized to be directly

347    proportional to the shared evolutionary histories, or branch length distances between taxa

348    (Blomberg et al., 2003; Kamilar & Cooper, 2015). We considered K > 1 from the

349    randomization test as indicative of a "strong" signal that exceeds the amount of signal

350    expected under a Brownian motion model of evolution (Blomberg et al., 2003). Values of

351    $0.8 < K < 1$ were considered to be indicative of a "moderate" signal, while values that are

352    << 0.8 indicate a weak signal, i.e. greater plasticity due to adaptation to current conditions

353    in a trait (Blomberg et al., 2003). These values were based on previous comparative studies

354    of nonhuman primate behavioral traits that also examined phylogenetic signals among

355    smaller numbers of species (Balasubramaniam et al., 2012a; Thierry et al., 2008). We

Balasubramaniam et al. 16

356    avoided splitting terminal species' nodes into multiple nodes to represent groups within

357    species. Although doing so offers the potential advantage of increased statistical power, it

358    would also artificially inflate phylogenetic signals (Blomberg et al., 2003; Thierry et al.,

359    2008). Blomberg's K generates identical results to Pagel's Lambda (Pagel, 1997, 1999), an

360    alternative indicator of phylogenetic signal. However, we chose to report K since this

361    statistic is more useful in informing about trait variation relative to Brownian evolution

362    (Kamilar & Cooper, 2015). In addition, we conducted randomization tests to compare the

363    MSE of phylogenetically transformed data to those computed from 1000 randomized

364    datasets generated by scattering the behavioral scores randomly on a phylogeny. In addition

365    to handling the intrinsic dependency of the data, such tests indicate whether any observed

366    phylogenetic signal is greater than that expected by chance. Although they had low

367    statistical power of 20-35% (Blomberg et al., 2003), randomization tests have nonetheless

368    been used in previous studies of similarly small sample sizes (7-10 species:

369    Balasubramaniam et al., 2012a; Thierry et al., 2008).

370          To examine whether grooming network traits were linked to dominance traits (Q2)

371    or social style scale (Q3) across species, and to assess the potential impact of

372    sociodemographic factors (Q4) on such covariations, we constructed General Linear

373    Mixed-effects Models (GLMMs: Bates et al., 2016). We implemented an Information-

374    Theoretical approach (Burnham et al., 2011; Grueber et al., 2011) using the *lme4* and

375    *MuMIn* R packages. Given the relatively small number of species, we used neither

376    Phylogenetic Least Squares regression (PGLS: Nunn, 2011), nor permutation-based

377    MCMC models (Croft et al., 2011; Farine & Whitehead, 2015) that are recommended for

378    examining variation in phylogenetic distances and network sampling effort respectively.

379    Instead, we indirectly tested for the effects of phylogeny by assessing covariation with

380    social style grade, since social style and phylogeny have been shown to strongly covary

381    across macaques (Thierry et al., 2000). To rule out the effect of network sampling effort on

382    our results, we replicated our GLMMs using mean network measures computed from

383    permuted datasets of varying degrees of sampling effort (20% - 80% of edges: see above).

384         We first generated 3 global models, one for each grooming network trait treated as

385    the outcome variable. While eigenvector coefficient and Newman's modularity were both

386    normally distributed (modularity: Shapiro-wilcoxon test: $w = 0.95, p = 0.13$), clustering

387    coefficient was arcsine-transformed to meet normality assumptions ($w = 0.98, p = 0.65$).

388    As recommended by I-T approaches (Burnham et al., 2011; Grueber et al., 2011), our

389    global models were constructed by the inclusion of just those covariates that catered to

390    testing our specific predictions (Q2-Q4). Specifically, dominance traits (transitivity and

391    dominance certainty), social style category, and sociodemographic factors (group size, sex

392    ratio, and living condition category) were included as fixed effects. Since the effect of

393    group size on grooming networks could be more pronounced among free-living groups

394    (Griffin & Nunn, 2012; Sueur et al., 2011b), we also examined a potential interaction

395    between group size and living condition. Species was set as a random effect to avoid

396    pseudoreplication issues. We next used the *arm* package in R to z standardize ($\mu = 0, SD = $

397    *1*) the predictors in the global model, which is essential for interpreting parameter estimates

398    after model averaging (Gelman et al., 2009). We then used the automated 'dredge' function

399    in the *MuMIn* R package to generate a 'complete' set of 80 models from multiple possible

400    combinations of predictors from the global models (Grueber et al., 2011) (Supplementary

401    Tables 4-6). This included a 'null' or an intercept-only model with just species as a random

Balasubramaniam et al. 18

402    effect for the sake of comparison. From each full model set, we identified candidate models

403    that included only models whose difference in AICc scores were < 4 from the model with

404    the lowest AICc score (Burnham et al., 2011) (models in bold font in Supplementary Tables

405    4-6). We confirmed that model diagnostics criteria were met for each candidate model, and

406    ruled out multicollinearity issues for models with multiple predictors (r < 0.8 for all pairs of

407    predictors; GVIF < 4 for each: the *car* package in R: Fox & Weisberg, 2011). We then

408    determined parameter estimates by model-averaging each set of candidate models using the

409    zero-averaging approach (Burnham & Anderson, 2002; Grueber et al., 2011). Since this

410    approach weakens the effect sizes of predictors that only appear in a minority of models, it

411    is more useful (than the natural averaging method) in cases where the aim is to determine

412    which (among multiple) factors have the strongest effect on a response variable (Grueber et

413    al., 2011; Nakagawa & Freckleton, 2010). For all parameter interpretations, we set the

414    alpha level at 0.05.

415    **Results:**

416    *(Q1) Tests for phylogenetic signals:*

417         Mean species-level scores of both dominance network traits -- transitivity and

418    dominance certainty -- showed moderate phylogenetic signals (Table 3). When we repeated

419    the analyses including only free-living groups (27 datasets across 7 species), the results

420    showed a strong phylogenetic signal for dominance traits (K statistics >>1: Table 3). In

421    comparison, grooming traits -- especially eigenvector and clustering coefficient -- showed

422    weak phylogenetic signals (Table 3). Although Newman's modularity showed a moderate

423    signal as indicated by the K statistic, randomization tests neither reached significance nor

424    showed a non-significant trend for this trait (Table 3). Given the relatively small number of

425    species, our tests of phylogenetic signals lacked power (~ 20-35%). Yet, results from the

426    randomization significance tests were mostly consistent with our estimations of the strength

427    of the signals from the K statistic (Table 3). Moreover, they were also robust to

428    phylogenetic branch length variation, with results from the consensus phylogeny being

429    largely consistent with those across 10 phylogenetic trees extracted from the *10KTrees*

430    website (Supplementary Table 3).

431    *(Q2-4) The effect of dominance traits, social style, and sociodemographic factors on*

432    *grooming traits:*

433          Table 4 shows the model-averaged coefficients and parameter estimates from

434    candidate GLMM sets shortlisted using our dAICc criterion, from the complete model sets

435    for grooming Newman's modularity and clustering coefficient. Our criterion shortlisted 8

436    models for modularity, and 7 for clustering coefficient. Neither candidate model set

437    included the 'random effect only' model, which had a dAICc > 12 from the candidate sets

438    (Supplementary Table 6, 7). Model averaged coefficients revealed that group size strongly

439    influenced modularity and clustering coefficient in predicted directions. Larger groups

440    showed more modular, but less dense clusters or redundant ties than smaller groups, which

441    showed the opposite characteristics (Table 4; Figure 2). Further, group size was both

442    present, and the most important predictor in all candidate models for both modularity and

443    clustering coefficient (Table 4). We also detected a significant effect of living condition,

444    with captive groups showing less modular networks and greater density/ redundancy of

445    cluster ties than free-living groups (Table 4; Figure 2). However, there was no interaction

446    between group size and living condition (Table 4), suggesting that the effect of group size

447    were independent of living condition. Sex ratio also showed no effect. Finally, neither

Balasubramaniam et al. 20

448　dominance traits nor social style grade strongly influenced these grooming network traits in

449　predicted directions (Table 4). In fact, social style did not make the candidate models for

450　modularity.

451　　In contrast to Newman's modularity and clustering coefficient, candidate model

452　selection for grooming eigenvector centrality coefficient failed to eliminate the 'random

453　effect only' model (Supplementary Table 5). Zero-based model averaging revealed that

454　none of the predictors had a strong effect on these indices (Supplementary Table 8).

455　　Finally, replications of our GLMMs using network measures computed from

456　permuted datasets revealed that our findings, particularly for group size, were highly

457　consistent across varying degrees of sampling effort. As per findings from the complete

458　data, group size showed positive associations with modularity, and negative associations

459　with clustering coefficient for all degrees of sampling effort (e.g. at 60% and 20% effort:

460　Supplementary Tables 9, 10). On the other hand, the effect of living condition on grooming

461　clustering coefficient weakened at lower sampling effort (Supplementary Tables 9, 10).

462　**Discussion:**

463　　In group-living animals, the evolutionary origins of variation in aspects of social

464　structure remain much debated. Here we used a social network approach to examine the

465　impact of phylogenetic relatedness, specifically phylogenetic signals and trait covariation,

466　as well as sociodemographic factors like group size and living condition on interspecific

467　variation in higher-order aspects of dominance and grooming social structure across

468　macaques. We found that while dominance social network traits showed strong

469　phylogenetic signals, grooming network traits showed weak signals and were not strongly

470　covariant with social style or with dominance traits. Rather, two aspects of grooming

471 network structure – modularity and clustering coefficient – were strongly influenced by

472 group size independently of current living condition. Below we discuss our findings in

473 depth, and offer avenues for future comparative assessments of primate social network

474 structure.

475     Previous studies among macaques have established strong phylogenetic signals in

476 some aspects of social structure (e.g. dominance steepness and counter-aggression:

477 Balasubramaniam et al., 2012a), but moderate-to-weak signals in others (e.g. kin-bias:

478 Thierry et al., 2008). Consistent with this pattern, we found moderate to strong

479 phylogenetic signals for aspects of female dominance network traits, but moderate or weak

480 signals for grooming networks. Specifically, both transitivity and dominance certainty

481 exhibited degrees of signal that are close in strength to what is expected under a Brownian

482 motion model of evolution (Blomberg et al., 2003). In other words, the covariance between

483 dominance trait values of adjacent taxa strongly proportional to their shared evolutionary

484 histories indicated by their phylogenetic branch length distances (Kamilar & Cooper,

485 2015). This finding extends earlier findings of strong phylogenetic signals on group-level

486 aspects of dominance structure that were based on dyadic interactions (e.g., hierarchical

487 steepness, counter-aggression: Balasubramaniam et al., 2012a) to broader patterns of triadic

488 motifs (transitivity) and network-wide flow patterns (dominance certainty). It also extends

489 it to indirect connections that reflect the higher-order structure of the flow of dominance

490 information through pathways that connect both interacting and non-interacting individuals

491 (dominance certainty: Fujii et al., 2013; Fushing et al., 2011). Phylogenetic signals were

492 even stronger when we analyzed only free-living groups of macaques, despite a reduction

493 in sample size from 10 to 7 species (Blomberg et al., 2003). This may be due to the

494    differences in living conditions between groups of closely related species. In captivity,

495    spatial constraints and/or management strategies may force animals to interact that might

496    otherwise avoid one another after one or two decided outcomes (Duboscq et al., 2013;

497    McCowan et al., 2008). This may result in greater than expected degrees of reversals in

498    agonistic success and hence, greater uncertainty in dominance relationships. Unfortunately,

499    limited datasets prevented an analysis of phylogenetic signals among captive groups alone

500    (11 out of 38 datasets: 5 species). Nevertheless, the detection of strong phylogenetic signals

501    among free-living macaques (27 out of 38 datasets: 7 species) builds on previous studies

