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

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

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12 5 Petit, O.^l, Schino, G.^m, Sosa, S.ⁿ, Sueur, C.^o, Thierry, B.^o, de Waal, F. B. M.^p & McCowan,
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Abstract:

Among nonhuman primates, the evolutionary underpinnings of variation in social structure remain debated, with both ancestral relationships and adaptation to current conditions hypothesized to play determining roles. Here we assess whether interspecific variation in higher-order aspects of female macaque (genus: *Macaca*) dominance and grooming social structure show phylogenetic signals, i.e. greater similarity among more closely-related species. We use a social network approach to describe higher-order characteristics of social structure, based on both direct interactions and secondary pathways that connect group members. We also ask whether network traits covary with each other, with species-typical social style grades, and/or with sociodemographic characteristics, specifically group size, sex-ratio, and current living condition (captive vs. free-living). We assembled 34-38 datasets of female-female dyadic aggression and allogrooming among captive and free-living macaques representing 10 species. We calculated dominance (transitivity, certainty), and grooming (centrality coefficient, Newman's modularity, clustering coefficient) network traits as aspects of social structure. Computations of K statistics and randomization tests on multiple phylogenies revealed moderate-strong phylogenetic signals in dominance traits, but moderate-weak signals in grooming traits. GLMMs showed that grooming traits did not covary with dominance traits and/or social style grade. Rather, modularity and clustering coefficient, but not centrality coefficient, were strongly predicted by group size and current living condition. Specifically, larger groups showed more modular networks with sparsely-connected clusters than smaller groups. Further, this effect was independent of variation in living condition, and/or sampling effort. In summary, our results reveal that female dominance networks were more

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3 55 phylogenetically conserved across macaque species than grooming networks, which were
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5 56 more labile to sociodemographic factors. Such findings narrow down the processes that
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7 57 influence interspecific variation in two core aspects of macaque social structure. Future
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9 58 directions should include using phylogeographic approaches, and addressing challenges in
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11 59 examining the effects of socioecological factors on primate social structure.
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15 **Key words:**

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18 61 Social networks, phylogenetic signals, social style, group size, macaques
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20 **Introduction:**