502    that have either included both captive and free living groups (Balasubramaniam et al.,

503    2012a) or only captive groups (Thierry et al., 2008). Since previous comparative studies

504    across primates have shown a general lack of correspondence between phylogeny and

505    socioecology (Koenig et al., 2013; Ménard, 2004; Okamoto & Matsumura, 2002), it is

506    unlikely that the observed phylogenetic signals in dominance traits are 'artifacts' of

507    correlations between phylogeny and current socioecological factors. Further, the signals

508    were detected despite the fact that a fraction of the free-living groups in our dataset were

509    exposed to food provisioning by humans (Table 1), although predation pressure, another

510    socioecological factor (van Schaik, 1989), was anecdotally either uniformly low or absent

511    across the study populations. Taken together, our findings suggest that phylogeny predicts a

512    major component of the interspecific variance in dominance structure among free-living

513    macaques. Nevertheless, these findings do not entirely rule out an adaptive component. For

514    instance, the concept of social reaction norms proposes that aspects of social structure may

515    change dynamically by responding to socioecological and environmental factors, but within

516    the limits posed by a species- or phylogenetic lineage-typical range of responses that may

517 in turn be linked to phylogenetic closeness (Berman & Thierry, 2010). Moreover,

518 phylogenetic signals, rather than being linked to ancestral genetic splits, may be outcomes

519 of adaptations by ancestral species dispersing into historically similar environments

520 (Kamilar & Cooper, 2015). We suggest that future assessments of the bases of phylogenetic

521 signals in social network traits focus on phylogeographic approaches (Lemey et al., 2009;

522 Ree & Smith, 2008). Specifically, a comparison of the reconstructed social networks and

523 geographic ranges of ancestral primate taxa may provide better insights into whether

524 phylogenetic signals in primate social networks are indeed 'artifacts' of adaptive responses

525 in their evolutionary past.

526        In comparison to dominance traits, grooming networks, particularly eigenvector and

527 clustering coefficients, showed moderate (modularity) or weak (eigenvector and clustering

528 coefficient) phylogenetic signals. Further, grooming traits did not covary with dominance

529 traits in the directions predicted. A possible explanation is that covariation between social

530 network traits is not always linear (but see Thierry et al.'s (2008) findings on covariation

531 between traits associated with conciliatory tendencies across macaques). Further, it may be

532 discernible at levels of organization other than species, for instance, across phylogenetic

533 lineages (Thierry, 2000). Yet the lack of a strong effect of species-typical social style on

534 grooming networks may be seen as evidence to refute this argument given that social style

535 and phylogeny are correlated (Thierry et al., 2000). A more likely explanation is that

536 grooming traits may come under the additional influence of current socioecological and/or

537 sociodemographic factors.

538        Among all the primate genera, macaques are presently unique in the extent to which

539 interspecific variation in social traits is consistent with phylogeny, and covariant with social

540  style (Balasubramaniam et al., 2012a; Sueur et al., 2011b; Thierry et al., 2008; Thierry et

541  al., 2000). Yet we found that group size had a stronger influence on grooming modularity

542  and clustering coefficient than either dominance traits or social styles. Specifically, larger

543  groups of macaques showed more modular grooming networks, as well as less density/

544  redundancy in connections among localized, triadic clusters.

545      It is conceivable that the effect of group size on grooming traits may have been an

546  artifact of intergroup differences in (1) living condition (McCowan et al., 2008; Duboscq et

547  al., 2013) and/or (2) chance interactions (Griffin & Nunn, 2012; Nunn et al., 2015). In our

548  dataset, for instance, captive groups were both significantly smaller (see Methods) and, as

549  expected due to spatial constraints, showed less modular grooming networks with more

550  densely connected clusters (see Results) than free-living groups. Yet we found no effect of

551  an interaction between group size and living condition on grooming traits, suggesting that

552  the effect of group size on grooming traits was independent of the effect of living condition.

553  Moreover, the permuted datasets revealed that both the grooming traits themselves, and the

554  strong relationships between group size and grooming traits, were robust to variation in

555  sampling effort. Together, these findings suggest that the effect of group size on grooming

556  traits, rather than being artefactual, may more likely have socioecological underpinnings.

557  Specifically, one school of thought is that living in larger groups may heighten levels of

558  within-group contest competition (or WGC) for resources (Koenig et al., 2013; Sterck et

559  al., 1997; van Schaik, 1989). This may lead to despotic, nepotistic primate societies

560  characterized by both steep and transitive dominance structure (Majolo et al., 2009), and

561  more modular, sparsely connected grooming community structures (the social bottleneck

562  hypothesis: Griffin & Nunn, 2012). In comparison, smaller groups may show weaker WGC

Balasubramaniam et al. 25

563  and the opposite characteristics that are indicative of greater social tolerance. An alternative

564  perspective is that individuals in large groups may face spatial or time constraints on their

565  abilities to interact consistently with all other group members (Berman & Thierry, 2010;

566  Dunbar, 1992; Korstjens et al., 2010; Puga & Sueur, 2017). This may in turn result in

567  modular or clustered but sparser social networks in larger groups, in which individuals may

568  come into contact with each other less frequently (Griffin & Nunn, 2012). Given the lack of

569  a clear association between group size and dominance networks in our dataset (e.g. Group

570  size vs. dominance certainty: $n = 38, r = 0.02, p = 0.88$), our findings point to a

571  spatiotemporal rather than a resource-competition based explanation. Yet final conclusions

572  await the expansion of our dataset to include additional groups and species, and comparable

573  operational measures of resource distribution (see below).

574       Unlike grooming modularity and clustering coefficient, grooming centrality

575  coefficient was not influenced by dominance traits, social style, or sociodemographic

576  factors. One reason for this lack of concordance could be due to the way this index was

577  computed. For instance, the exclusion of males from our grooming networks, unlike in

578  Sueur et al.'s (2011b) study, may have masked skew in grooming centrality towards

579  dominants. In despotic macaques, high-ranking males may be among the most attractive

580  grooming partners for females who may gain benefits such as access to social support

581  and/or resources (Schino, 2001; Silk et al., 2003; Sueur et al., 2011b). It is possible that

582  female dominance status could be related to centralization in the grooming network that is

583  based on *specific types* of grooming connections rather than their overall connectedness.

584  These could be grooming connections with non-kin, grooming that is directed up the

585  hierarchy in exchange for access to rank-related benefits such as resource tolerance and

586　support in conflicts, and/or grooming that is reciprocated in the short or long-term

587　(reviewed in Henzi & Barrett, 1999). Should comparative data be available, such

588　assessments may generate centralization indices that better reflect female social structure.

589　　　　Alternatively, it is conceivable that intergroup variation in centrality coefficients

590　may be influenced by additional socioecological variables (Griffin & Nunn, 2012; Sterck et

591　al., 1997), and/or intraspecific variation (Borgeaud et al., 2016; Romano et al., 2016).

592　Yet assessments of the socioecological bases of variation in sociality have proved to be

593　complicated. For instance, we currently lack a consistent operational measure of resource

594　abundance and distribution that may be used in comparative contexts across a wide range of

595　taxa (Clutton-Brock & Janson, 2012). Another challenge is assessing the effects of

596　infectious disease risk on social networks. For instance, increased parasite infection risk

597　may lead to the evolution of more modular networks because individuals engage fewer

598　social partners (Griffin & Nunn, 2012; Nunn et al., 2015). At the same time, possessing

599　more partners can also reduce infection risk via socially buffering individuals against

600　susceptibility to infectious agents (Balasubramaniam et al., 2016; Duboscq et al., 2016;

601　Young et al., 2014). Third, the spatial distribution of females may also influence male

602　reproductive tactics, i.e. the extent to which males show reproductive skew by

603　monopolizing mating opportunities which may in turn influence female social networks

604　(Schülke & Ostner, 2008, 2013). More definitive conclusions await the ability to draw

605　interspecies links between reproductive skew and female social networks, and indeed male-

606　male social relationships. Finally, in comparison to interspecific variation, few comparative

607　studies have assessed the evolutionary origins of inter-individual or intergroup variation

608　(Clutton-Brock & Janson, 2012). In addition to impacting group-level outcomes, selection

609 pressures may act on the spatial orientation, behavioral strategies, and personalities of

610 individuals, any or all of which may in turn affect social networks (Borgeaud et al., 2016;

611 Capitanio, 1999; Krause et al., 2010; Lusseau & Newman, 2004; Puga & Sueur, 2017; Sih

612 et al., 2004). Although beyond the scope of this study, adopting similar comparative,

613 evolutionary approaches to assess the influence of intraspecific variation in spatial and

614 social strategies on social network structure may be a logical next step.

632    KNB, BAB and BJM were supported by the University of California at Davis, the National

633    Institute of Health (NIH: R01-HD068335), and the National Science Foundation (NSF:

634    NSF-V451CNH). The International Animal Care and Use Committee of the University of

635    California at Davis approved the research.

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900    **Table 1: Macaque datasets analyzed in the study**

| Species (*Macaca*) | Social Style | Study Location | Source or Citation | Group Size | Adult Females | Sampling Effort[b] | Living Condition[c] |
|---|---|---|---|---|---|---|---|
| *fuscata*[a] | 1 | Yakushima, Japan | Ventura et al. (2006) | 25 | 8 | 25 (NA) | Free-living |
| *fuscata*[a] | 1 | Yakushima, Japan | Ventura et al. (2006) | 50 | 21 | 7 (NA) | Free-living |
| *Fuscata* | 1 | Koshima, Japan | Duboscq et al. (2016); Romano et al. (2016) | 45 | 21 | 10 | Free-living |
| *Fuscata* | 1 | Koshima, Japan | Duboscq et al. (2016); Romano et al. (2016) | 45 | 20 | 5 | Free-living |
| *Fuscata* | 1 | Koshima, Japan | Duboscq et al. (2016); Romano et al. (2016) | 45 | 20 | 16 | Free-living |
| *Fuscata* | 1 | Rome Zoo, Italy | Schino et al. (2007) | 57 | 23 | 291 (280) | Captive |
| *Fuscata* | 1 | Rome Zoo, Italy | Schino et al. (2007) | 57 | 23 | 229 (224) | Captive |
| *Fuscata* | 1 | Paris Zoo, France | Petit et al. (1997) | 22-24 | 9 | 180 (8) | Captive |
| *mulatta* | 1 | University of Cambridge, Madingley, UK | Desportes & Thierry (unpub) | 16 | 7 | 72 (8) | Captive |
| *mulatta* | 1 | Cayo Santiago, Puerto Rico | Balasubramaniam et al. (2014) | 135 | 30 | 18 | Free-living [d] |
| *mulatta* | 1 | Cayo Santiago, Puerto Rico | Balasubramaniam et al. (2014) | 33 | 10 | 16 | Free-living [d] |
| *mulatta*[a] | 1 | Yerkes Primate Center, USA | de Waal & Luttrell (1989) | 51-62 | 13 | 675 (NA) | Captive |
| *assamensis* | 2 | Tukreshwari Temple, Assam, India | Cooper & Bernstein (2008) | 28 | 14 | - | Free-living [d] |
| *assamensis* | 2 | Tham Pla Temple, Thailand | Ogawa (*unpub*) | 47 | 14 | 9 | Free-living [d] |
| *assamensis* | 2 | Shivapuri Nagarjun National Park, Nepal | Ogawa & Koirala (*unpub*) | 25 | 8 | 10 | Free-living |
| *fascicularis* | 2 | Primatological Station, Kassel University, Germany | Butovskaya et al. (1995) | 9 | 7 | 47 (3) | Captive |
| *fascicularis* | 2 | Primatological Station, Kassel University, Germany | Butovskaya et al. (1995) | 13 | 9 | 50 (3) | Captive |
| *thibetana* | 2 | Mt. Huangshan, China | Balasubramaniam et al. (2011) | 39 | 8 | 47 | Free-living [d] |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *thibetana* | 2 | Mt. Huangshan, China | Balasubramaniam et al. (2011) | 42 | 9 | 47 | Free-living [d] |
| *thibetana* | 2 | Mt. Huangshan, China | Balasubramaniam et al. (2011) | 42 | 9 | 38 | Free-living [d] |
| *thibetana* | 2 | Mt. Huangshan, China | Balasubramaniam et al. (2011) | 52 | 10 | 11 | Free-living [d] |
| *thibetana* | 2 | Mt. Huangshan, China | Balasubramaniam et al. (2011) | 49 | 10 | 12 | Free-living [d] |
| *thibetana* | 2 | Mt. Huangshan, China | Balasubramaniam et al. (2011) | 37 | 10 | 20 | Free-living [d] |
| *arctoides*[a] | 3 | Yerkes Primate Center, USA | de Waal & Luttrell (1989) | 14 | 12 | 225 (NA) | Captive |
| *radiata* | 3 | Mysore, India | Cooper et al. (2007) | 41-49 | 13 | - | Free-living [d] |
| *sylvanus* | 3 | Middle Atlas Mountains, Morocco | McFarland & Majolo (2011) | 19 | 8 | 32 | Free-living |
| *sylvanus* | 3 | Middle Atlas Mountains, Morocco | McFarland & Majolo (2011) | 29 | 10 | 10 | Free-living |
| *sylvanus* | 3 | Middle Atlas Mountains, Morocco | Molesti & Majolo (2013) | 18 | 7 | - (12) | Free-living |
| *sylvanus* | 3 | Rocamadour, France | Sosa (2014) | 55 | 24 | 14 | Free-living [d] |
| *sylvanus* | 3 | Rocamadour, France | Sosa (2014) | 55 | 24 | 8 | Free-living [d] |
| *sylvanus* | 3 | Rocamadour, France | Sosa (2014) | 55 | 24 | 12 | Free-living [d] |
| *nigra* | 4 | Tangkoko Reserve, Indonesia | Duboscq et al. (2013) | 50 | 18 | 24 | Free-living |
| *nigra* | 4 | Tangkoko Reserve, Indonesia | Duboscq et al. (2013) | 80 | 21 | 45 | Free-living |
| *nigra* | 4 | Tangkoko Reserve, Indonesia | Duboscq et al. (2013) | 80 | 21 | 43 | Free-living |
| *nigra* | 4 | Tangkoko Reserve, Indonesia | Duboscq et al. (2013) | 80 | 24 | 22 | Free-living |
| *tonkeana* | 4 | Primatology Center, Strasbourg, France | Thierry (1985); Demaria & Thierry (2001) | 16 | 9 | 104 (8) | Captive |
| *tonkeana* | 4 | Orangerie Zoo, Strasbourg, France | De Marco et al. (2010) | 21 | 7 | 110 (5) | Captive |
| *tonkeana* | 4 | Primatology Center, Strasbourg, France | Thierry (1985); Demaria & Thierry (2001) | 29 | 11 | 87 (6) | Captive |

901 Groups excluded from computation and analyses of grooming network metrics on account of either (a) non-availability of data,
902 or (b) too few (< 7) individuals
903 Calculated as the mean observation time per subject in hours, for datasets collected using focal animal (mean focal observation
904 time), all-occurrences (total observation time of the group), and/or scan sampling (number of scans per subject times the
905 duration of the scan (derived from Romano et al. (2016)). Blank entries represent datasets in which *ad-libitum* sampling was
906 used. Entries in parentheses represent sampling effort for grooming datasets, where different from aggression
907 Criteria for designation of group's living-condition: Free-living: within their natural geographic distribution, or an unfenced
908 area outside of their natural geographic distribution; Captive: housed within a fenced enclosure
909 Free-living groups that were regularly food-provisioned by humans
910 Codes for Social Style (Thierry, 2007): (1) Highly Despotic, (2) Mildly Despotic, (3) Mildly Tolerant, (4) Highly Tolerant

911     **Table 2: Definitions of Social Network Traits**

| Trait | Description | Data Source | Code Source |
|---|---|---|---|
| **Dominance** | | | |
| Triangle transitivity | A transitive triangle is 3 individuals connected in the following manner: *a* wins its encounters with *b*, *b* with *c*, and *a* with *c* (Snijders, 2012). Group-level triangle transitivity is number of such "triangles" divided by all possible triangles within a group | Aggression network matrix | *Perc* R package (Fujii et al. 2015) |
| Dominance certainty | Based on a tally of all directed network paths between *a* and *b*, dyadic dominance certainty is the degree of consistency in direction of all dominance paths. It reflects the probability that *a* will win against *b*. Group-level dominance certainty is the mean of the row-wise averages of just the win-probabilites for each individual | Aggression network matrix | *Perc* R package (Fujii et al. 2015) |
| **Grooming** | | | |
| Centrality Coefficient | The Pearson's R correlation coefficient between the eigenvector centrality scores and David's scores of all the individuals in the group. This metric reveals the extent to which dominant individuals are more central and have extended secondary grooming connections compared to subordinates | Groom network string | *Statnet* R package (Handcock et al., 2006) |
| Newman's Modularity | The extent to which a network can be divided into communities of individuals which interact more among themselves (than expected by chance), than with members from another community. Higher values (approaching 1) indicate greater division into distinct sub-groups than lower values (closer to 0), which indicate little or no sub-divisioning | Groom network string | *Igraph* R package (Csardi & Nepusz, 2006) |
| Global clustering coefficient | Similar in calculation to triangle transitivity, but with edge direction not considered. The proportion of triplets (i.e. sets of 3 individuals) that are completely connected to each other (or form a closed triangle) relative to the total number of *potential* triplets. | Groom network string | *Igraph* R package (Csardi & Nepusz, 2006) |

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Balasubramaniam et al. 42

917　**Table 3: Results of tests for phylogenetic signals among macaque dominance and**

918　**grooming social network traits. K: Blomberg's Kappa coefficient; P: significance from**

919　**Randomization tests (Blomberg et al. 2003)**

920

| Behavioral Metric | All Datasets (10 species) | | Free-living Groups (7 species) | |
|---|---|---|---|---|
| | K | P | K | P |
| Dominance Metrics | | | | |
| Transitivity | 0.892 | 0.081(*) | **1.704** | **0.022*** |
| Dominance Certainty | 0.893 | 0.078(*) | **1.634** | **0.023*** |
| Grooming Network Metrics | | | | |
| Eigenvector Coefficient | 0.654 | 0.205 | 0.722 | 0.238 |
| Newman's Modularity | **0.872** | 0.110 | 0.959 | 0.110 |
| Clustering coefficient | 0.406 | 0.567 | 0.836 | 0.165 |

921　**Bold font:** K values (> 1) indicate strong phylogenetic signals
922　* P < 0.05; (*) 0.05 < P < 0.1
923　Phylogenetic tree used was the Bayesian MCMC consensus tree from the 10ktrees website (Arnold et al. 2010)
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925
926

927 **Table 4: Summary of zero-averaged coefficients from the candidate models for**

928 **Newman's modularity and clustering coefficient of grooming networks.**

| | B | Adj SE | z | Pr (>\|z\|) | Importance |
|---|---|---|---|---|---|
| **(A) Newman's Modularity (8 candidate models)** | | | | | |
| Intercept | 0.19 | 0.03 | 5.82 | <0.01** | |
| **Living Condition (Captive vs. Free living)** | **0.15** | **0.04** | **4.16** | **<0.01**** | **1** |
| Sex Ratio (proportion of females) | 0.04 | 0.05 | 0.86 | 0.39 | 0.57 |
| **Group Size** | **0.09** | **0.03** | **3.27** | **<0.01**** | **1** |
| Dominance Certainty | 0.00 | 0.02 | 0.21 | 0.84 | 0.15 |
| Transitivity | 0.00 | 0.01 | 0.15 | 0.88 | 0.13 |
| Group Size: Living Condition | 0.00 | 0.03 | 0.08 | 0.94 | 0.13 |
| **(B) Clustering Coefficient (7 candidate models)** | | | | | |
| Intercept | 0.92 | 0.14 | 6.71 | <0.01** | |
| **Living Condition (Captive vs. Free living)** | **-0.44** | **0.20** | **2.25** | **0.02*** | **0.93** |
| Dominance Certainty | 0.34 | 0.19 | 1.75 | 0.08 | 0.83 |
| **Group Size** | **-0.21** | **0.09** | **2.43** | **0.02*** | **1** |
| Group Size: Living Condition | 0.03 | 0.12 | 0.26 | 0.79 | 0.14 |
| Social Style (Grade 1 vs. Grade 2) | 0.02 | 0.11 | 0.18 | 0.85 | 0.12 |
| Social Style (Grade 1 vs. Grade 3) | 0.06 | 0.20 | 0.31 | 0.76 | |
| Social Style (Grade 1 vs. Grade 4) | 0.09 | 0.28 | 0.34 | 0.73 | |
| Sex Ratio (proportion of females) | 0.01 | 0.04 | 0.14 | 0.89 | 0.09 |
| Transitivity | 0.00 | 0.03 | 0.02 | 0.98 | 0.08 |

981 [a] Effect sizes are standardized, comparable values (Gelman et al., 2009)

982 Data are from 34 groups of 9 macaque species

983 * $p \leq 0.05$ ** $p < 0.01$

Balasubramaniam et al. 44

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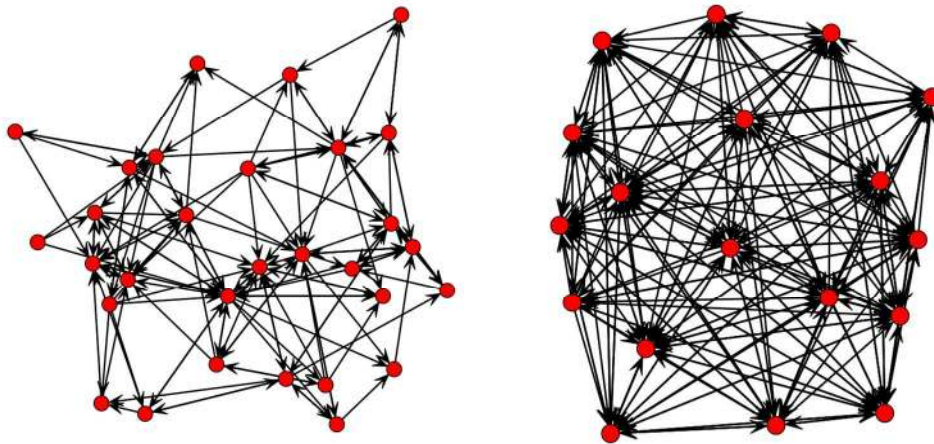
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986 Figure 1: Grooming social networks from a (A) rhesus macaque (*M. mulatta*)

987 (Balasubramaniam et al. 2014; n = 29 individuals), and a (B) Sulawesi crested macaque (*M.*

988 *nigra*) (Duboscq et al. 2013; n = 19 individuals) group. Circles represent individual adult

989 females, and lines connecting them represent edges (unweighted) of grooming relationships

990 between females

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Balasubramaniam et al. 45

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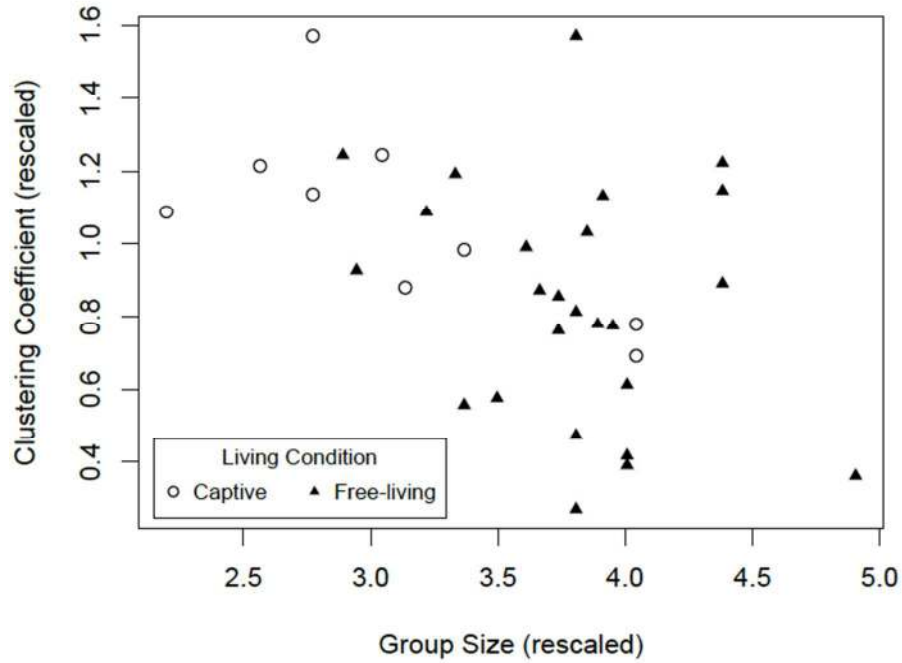


1012 Figure 2: Influence of group size on grooming clustering coefficient across 34 datasets of

1013 captive and free-living macaque groups representing 9 species

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- We assessed the bases for variation in macaque social network structure

- Dominance traits showed phylogenetic signals, but grooming traits were linked to group size

- Social networks are influenced by both ancestral and sociodemographic factors

**Supplementary Figure 1: Consensus tree of phylogenetic relationships among 10 species of macaques extracted from the 10ktrees website (Arnold et al., 2010), on which tests of phylogenetic signals were conducted**
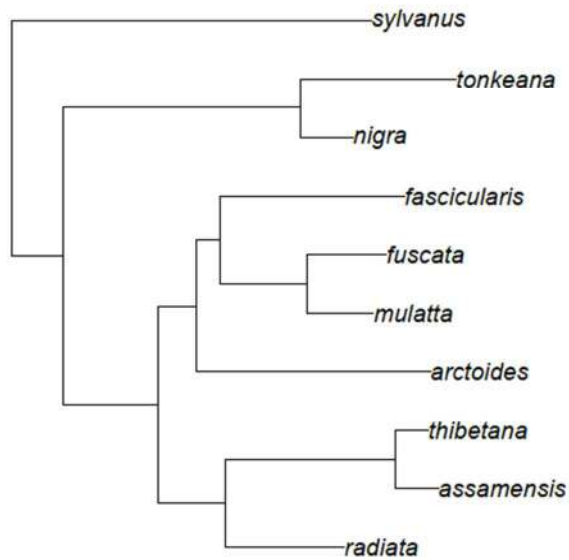
Supplementary Figure 2: Plots of grooming network measures against % sampling effort. Data-points represent means computed from values across 200 networks permuted from a natural dataset, and error bars represent standard deviations. Data-points at 100% sampling effort represent the value of the original network measure. The four groups selected were largest in size (e.g. Group 10: 135 individuals), or had the lowest observation times (e.g. Group 4: 5 hours/ subject)
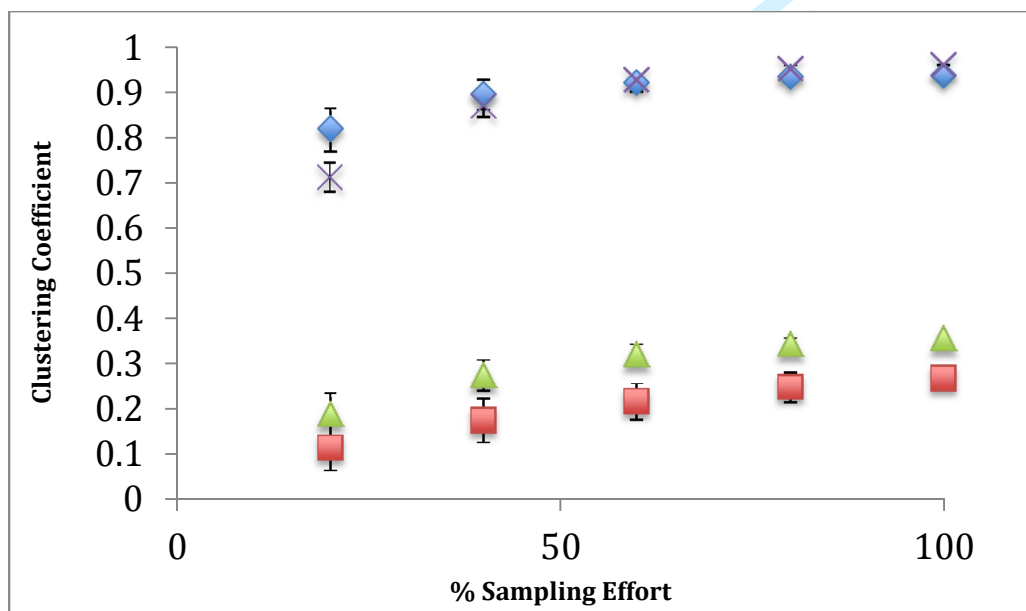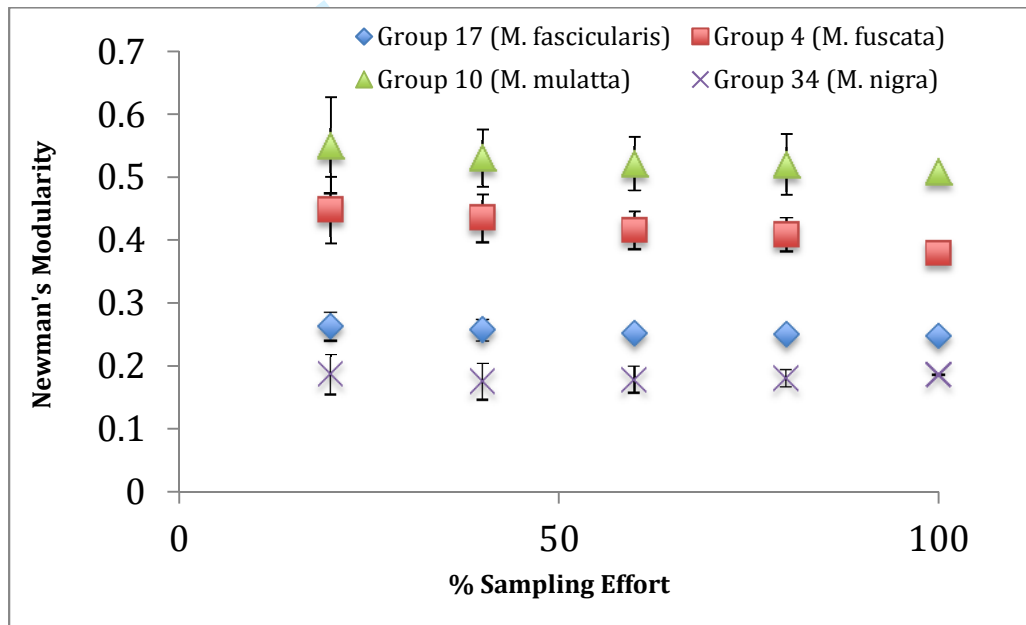
**Supplementary Figure 3: Scatterplots between sampling effort and (A) group size, (B) dominance certainty, and (C) grooming Newman's modularity across the datasets. Datasets that used *Ad libitum* sampling (B: 3/38; C: 2/34), and/or were outliers (B: 1/38 dataset sampled for 675 hours per subject; C: 2/34 datasets sampled for 224 and 280 hours per subject respectively) have been omitted**

**(A)**

**(B)**



**(C)**

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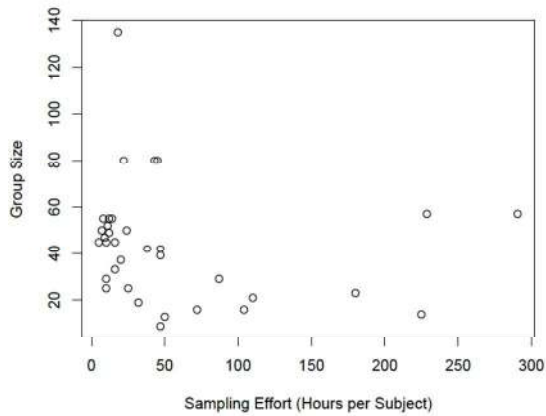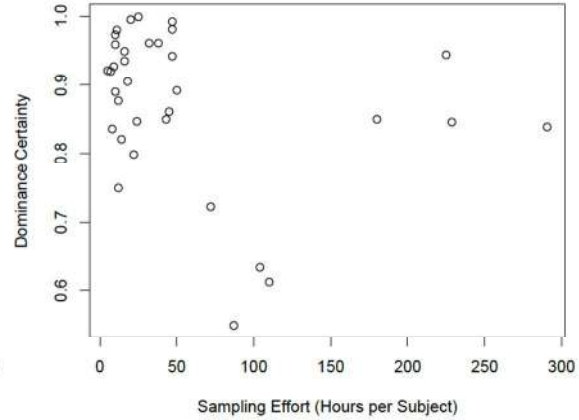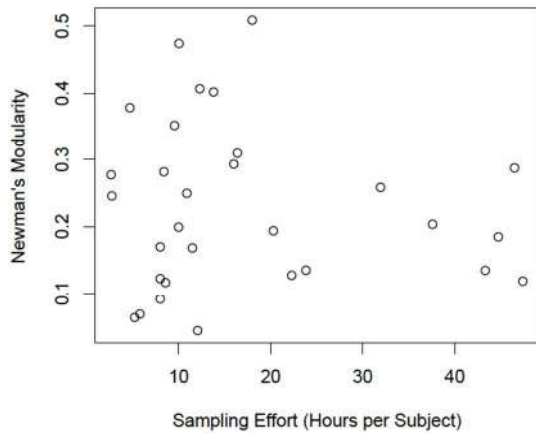
**Supplementary Table 1: Measures of dominance and grooming network traits, computed for each macaque dataset**

| | | Dominance Measures | | Grooming Measures | | |
|---|---|---|---|---|---|---|
| Dataset | Species | Transit-ivity | Dominance Certainty | Centrality Coefficient | Newman's Modularity | Clustering Coefficient |
| 1 | *M. fuscata* | 1.000 | 0.999 | NA | NA | NA |
| 2 | *M. fuscata* | 1.000 | 0.920 | NA | NA | NA |
| 3 | *M. fuscata* | 1.000 | 0.973 | 0.533 | 0.352 | 0.273 |
| 4 | *M. fuscata* | 1.000 | 0.921 | 0.429 | 0.379 | 0.732 |
| 5 | *M. fuscata* | 1.000 | 0.949 | 0.522 | 0.309 | 0.544 |
| 6 | *M. fuscata* | 0.983 | 0.839 | 0.649 | 0.202 | 0.297 |
| 7 | *M. fuscata* | 0.975 | 0.846 | 0.528 | 0.202 | 0.362 |
| 8 | *M. fuscata* | 1.000 | 0.850 | -0.440 | 0.123 | 0.229 |
| 9 | *M. mulatta* | 1.000 | 0.992 | NA | NA | NA |
| 10 | *M. mulatta* | 0.714 | 0.722 | 0.618 | 0.170 | 0.093 |
| 11 | *M. mulatta* | 0.957 | 0.905 | 0.393 | 0.508 | 0.646 |
| 12 | *M. mulatta* | 1.000 | 0.935 | 0.493 | 0.293 | 0.455 |
| 13 | *M. assamensis* | 1.000 | 0.955 | 0.341 | 0.182 | 0.071 |
| 14 | *M. assamensis* | 0.972 | 0.927 | 0.449 | 0.117 | 0.142 |
| 15 | *M. assamensis* | 1.000 | 0.959 | 0.071 | 0.199 | 0.115 |
| 16 | *M. fascicularis* | 1.000 | 0.981 | 0.033 | 0.277 | 0.115 |
| 17 | *M. fascicularis* | 0.988 | 0.892 | -0.303 | 0.246 | 0.063 |
| 18 | *M. thibetana* | 1.000 | 0.942 | 0.849 | 0.287 | 0.234 |
| 19 | *M. thibetana* | 1.000 | 0.992 | 0.532 | 0.119 | 0.245 |
| 20 | *M. thibetana* | 1.000 | 0.961 | -0.091 | 0.204 | 0.309 |
| 21 | *M. thibetana* | 1.000 | 0.980 | 0.676 | 0.250 | 0.3 |
| 22 | *M. thibetana* | 1.000 | 0.877 | -0.038 | 0.169 | 0.297 |
| 23 | *M. thibetana* | 1.000 | 0.995 | 0.675 | 0.194 | 0.164 |
| 24 | *M. arctoides* | 0.976 | 0.944 | NA | NA | NA |
| 25 | *M. radiata* | 0.984 | 0.962 | -0.281 | 0.086 | 0 |
| 26 | *M. sylvanus* | 1.000 | 0.961 | 0.581 | 0.258 | 0.2 |
| 27 | *M. sylvanus* | 0.917 | 0.890 | -0.644 | 0.474 | 0.471 |
| 28 | *M. Sylvanus* | 1.000 | 0.979 | 0.825 | 0.043 | 0.053 |
| 29 | *M. sylvanus* | 0.881 | 0.821 | 0.350 | 0.402 | 0.425 |

| 30 | *M. sylvanus* | 0.935 | 0.836 | 0.385 | 0.282 | 0.619 |
| 31 | *M. sylvanus* | 0.902 | 0.749 | 0.308 | 0.407 | 0.595 |
| 32 | *M. nigra* | 0.958 | 0.847 | -0.468 | 0.136 | 0.095 |
| 33 | *M. nigra* | 0.906 | 0.861 | 0.027 | 0.185 | 0.06 |
| 34 | *M. nigra* | 0.898 | 0.850 | 0.065 | 0.135 | 0.089 |
| 35 | *M. nigra* | 0.941 | 0.799 | 0.055 | 0.128 | 0.222 |
| 36 | *M. tonkeana* | 1.000 | 0.633 | -0.075 | 0.091 | 0 |
| 37 | *M. tonkeana* | 1.000 | 0.612 | -0.477 | 0.063 | 0.053 |
| 38 | *M. tonkeana* | 0.750 | 0.550 | 0.370 | 0.068 | 0.168 |

**NA: Grooming network measures unavailable or not calculated owing to dataset restrictions (see Table 1)**

**Supplementary Table 2: Wilcoxon rank-sum tests comparing grooming network measures -- (A) modularity and (B) clustering coefficient – between the original dataset (n = 34), and permuted datasets with reduced sampling effort (80% - 20% of the total number of edges). Cells contain W coefficients and p values within parentheses**

**(A) Modularity**

| | | % Sampling Effort | | | | |
|---|---|---|---|---|---|---|
| | | Original Dataset | 80 | 60 | 40 | 20 |
| % Sampling Effort | Original Dataset | x | | | | |
| | 80 | 560 (0.83) | x | | | |
| | 60 | 552 (0.76) | 565 (0.88) | x | | |
| | 40 | 527 (0.54) | 531 (0.57) | 539 (0.64) | x | |
| | 20 | 458 (0.14) | 463 (0.16) | 472 (0.20) | 498 (0.33) | x |

**(B) Clustering Coefficient**

| | | % Sampling Effort | | | | |
|---|---|---|---|---|---|---|
| | | Original Dataset | 80 | 60 | 40 | 20 |
| % Sampling Effort | Original Dataset | x | | | | |
| | 80 | 625 (0.57) | x | | | |
| | 60 | 688 (0.18) | 644 (0.42) | x | | |
| | 40 | 718 (0.02) | 731 (0.06) | 683 (0.20) | x | |
| | 20 | **924 (<0.01*)** | **893 (<0.01*)** | **848 (<0.01*)** | 774 (0.02) | x |

**\*p (Bonferroni-corrected alpha = 0.005) < 0.005**

**Supplementary Table 3: Correlations between mean sampling effort (mean observation hours per subject) and group size, dominance network measures, and grooming network measures**

| | | N[1] | Pearson's R | p ($p_{crit}$ = 0.02) |
|---|---|---|---|---|
| *Sampling Effort vs. Dominance Network Measures* | | | | |
| Sampling Effort | Group size | 34 | -0.17 | 0.32 |
| Sampling Effort | Dominance certainty | 34 | -0.27 | 0.12 |
| Sampling Effort | Transitivity | 34 | 0.00 | 0.99 |

| | | N[1] | Pearson's R | p ($p_{crit}$ = 0.01) |
|---|---|---|---|---|
| *Sampling Effort vs. Grooming Network Measures* | | | | |
| Sampling Effort | Group Size | 30 | 0.36 | 0.06 |
| Sampling Effort | Eigenvector coefficient | 30 | 0.18 | 0.35 |
| Sampling Effort | Newman's Modularity | 30 | -0.10 | 0.59 |
| Sampling Effort | Sparseness Coefficient | 30 | -0.13 | 0.50 |

[1]Datasets that used *Ad libitum* sampling (dominance measures: 3/38; grooming measures: 2/34), and/or were outliers (dominance measures: 1/38 dataset sampled for 675 hours per subject; grooming measures: 2/34 datasets sampled for 224 and 280 hours per subject respectively) were omitted from the analyses.

$p_{crit}$: critical p value set after implementing a Bonferroni correction for multiple comparisons

**Supplementary Table 4: Results of tests for phylogenetic signals among macaque dominance and grooming social Network traits, across a tree block of 10 phylogenetic trees extracted from the 10ktrees website (Arnold et al., 2010). K: Blomberg's Kappa coefficient; P: significance from Randomization tests (Blomberg et al. 2003)**

| Behavioral Metric | All Datasets (10 species) | | Free-living Groups (7 species) | |
|---|---|---|---|---|
| | K (m±sd) | P (m) | K (m±sd) | P (m) |
| *Dominance Metrics* | | | | |
| Transitivity | 0.84 ± 0.07 | 0.10 | **1.64 ± 0.06** | 0.03* |
| Dominance Certainty | 0.90 ± 0.08 | 0.10 | **1.58 ± 0.07** | 0.02* |
| *Grooming Network Metrics* | | | | |
| Eigenvector Coefficient | 0.66 ± 0.05 | 0.21 | 0.73 ± 0.05 | 0.23 |
| Newman's Modularity | 0.85 ± 0.03 | 0.10 | 0.94 ± 0.06 | 0.19 |
| Sparseness Coefficient | 0.39 ± 0.03 | 0.58 | 0.82 ± 0.05 | 0.16 |

**Bold font:** K values (> 1) indicate strong phylogenetic signals
* P < 0.05

**Supplementary Table 5: Model parameters and coefficients for all 80 sub-models within the full model set derived using the dredge function for the outcome variable groom eigenvector coefficient. Species was set as a random effect. Models in bold represent the candidate set (dAICc < 4 from the best-fit) selected for model averaging and interpretation.**

| Model | (Int) | LC | SS | DC | SR | GS | T | GS:LC | df | AICc | Δ | w |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1^ | 0.21 | | | | | | | | 3 | 40.50 | 0.00 | 0.11 |
| 2 | 0.23 | | | 0.22 | | | | | 4 | 40.60 | 0.10 | 0.11 |
| 3 | 0.22 | | | 0.38 | | | -0.28 | | 5 | 41.00 | 0.49 | 0.09 |
| 4 | 0.22 | 0.18 | | | | | | | 4 | 41.80 | 1.33 | 0.06 |
| 5 | 0.41 | | + | | | | | | 6 | 42.00 | 1.51 | 0.05 |
| 6 | 0.21 | | | | | 0.10 | | | 4 | 42.60 | 2.07 | 0.04 |
| 7 | 0.21 | | | | | | -0.08 | | 4 | 42.90 | 2.37 | 0.03 |
| 8 | 0.22 | | | | -0.06 | | | | 4 | 42.90 | 2.42 | 0.03 |
| 9 | 0.23 | | | 0.21 | | 0.09 | | | 5 | 43.10 | 2.62 | 0.03 |
| 10 | 0.23 | | | 0.21 | -0.05 | | | | 5 | 43.30 | 2.80 | 0.03 |
| 11 | 0.30 | -0.05 | | | | 0.13 | | -0.81 | 6 | 43.40 | 2.85 | 0.03 |
| 12 | 0.45 | 0.20 | + | | | | | | 7 | 43.40 | 2.92 | 0.03 |
| 13 | 0.22 | 0.07 | | 0.17 | | | | | 5 | 43.50 | 2.97 | 0.03 |
| 14 | 0.21 | | | 0.37 | | 0.08 | -0.27 | | 6 | 43.80 | 3.27 | 0.02 |
| 15 | 0.41 | | + | | | | -0.15 | | 7 | 44.00 | 3.47 | 0.02 |
| 16 | 0.21 | 0.22 | | | | | -0.13 | | 5 | 44.10 | 3.55 | 0.02 |
| 17 | 0.21 | 0.04 | | 0.36 | | | -0.28 | | 6 | 44.10 | 3.56 | 0.02 |
| 18 | 0.21 | | | 0.38 | -0.01 | | -0.28 | | 6 | 44.10 | 3.58 | 0.02 |
| 19 | 0.40 | | + | | | 0.13 | | | 7 | 44.30 | 3.77 | 0.02 |
| 20 | 0.42 | | + | | -0.12 | | | | 7 | 44.30 | 3.83 | 0.02 |
| 21 | 0.22 | 0.15 | | | | 0.05 | | | 5 | 44.60 | 4.04 | 0.02 |
| 22 | 0.46 | 0.25 | + | | | | -0.20 | | 8 | 44.70 | 4.17 | 0.01 |
| 23 | 0.21 | 0.20 | | | 0.04 | | | | 5 | 44.70 | 4.19 | 0.01 |
| 24 | 0.21 | | | | | 0.10 | -0.08 | | 5 | 45.20 | 4.65 | 0.01 |
| 25 | 0.41 | | + | 0.06 | | | | | 7 | 45.40 | 4.84 | 0.01 |
| 26 | 0.21 | | | | 0.01 | 0.11 | | | 5 | 45.50 | 4.94 | 0.01 |
| 27 | 0.30 | -0.15 | | 0.16 | | 0.16 | | -0.76 | 7 | 45.60 | 5.05 | 0.01 |
| 28 | 0.21 | | | | -0.05 | | -0.08 | | 5 | 45.60 | 5.05 | 0.01 |
| 29^ | 0.30 | 0.00 | | | | 0.11 | -0.15 | -0.86 | 7 | 45.70 | 5.21 | 0.01 |
| 30 | 0.30 | -0.20 | | 0.35 | | 0.15 | -0.29 | -0.82 | 8 | 45.80 | 5.29 | 0.01 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 31 | 0.30 | 0.00 | | | 0.24 | 0.24 | | -0.98 | 7 | 46.20 | 5.65 | 0.01 |
| 32 | 0.22 | 0.01 | | 0.19 | | 0.09 | | | 6 | 46.30 | 5.74 | 0.01 |
| 33 | 0.47 | 0.30 | + | -0.17 | | | | | 8 | 46.30 | 5.80 | 0.01 |
| 34 | 0.22 | | | 0.20 | 0.01 | 0.10 | | | 6 | 46.30 | 5.83 | 0.01 |
| 35 | 0.39 | | + | | | 0.13 | -0.15 | | 8 | 46.40 | 5.93 | 0.01 |
| 36 | 0.42 | | + | | -0.12 | | -0.15 | | 8 | 46.50 | 6.00 | 0.01 |
| 37 | 0.22 | 0.06 | | 0.17 | -0.02 | | | | 6 | 46.60 | 6.05 | 0.01 |
| 38 | 0.44 | 0.17 | + | | | 0.04 | | | 8 | 46.80 | 6.31 | 0.01 |
| 39 | 0.45 | 0.18 | + | | -0.03 | | | | 8 | 46.90 | 6.34 | 0.01 |
| 40 | 0.21 | 0.20 | | | | 0.03 | -0.13 | | 6 | 47.00 | 6.49 | 0 |
| 41 | 0.20 | 0.27 | | | 0.09 | | -0.15 | | 6 | 47.00 | 6.50 | 0 |
| 42 | 0.21 | -0.01 | | 0.38 | | 0.08 | -0.28 | | 7 | 47.10 | 6.56 | 0 |
| 43 | 0.20 | | | 0.39 | 0.07 | 0.11 | -0.29 | | 7 | 47.20 | 6.72 | 0 |
| 44 | 0.21 | 0.06 | | 0.35 | 0.02 | | -0.28 | | 7 | 47.40 | 6.92 | 0 |
| 45 | 0.41 | | + | | -0.07 | 0.09 | | | 8 | 47.50 | 6.97 | 0 |
| 46 | 0.21 | 0.18 | | | 0.08 | 0.08 | | | 6 | 47.60 | 7.08 | 0 |
| 47 | 0.40 | | + | 0.00 | | 0.13 | | | 8 | 47.70 | 7.22 | 0 |
| 48 | 0.31 | 0.09 | | | 0.32 | 0.24 | -0.20 | -1.09 | 8 | 47.80 | 7.25 | 0 |
| 49 | 0.42 | | + | 0.02 | -0.11 | | | | 8 | 47.80 | 7.27 | 0 |
| 50 | 0.40 | | + | 0.26 | | | -0.25 | | 8 | 47.90 | 7.37 | 0 |
| 51 | 0.45 | 0.01 | + | | | 0.11 | | -0.61 | 9 | 48.00 | 7.51 | 0 |
| 52 | 0.20 | | | | 0.03 | 0.11 | -0.08 | | 6 | 48.20 | 7.73 | 0 |
| 53 | 0.45 | 0.24 | + | | | 0.01 | -0.20 | | 9 | 48.40 | 7.91 | 0 |
| 54 | 0.46 | 0.25 | + | | 0.01 | | -0.20 | | 9 | 48.40 | 7.91 | 0 |
| 55 | 0.46 | 0.25 | + | -0.01 | | | -0.20 | | 9 | 48.40 | 7.91 | 0 |
| 56 | 0.47 | 0.07 | + | | | 0.09 | -0.24 | -0.73 | 10 | 48.70 | 8.14 | 0 |
| 57 | 0.30 | -0.07 | | 0.09 | 0.23 | 0.25 | | -0.94 | 8 | 49.40 | 8.89 | 0 |
| 58 | 0.30 | -0.08 | | 0.32 | 0.30 | 0.27 | -0.32 | -1.02 | 9 | 49.50 | 8.94 | 0 |
| 59 | 0.41 | | + | 0.17 | -0.09 | | -0.22 | | 9 | 49.60 | 9.05 | 0 |
| 60 | 0.22 | 0.03 | | 0.18 | 0.04 | 0.10 | | | 7 | 49.70 | 9.21 | 0 |
| 61 | 0.40 | | + | | -0.07 | 0.09 | -0.15 | | 9 | 49.90 | 9.40 | 0 |
| 62 | 0.47 | 0.28 | + | -0.17 | | 0.03 | | | 9 | 50.00 | 9.51 | 0 |
| 63 | 0.47 | 0.30 | + | -0.17 | 0.00 | | | | 9 | 50.10 | 9.54 | 0 |
| 64 | 0.20 | 0.25 | | | 0.12 | 0.07 | -0.15 | | 7 | 50.10 | 9.59 | 0 |
| 65 | 0.44 | 0.16 | + | | -0.02 | 0.03 | | | 9 | 50.50 | 10.03 | 0 |
| 66 | 0.20 | 0.03 | | 0.38 | 0.09 | 0.11 | -0.29 | | 8 | 50.80 | 10.26 | 0 |
| 67 | 0.39 | | + | 0.21 | | 0.09 | -0.24 | | 9 | 51.00 | 10.49 | 0 |
| 68 | 0.41 | | + | 0.00 | -0.07 | 0.09 | | | 9 | 51.20 | 10.71 | 0 |
| 69 | 0.48 | 0.12 | + | -0.18 | | 0.10 | | -0.63 | 10 | 51.30 | 10.83 | 0 |
| 70 | 0.45 | 0.25 | + | | 0.01 | 0.01 | -0.20 | | 10 | 52.50 | 11.97 | 0 |
| 71 | 0.45 | 0.25 | + | 0.00 | | 0.01 | -0.20 | | 10 | 52.50 | 11.98 | 0 |
| 72 | 0.46 | 0.26 | + | -0.01 | 0.01 | | -0.20 | | 10 | 52.50 | 11.98 | 0 |

| | Int | DC | | SR | GS | LC | SS | T | df | AICc | Δ | weight |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 73 | 0.47 | 0.06 | + | 0.01 | | 0.09 | -0.25 | -0.73 | 11 | 53.10 | 12.57 | 0 |
| 74 | 0.47 | 0.28 | + | -0.17 | 0.01 | 0.03 | | | 10 | 54.10 | 13.57 | 0 |
| 75 | 0.49 | 0.05 | + | | 0.26 | 0.22 | | -0.95 | 10 | 55.10 | 14.55 | 0 |
| 76 | 0.50 | 0.15 | + | | 0.28 | 0.21 | -0.26 | -1.04 | 11 | 55.10 | 14.59 | 0 |
| 77 | 0.45 | 0.25 | + | -0.01 | 0.01 | 0.01 | -0.20 | | 11 | 56.90 | 16.41 | 0 |
| 78 | 0.50 | 0.14 | + | -0.14 | 0.23 | 0.20 | | -0.92 | 11 | 58.20 | 17.64 | 0 |
| 79 | 0.36 | | + | 0.40 | 0.15 | 0.14 | -0.30 | | 10 | 58.80 | 18.27 | 0 |
| 80 | 0.47 | 0.02 | + | 0.31 | 0.38 | 0.28 | -0.34 | -1.12 | 12 | 62.20 | 21.66 | 0 |

^ 'null' model with just the intercept and random effect term

Random term: 1|Species

Int: Intercept; DC: Dominance Certainty; SR: Sex Ratio; GS: Group Size; LC: Living Condition; SS: Social Style; T: Transitivity

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**Supplementary Table 6: Model parameters and coefficients for all 80 sub-models within the full model set derived using the dredge function for the outcome variable groom Newman's Modularity. Species was set as a random effect. Models in bold represent the candidate set (8 models: dAICc < 4 from the best-fit) selected for model averaging and interpretation.**

| Model | (Int) | | | B Coefficients | | | | | df | AICc | Δ | w |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | LC | SS | DC | SR | GS | T | GS:LC | | | | |
| **1** | **0.19** | **0.15** | | | **0.07** | **0.10** | | | **6** | **-72.40** | **0.00** | **0.29** |
| **2** | **0.20** | **0.14** | | | | **0.08** | | | **5** | **-71.70** | **0.65** | **0.21** |
| **3** | **0.19** | **0.16** | | **-0.03** | **0.07** | **0.10** | | | **7** | **-69.60** | **2.77** | **0.07** |
| **4** | **0.19** | **0.15** | | | **0.07** | **0.10** | **-0.01** | | **7** | **-69.30** | **3.06** | **0.06** |
| **5** | **0.19** | **0.15** | | | **0.07** | **0.10** | | **0.00** | **7** | **-69.10** | **3.30** | **0.06** |
| **6** | **0.20** | **0.16** | | **-0.03** | | **0.08** | | | **6** | **-69.10** | **3.31** | **0.06** |
| **7** | **0.19** | **0.15** | | | | **0.08** | | **0.04** | **6** | **-68.90** | **3.43** | **0.05** |
| **8** | **0.20** | **0.15** | | | | **0.08** | **-0.01** | | **6** | **-68.90** | **3.46** | **0.05** |
| 9 | 0.29 | 0.15 | + | | 0.07 | 0.10 | | | 9 | -66.40 | 6.00 | 0.02 |
| 10 | 0.19 | 0.16 | | -0.03 | 0.07 | 0.10 | 0.00 | | 8 | -66.00 | 6.35 | 0.01 |
| 11 | 0.19 | 0.16 | | -0.03 | 0.07 | 0.10 | | -0.01 | 8 | -66.00 | 6.35 | 0.01 |
| 12 | 0.19 | 0.16 | | -0.02 | | 0.07 | | 0.03 | 7 | -66.00 | 6.42 | 0.01 |
| 13 | 0.30 | 0.14 | + | | | 0.08 | | | 8 | -65.90 | 6.49 | 0.01 |
| 14 | 0.19 | 0.15 | | | | 0.08 | -0.01 | 0.03 | 7 | -65.80 | 6.54 | 0.01 |
| 15 | 0.20 | 0.16 | | -0.02 | | 0.08 | 0.00 | | 7 | -65.80 | 6.57 | 0.01 |
| 16 | 0.19 | 0.15 | | | 0.07 | 0.10 | -0.01 | 0.00 | 8 | -65.70 | 6.65 | 0.01 |
| 17 | 0.30 | 0.18 | + | -0.06 | 0.07 | 0.09 | | | 10 | -65.50 | 6.84 | 0.01 |
| 18 | 0.30 | 0.17 | + | -0.05 | | 0.07 | | | 9 | -64.20 | 8.20 | 0.01 |
| 19 | 0.19 | 0.17 | | | | | | | 4 | -63.90 | 8.48 | 0 |
| 20 | 0.29 | 0.15 | + | | | 0.07 | | 0.05 | 9 | -62.70 | 9.64 | 0 |
| 21 | 0.29 | 0.15 | + | | 0.07 | 0.10 | -0.01 | | 10 | -62.50 | 9.90 | 0 |
| 22 | 0.19 | 0.16 | | -0.02 | | 0.07 | 0.00 | 0.03 | 8 | -62.40 | 9.98 | 0 |
| 23 | 0.19 | 0.21 | | -0.05 | | | | | 5 | -62.30 | 10.06 | 0 |
| 24 | 0.30 | 0.15 | + | | | 0.08 | -0.01 | | 9 | -62.30 | 10.09 | 0 |
| 25 | 0.29 | 0.15 | + | | 0.07 | 0.10 | | 0.01 | 10 | -62.20 | 10.15 | 0 |
| 26 | 0.19 | 0.16 | | -0.03 | 0.07 | 0.10 | 0.00 | -0.01 | 9 | -62.10 | 10.26 | 0 |
| 27 | 0.32 | 0.21 | + | -0.09 | | | | | 8 | -61.90 | 10.43 | 0 |
| 28 | 0.19 | 0.18 | | | | | -0.01 | | 5 | -61.40 | 10.99 | 0 |
| 29 | 0.30 | 0.19 | + | -0.08 | 0.07 | 0.09 | 0.01 | | 11 | -61.40 | 11.00 | 0 |
| 30 | 0.19 | 0.17 | | | 0.00 | | | | 5 | -61.10 | 11.31 | 0 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 31 | 0.31 | 0.17 | + | | | | | | 7 | -61.00 | 11.34 | 0 |
| 32 | 0.30 | 0.18 | + | -0.06 | 0.07 | 0.09 | | 0.00 | 11 | -60.90 | 11.48 | 0 |
| 33 | 0.30 | 0.18 | + | -0.05 | | 0.07 | | 0.04 | 10 | -60.60 | 11.81 | 0 |
| 34 | 0.32 | 0.23 | + | -0.10 | 0.03 | | | | 9 | -60.30 | 12.08 | 0 |
| 35 | 0.31 | 0.17 | + | -0.06 | | 0.07 | 0.01 | | 10 | -60.20 | 12.17 | 0 |
| 36 | 0.19 | | | 0.07 | | 0.11 | | | 5 | -60.20 | 12.21 | 0 |
| 37 | 0.19 | | | | | 0.12 | | | 4 | -59.80 | 12.57 | 0 |
| 38 | 0.19 | 0.21 | | -0.05 | 0.01 | | | | 6 | -59.30 | 13.05 | 0 |
| 39 | 0.19 | 0.20 | | -0.05 | | | 0.00 | | 6 | -59.30 | 13.09 | 0 |
| 40 | 0.29 | 0.15 | + | | | 0.07 | -0.01 | 0.04 | 10 | -58.70 | 13.68 | 0 |
| 41 | 0.32 | 0.22 | + | -0.11 | | | 0.02 | | 9 | -58.60 | 13.79 | 0 |
| 42 | 0.19 | | | 0.07 | 0.05 | 0.13 | | | 6 | -58.40 | 13.99 | 0 |
| 43 | 0.19 | 0.18 | | | 0.00 | | -0.01 | | 6 | -58.30 | 14.02 | 0 |
| 44 | 0.29 | 0.15 | + | | 0.07 | 0.10 | -0.01 | 0.01 | 11 | -57.90 | 14.50 | 0 |
| 45 | 0.19 | | | | 0.05 | 0.13 | | | 5 | -57.90 | 14.51 | 0 |
| 46 | 0.31 | 0.18 | + | | | | -0.01 | | 8 | -57.80 | 14.55 | 0 |
| 47 | 0.19 | | | | | 0.11 | 0.02 | | 5 | -57.70 | 14.63 | 0 |
| 48 | 0.32 | 0.17 | + | | 0.01 | | | | 8 | -57.70 | 14.71 | 0 |
| 49 | 0.27 | | + | | | 0.11 | | | 7 | -57.60 | 14.78 | 0 |
| 50 | 0.19 | | | 0.08 | | 0.11 | -0.01 | | 6 | -57.20 | 15.19 | 0 |
| 51 | 0.33 | 0.23 | + | -0.12 | 0.03 | | 0.02 | | 10 | -56.40 | 15.92 | 0 |
| 52 | 0.30 | 0.18 | + | -0.06 | | 0.07 | 0.01 | 0.04 | 11 | -56.30 | 16.10 | 0 |
| 53 | 0.30 | 0.19 | + | -0.08 | 0.07 | 0.09 | 0.01 | 0.00 | 12 | -56.20 | 16.13 | 0 |
| 54 | 0.19 | 0.21 | | -0.06 | 0.01 | | 0.00 | | 7 | -56.00 | 16.33 | 0 |
| 55 | 0.19 | | | | 0.05 | 0.13 | 0.03 | | 6 | -55.70 | 16.66 | 0 |
| 56 | 0.19 | | | 0.08 | 0.05 | 0.13 | -0.01 | | 7 | -55.10 | 17.23 | 0 |
| 57 | 0.31 | 0.18 | + | | 0.02 | | -0.01 | | 9 | -54.20 | 18.15 | 0 |
| 58 | 0.27 | | + | | | 0.11 | 0.02 | | 8 | -54.10 | 18.27 | 0 |
| 59 | 0.27 | | + | 0.06 | | 0.11 | | | 8 | -53.40 | 19.00 | 0 |
| 60 | 0.27 | | + | | 0.04 | 0.13 | | | 8 | -53.30 | 19.05 | 0 |
| 61 | 0.27 | | + | 0.08 | 0.06 | 0.13 | | | 9 | -49.90 | 22.50 | 0 |
| 62 | 0.27 | | + | | 0.04 | 0.12 | 0.02 | | 9 | -49.70 | 22.65 | 0 |
| 63 | 0.27 | | + | 0.06 | | 0.11 | 0.00 | | 9 | -49.50 | 22.82 | 0 |
| 64^ | 0.19 | | | | | | | | 3 | -49.20 | 23.12 | 0 |
| 65 | 0.19 | | | 0.07 | | | | | 4 | -49.00 | 23.33 | 0 |
| 66 | 0.19 | | | | -0.05 | | | | 4 | -47.70 | 24.7 | 0 |
| 67 | 0.19 | | | | | | 0.03 | | 4 | -47.30 | 25.03 | 0 |
| 68 | 0.19 | | | 0.07 | -0.04 | | | | 5 | -47.10 | 25.25 | 0 |
| 69 | 0.29 | | + | | | | | | 6 | -47.10 | 25.29 | 0 |
| 70 | 0.19 | | | 0.08 | | | 0.00 | | 5 | -46.20 | 26.12 | 0 |
| 71 | 0.29 | | + | | -0.05 | | | | 7 | -46.20 | 26.2 | 0 |
| 72 | 0.27 | | + | 0.08 | 0.06 | 0.13 | 0.00 | | 10 | -45.70 | 26.7 | 0 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 73 | 0.19 | | | -0.05 | 0.03 | | 5 | -45.50 | 26.89 | 0 |
| 74 | 0.29 | + | 0.07 | | | | 7 | -44.70 | 27.63 | 0 |
| 75 | 0.19 | | 0.08 | -0.05 | 0.00 | | 6 | -44.10 | 28.26 | 0 |
| 76 | 0.29 | + | | | 0.03 | | 7 | -44.00 | 28.33 | 0 |
| 77 | 0.29 | + | | -0.05 | 0.03 | | 8 | -42.30 | 30.07 | 0 |
| 78 | 0.29 | + | 0.07 | -0.04 | | | 8 | -42.10 | 30.26 | 0 |
| 79 | 0.29 | + | 0.07 | | 0.00 | | 8 | -41.20 | 31.18 | 0 |
| 80 | 0.29 | + | 0.06 | -0.04 | 0.00 | | 9 | -38.20 | 34.13 | 0 |

^ 'null' model with just the intercept and random effect term

Random term: 1|Species

Int: Intercept; DC: Dominance Certainty; SR: Sex Ratio; GS: Group Size; LC: Living Condition; SS: Social Style; T: Transitivity

**Supplementary Table 7: Model parameters and coefficients for all 80 submodels within the full model set derived using the dredge function for the outcome variable groom clustering coefficient. Species was set as a random effect. Models in bold represent the candidate set (7 models: dAICc < 4 from the best-fit) selected for model averaging and interpretation.**

| Model | (Int) | B Coefficients | | | | | | | df | AICc | Δ | w |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | LC | SS | DC | SR | GS | T | GS: LC | | | | |
| **1** | **0.97** | **-0.49** | | **0.37** | | **-0.20** | | | **6** | **7.50** | **0.00** | **0.28** |
| **2** | **0.94** | **-0.49** | | **0.41** | | **-0.22** | | **0.23** | **7** | **9.70** | **2.17** | **0.10** |
| **3** | **0.62** | **-0.54** | **+** | **0.46** | | **-0.19** | | | **9** | **10.00** | **2.44** | **0.08** |
| **4** | **0.97** | **-0.51** | | **0.39** | **0.07** | **-0.18** | | | **7** | **10.50** | **2.95** | **0.06** |
| **5** | **0.97** | **-0.49** | | **0.36** | | **-0.20** | **0.01** | | **7** | **10.70** | **3.18** | **0.06** |
| **6** | **0.97** | **-0.21** | | | | **-0.26** | | | **5** | **10.90** | **3.40** | **0.05** |
| **7** | **0.97** | | | | | **-0.31** | | | **4** | **11.10** | **3.61** | **0.05** |
| 8 | 0.97 | -0.63 | | 0.46 | | | | | 5 | 11.70 | 4.16 | 0.04 |
| 9 | 0.97 | -0.29 | | | | -0.26 | 0.11 | | 6 | 12.10 | 4.56 | 0.03 |
| 10 | 0.57 | -0.67 | + | 0.55 | | | | | 8 | 12.20 | 4.66 | 0.03 |
| 11 | 0.96 | -0.63 | | 0.50 | 0.19 | | | | 6 | 12.70 | 5.15 | 0.02 |
| 12 | 0.94 | -0.50 | | 0.42 | 0.05 | -0.21 | | 0.22 | 8 | 13.00 | 5.49 | 0.02 |
| 13 | 0.94 | -0.49 | | 0.40 | | -0.22 | 0.01 | 0.23 | 8 | 13.10 | 5.61 | 0.02 |
| 14 | 0.60 | -0.54 | + | 0.49 | | -0.21 | | 0.23 | 10 | 13.40 | 5.90 | 0.02 |
| 15 | 0.97 | | | | | -0.31 | 0.04 | | 5 | 13.70 | 6.16 | 0.01 |
| 16 | 0.97 | | | 0.04 | | -0.31 | | | 5 | 13.80 | 6.27 | 0.01 |
| 17 | 0.62 | -0.54 | + | 0.48 | | -0.19 | -0.02 | | 10 | 13.80 | 6.28 | 0.01 |
| 18 | 0.96 | -0.20 | | | | -0.27 | | 0.07 | 6 | 13.80 | 6.29 | 0.01 |
| 19 | 0.97 | -0.22 | | | -0.03 | -0.27 | | | 6 | 13.90 | 6.32 | 0.01 |
| 20 | 0.97 | -0.50 | | 0.38 | 0.06 | -0.19 | 0.00 | | 8 | 13.90 | 6.39 | 0.01 |
| 21 | 0.97 | | | | 0.00 | -0.31 | | | 5 | 13.90 | 6.40 | 0.01 |
| 22 | 0.62 | -0.55 | + | 0.47 | 0.07 | -0.17 | | | 10 | 14.50 | 6.99 | 0.01 |
| 23 | 0.97 | -0.63 | | 0.48 | | | -0.02 | | 6 | 14.60 | 7.08 | 0.01 |
| 24 | 0.96 | -0.27 | | | | -0.27 | 0.11 | 0.11 | 7 | 15.10 | 7.55 | 0.01 |
| 25 | 0.97 | -0.29 | | | -0.01 | -0.26 | 0.11 | | 7 | 15.30 | 7.74 | 0.01 |
| 26 | 0.56 | -0.67 | + | 0.59 | | | -0.04 | | 9 | 15.60 | 8.03 | 0.01 |
| 27 | 0.96 | -0.63 | | 0.51 | 0.19 | | -0.02 | | 7 | 15.80 | 8.29 | 0 |
| 28 | 0.57 | -0.67 | + | 0.56 | 0.18 | | | | 9 | 16.20 | 8.71 | 0 |
| 29 | 0.73 | | + | | | -0.31 | | | 7 | 16.50 | 8.98 | 0 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 30 | 0.97 | | | 0.02 | | -0.31 | 0.03 | | 6 | 16.70 | 9.14 | 0 |
| 31 | 0.97 | | | | 0.00 | -0.31 | 0.04 | | 6 | 16.70 | 9.15 | 0 |
| 32 | 0.97 | -0.32 | | | | | | | 4 | 16.70 | 9.17 | 0 |
| 33 | 0.94 | -0.50 | | 0.41 | 0.04 | -0.21 | 0.01 | 0.22 | 9 | 16.80 | 9.24 | 0 |
| 34 | 0.97 | | | 0.05 | 0.01 | -0.31 | | | 6 | 16.80 | 9.26 | 0 |
| 35 | 0.96 | -0.20 | | | -0.04 | -0.28 | | 0.10 | 7 | 16.90 | 9.37 | 0 |
| 36 | 0.69 | -0.23 | + | | | -0.26 | | | 8 | 17.30 | 9.79 | 0 |
| 37 | 0.60 | -0.54 | + | 0.50 | | -0.21 | -0.02 | 0.22 | 11 | 17.70 | 10.13 | 0 |
| 38 | 0.97 | -0.39 | | | | | 0.12 | | 5 | 17.70 | 10.19 | 0 |
| 39 | 0.60 | -0.55 | + | 0.49 | 0.05 | -0.19 | | 0.22 | 11 | 18.20 | 10.67 | 0 |
| 40 | 0.73 | | + | 0.13 | | -0.31 | | | 8 | 18.40 | 10.83 | 0 |
| 41 | 0.95 | -0.27 | | | -0.04 | -0.28 | 0.11 | 0.13 | 8 | 18.50 | 10.93 | 0 |
| 42 | 0.62 | -0.55 | + | 0.49 | 0.06 | -0.17 | -0.02 | | 11 | 18.70 | 11.16 | 0 |
| 43 | 0.96 | -0.29 | | | 0.11 | | | | 5 | 19.00 | 11.48 | 0 |
| 44 | 0.69 | -0.31 | + | | | -0.25 | 0.12 | | 9 | 19.00 | 11.51 | 0 |
| 45 | 0.74 | | + | | | -0.31 | 0.05 | | 8 | 19.50 | 11.93 | 0 |
| 46^ | 0.97 | | | | | | | | 3 | 19.60 | 12.11 | 0 |
| 47 | 0.56 | -0.66 | + | 0.60 | 0.18 | | -0.04 | | 10 | 19.80 | 12.31 | 0 |
| 48 | 0.97 | | | 0.02 | 0.01 | -0.31 | 0.03 | | 7 | 19.90 | 12.35 | 0 |
| 49 | 0.96 | -0.37 | | | 0.12 | | 0.12 | | 6 | 20.20 | 12.65 | 0 |
| 50 | 0.73 | | + | | 0.02 | -0.30 | | | 8 | 20.20 | 12.71 | 0 |
| 51 | 0.97 | | | | 0.18 | | | | 4 | 20.60 | 13.07 | 0 |
| 52 | 0.62 | -0.33 | + | | | | | | 7 | 20.70 | 13.16 | 0 |
| 53 | 0.68 | -0.23 | + | | | -0.26 | | 0.06 | 9 | 21.00 | 13.50 | 0 |
| 54 | 0.69 | -0.23 | + | | -0.01 | -0.26 | | | 9 | 21.10 | 13.61 | 0 |
| 55 | 0.73 | | + | 0.14 | | -0.31 | -0.01 | | 9 | 22.00 | 14.48 | 0 |
| 56 | 0.97 | | | | | | 0.03 | | 4 | 22.10 | 14.58 | 0 |
| 57 | 0.98 | | | 0.03 | | | | | 4 | 22.20 | 14.70 | 0 |
| 58 | 0.73 | | + | 0.13 | 0.04 | -0.30 | | | 9 | 22.40 | 14.86 | 0 |
| 59 | 0.62 | -0.41 | + | | | | 0.13 | | 8 | 22.40 | 14.90 | 0 |
| 60 | 0.60 | -0.54 | + | 0.51 | 0.04 | -0.19 | -0.02 | 0.21 | 12 | 22.80 | 15.28 | 0 |
| 61 | 0.68 | -0.30 | + | | | -0.26 | 0.12 | 0.12 | 10 | 23.00 | 15.46 | 0 |
| 62 | 0.97 | | | | 0.18 | | 0.03 | | 5 | 23.20 | 15.68 | 0 |
| 63 | 0.69 | -0.31 | + | | 0.01 | -0.25 | 0.12 | | 10 | 23.20 | 15.72 | 0 |
| 64 | 0.97 | | | 0.06 | 0.19 | | | | 5 | 23.30 | 15.75 | 0 |
| 65 | 0.67 | | + | | | | | | 6 | 23.40 | 15.87 | 0 |
| 66 | 0.74 | | + | | 0.02 | -0.30 | 0.05 | | 9 | 23.50 | 15.94 | 0 |
| 67 | 0.62 | -0.32 | + | | 0.11 | | | | 8 | 24.70 | 17.21 | 0 |
| 68 | 0.97 | | | 0.01 | | | 0.02 | | 5 | 24.90 | 17.39 | 0 |
| 69 | 0.68 | -0.23 | + | | -0.02 | -0.27 | | 0.07 | 10 | 25.10 | 17.52 | 0 |
| 70 | 0.67 | | + | | 0.18 | | | | 7 | 25.50 | 17.92 | 0 |
| 71 | 0.97 | | | 0.05 | 0.19 | | 0.01 | | 6 | 26.20 | 18.67 | 0 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 72 | 0.67 | | + | 0.11 | | | | | 7 | 26.30 | 18.76 | 0 |
| 73 | 0.67 | | + | | | | 0.03 | | 7 | 26.30 | 18.77 | 0 |
| 74 | 0.73 | | + | 0.14 | 0.04 | -0.30 | -0.01 | | 10 | 26.40 | 18.84 | 0 |
| 75 | 0.62 | -0.40 | + | | 0.13 | | 0.13 | | 9 | 26.80 | 19.30 | 0 |
| 76 | 0.68 | -0.30 | + | | -0.01 | -0.26 | 0.12 | 0.12 | 11 | 27.40 | 19.88 | 0 |
| 77 | 0.67 | | + | 0.15 | 0.21 | | | | 8 | 28.00 | 20.44 | 0 |
| 78 | 0.67 | | + | | 0.18 | | 0.04 | | 8 | 28.50 | 21.01 | 0 |
| 79 | 0.67 | | + | 0.12 | | | -0.02 | | 8 | 29.80 | 22.22 | 0 |
| 80 | 0.66 | | + | 0.17 | 0.21 | | -0.03 | | 9 | 31.70 | 24.13 | 0 |

^ 'null' model with just the intercept and random effect term

Random term: 1|Species

Int: Intercept; DC: Dominance Certainty; SR: Sex Ratio; GS: Group Size; LC: Living Condition; SS: Social Style; T: Transitivity

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**Supplementary Table 8: Summary of zero-averaged coefficients of the predictors**

**from the candidate models (dAICc < 4 from the model with the lowest AICc score)**

**for groom eigenvector coefficient**

|  | B | Adj SE | z | Pr (>\|z\|) | Importance |
|---|---|---|---|---|---|
| (Intercept) | 0.22 | 0.09 | 2.48 | 0.01* |  |
| Dominance Certainty | 0.06 | 0.14 | 0.43 | 0.67 | 0.23 |
| Transitivity | 0.02 | 0.09 | 0.23 | 0.82 | 0.14 |
| Living Condition (captive vs free living) | 0.01 | 0.05 | 0.17 | 0.86 | 0.09 |
| Sex Ratio | 0.00 | 0.04 | 0.09 | 0.93 | 0.07 |
| Group Size | -0.02 | 0.09 | 0.26 | 0.80 | 0.13 |
| Living Condition: Group Size | -0.01 | 0.11 | 0.10 | 0.92 | 0.01 |
| Social Style (grade 1 vs grade 2) | 0.00 | 0.03 | 0.07 | 0.94 | 0.02 |
| Social Style (grade 1 vs grade 3) | 0.00 | 0.04 | 0.09 | 0.93 |  |
| Social Style (grade 1 vs grade 4) | -0.01 | 0.07 | 0.12 | 0.90 |  |

*p < 0.05

**Supplementary Table 9: Summary of zero-averaged coefficients from the candidate models for Newman's modularity and clustering coefficient of permuted grooming networks of 60% sampling effort**

| (A) Newman's Modularity (8 candidate models) | | | | | |
|---|---|---|---|---|---|
| | B | Adj SE | z | Pr (>\|z\|) | Importance |
| Intercept | 0.22 | 0.04 | 6.026 | <0.01 | |
| **Living Condition (Captive vs. Free living)** | **0.15** | **0.03** | **4.64** | **<0.01**\*\* | **1** |
| Sex Ratio (proportion of females) | 0.07 | 0.05 | 1.47 | 0.14 | 0.82 |
| **Group Size** | **0.09** | **0.03** | **3.40** | **<0.01**\*\* | **1** |
| Dominance Certainty | 0.00 | 0.03 | 0.17 | 0.87 | 0.12 |
| Transitivity | 0.00 | 0.01 | 0.16 | 0.87 | 0.12 |
| Group Size: Living Condition | 0.00 | 0.01 | 0.05 | 0.96 | 0.1 |
| (B) Clustering Coefficient (7 candidate models) | | | | | |
| Intercept | 0.87 | 0.11 | 7.73 | <0.01\*\* | |
| **Group Size** | **-0.24** | **0.09** | **2.59** | **0.01**\* | **1** |
| Living Condition (Captive vs. Free living) | -0.23 | 0.23 | 0.96 | 0.34 | 0.57 |
| Dominance Certainty | 0.14 | 0.19 | 0.73 | 0.47 | 0.39 |
| Group Size: Living Condition | 0.03 | 0.11 | 0.24 | 0.81 | 0.08 |
| Sex Ratio (proportion of females) | 0.00 | 0.02 | 0.05 | 0.96 | 0.02 |
| Transitivity | 0.00 | 0.01 | 0.05 | 0.96 | 0.01 |

[a] Effect sizes are standardized, comparable values (Gelman et al., 2009)
Data are from 34 groups of 9 macaque species
\* $p \leq 0.05$   \*\* $p < 0.01$

**Supplementary Table 10: Summary of zero-averaged coefficients from the candidate models for Newman's modularity and clustering coefficient of permuted grooming networks of 20% sampling effort**

| (A) Newman's Modularity (8 candidate models) | | | | | |
|---|---|---|---|---|---|
| | B | Adj SE | z | Pr (>\|z\|) | Importance |
| Intercept | 0.25 | 0.04 | 6.25 | <0.01** | |
| **Living Condition (Captive vs. Free living)** | **0.14** | **0.03** | **4.52** | **<0.01**** | **1** |
| Sex Ratio (proportion of females) | 0.03 | 0.04 | 0.72 | 0.47 | 0.82 |
| **Group Size** | **0.10** | **0.02** | **4.31** | **<0.01**** | **1** |
| Dominance Certainty | 0.00 | 0.02 | 0.19 | 0.85 | 0.12 |
| Transitivity | 0.00 | 0.01 | 0.20 | 0.85 | 0.12 |
| Group Size: Living Condition | 0.00 | 0.03 | 0.17 | 0.86 | 0.1 |
| (B) Clustering Coefficient (7 candidate models) | | | | | |
| Intercept | 0.61 | 0.10 | 5.88 | <0.01** | |
| **Group Size** | **-0.20** | **0.07** | **2.82** | **0.00**** | **1** |
| Living Condition (Captive vs. Free living) | -0.23 | 0.15 | 1.48 | 0.14 | 0.83 |
| Dominance Certainty | 0.19 | 0.16 | 1.22 | 0.22 | 0.74 |
| Group Size: Living Condition | 0.14 | 0.21 | 0.66 | 0.51 | 0.41 |
| Sex Ratio (proportion of females) | 0.01 | 0.05 | 0.21 | 0.83 | 0.18 |
| Transitivity | -0.01 | 0.04 | 0.34 | 0.74 | 0.14 |

[a] Effect sizes are standardized, comparable values (Gelman et al., 2009)
Data are from 34 groups of 9 macaque species
\*　$p \leq 0.05$　\*\* $p < 0.01$