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22 63 In group-living animals, diversity in sociality may be characterized by variation in
23
24 64 social structure, i.e. the patterning and distribution of different types of interactions (e.g.
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26 65 competitive, affiliative, cooperative) and relationships among group members (Hinde,
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28 66 1976; Kappeler & Van Schaik, 2002). Several factors have been found to govern social
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30 67 structure, including but not restricted to kinship, age similarity, sex and dominance status
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32 68 (Hinde, 1976; Kappeler & Van Schaik, 2002). However, our understanding of the
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34 69 evolutionary and ecological factors that produce diverse social structures remains limited.
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36 70 Specifically, the extent to which such social structure has been influenced by species'
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38 71 ancestral relationships versus variation in current conditions remains debated (Clutton-
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40 72 Brock & Janson, 2012; Kasper & Voelkl, 2009; Koenig et al., 2013; Thierry, 2004). Here,
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42 73 we use Social Network Analysis to assess whether variation in aspects of social structure
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44 74 across multiple species of macaques (genus: *Macaca*) is related to species' phylogenetic
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46 75 relatedness (Blomberg et al., 2003; Thierry, 2004), and hypothesized tendencies for social
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48 76 traits to co-evolve with each other in suites or packages (de Waal & Luttrell, 1989; Thierry,
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50 77 2007). We also investigate the extent to which such covariation may be influenced by
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3 78 group-specific sociodemographic characteristics (Kasper & Voelkl, 2009; Sterck et al.,
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5 79 1997; Sueur et al., 2011b)
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8 80 A major explanatory framework for the evolution of variation in primate social
9
10 81 structure is related to species' ancestry or phylogenetic closeness (Blomberg et al., 2003).
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12 82 According to this framework, aspects of sociality are expected to show phylogenetic
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14 83 signals, i.e. to exhibit greater similarity in social structure among more closely-related than
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16 84 distantly-related species (Blomberg et al., 2003). Ecological adaptation is not ruled out but
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18 85 rather hypothesized to occur minimally, or in response to novel, drastic environmental
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20 86 changes (Blomberg et al., 2003; Chan, 1996; Matsumura, 1999). In the past, proponents of
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22 87 phylogenetic signals often referred to them as outcomes of phylogenetic constraints or
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24 88 phylogenetic inertia (Blomberg et al., 2003). However, more recent theory recognizes that
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26 89 phylogenetic signal refers to the observed patterns of trait similarity, rather than one or
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28 90 more evolutionary processes – e.g. random genetic drift, stabilizing selection, pleiotropy, or
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30 91 low rates of evolution -- by which such patterns may arise (reviewed in Kamilar & Cooper,
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32 92 2015). Rather than attempt to distinguish between possible processes or the rates at which
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34 93 they occur, here we simply aim to identify strong and weak phylogenetic signals in order to
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36 94 determine the extent to which social network structure covaries with macaques'
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38 95 phylogenetic closeness.
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45 96 Across animal societies, behavioral traits are more labile to evolutionary change in
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47 97 comparison to morphological and/or physiological characteristics (Blomberg et al., 2003).
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49 98 Primates are no exception, with traits like brain size, body mass and canine dimorphism
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51 99 exhibiting stronger phylogenetic signals than those related to social organization and
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53 100 activity budgets (Kamilar & Cooper, 2015). As such, phylogenetic signals for aspects of
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3 101 primate social network traits have been hard to identify. For instance, Kasper and Voelkl
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5 102 (2009) established that several aspects of affiliative social networks – e.g. community sub-
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7 103 group formation or modularity, mean centrality in the connectedness of individuals, and the
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9 104 density of network connections (see Methods for precise definitions) -- all showed greater
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11 105 variation between closely related than between distantly related species, i.e. weak
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13 106 phylogenetic signals and a substantial effect of socioecological or demographic factors on
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15 107 network structure. Similarly, Pasquaretta et al. (2014) found no effect of phylogenetic
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17 108 signals on the efficiency of information flow through affiliative social networks of
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19 109 primates, including humans. Tests for phylogenetic signals in aspects of sociality within
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21 110 specific primate families and genera have also revealed inconsistencies. In the genus
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23 111 *Eulemur*, group size and sex-ratio both strongly correlated with phylogenetic distances
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25 112 (Ossi & Kamilar, 2006). Yet among both baboons (genus: *Papio*) and squirrel monkeys
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27 113 (genus: *Saimiri*), interspecific variation in multiple forms of social organization seem to be
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29 114 strongly linked to ecological factors like food distribution, predation pressure, and
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31 115 intergroup feeding competition (Barton et al., 1996; Boinski, 1999; Henzi & Barrett, 2003).
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34 116 Nevertheless, among all primate genera, phylogenetic signals in social traits have
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36 117 been most consistently detected within the genus *Macaca*. Macaques constitute 23 species
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38 118 of Old World primates, with wide-spread geographic distributions in nature (Cords, 2013).
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40 119 Although all species show a predominantly similar social organization (multi-male, multi-
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42 120 female social groups, female philopatry and male dispersal), they show broad inter- and
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44 121 intraspecific variation in several aspects of female social structure (Thierry, 2007).
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46 122 Specifically, post-conflict affiliation, rates of affiliative contact (Thierry et al., 2008), the
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48 123 steepness of dominance hierarchies (Balasubramaniam et al., 2012a), and asymmetry in
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3 124 aggression (Balasubramaniam et al., 2012a; Thierry et al., 2008) all show phylogenetic
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5 125 signals, whereas grooming kin bias shows a weak signal (Thierry et al., 2008). These
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8 126 findings have led some proponents of phylogenetic explanations to posit that core aspects
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11 127 of macaque social structure may also be structurally linked, covarying with each other at
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13 128 the species level (Petit et al., 1997; Thierry et al., 2008). Thierry (2007) has characterized
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15 129 this tendency to covary by assigning macaque species to positions on a four-grade 'social
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17 130 style' scale that is broadly consistent with phylogenetic lineage splits (Thierry, 2007). At
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20 131 one extreme, 'grade-1' species (e.g. rhesus macaques (*Macaca mulatta*), Japanese
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22 132 macaques (*M. fuscata*)) of the Fascicularis lineage are hypothesized to show 'despotic'
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24 133 social structure, characterized by steep and asymmetric dominance hierarchies, low levels
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27 134 of post-conflict affiliation, intense affiliative kin-bias, and highly modular or sub-structured
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29 135 social networks in which grooming is both centralized among dominant individuals and is
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31 136 concentrated among more preferred partners. At the other extreme, 'grade-4' species (e.g.
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34 137 Tonkean macaques (*M. tonkeana*), crested macaques (*M. nigra*)) belonging to the Sulawesi
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36 138 lineage are hypothesized to be more 'tolerant' or 'egalitarian', showing shallower
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39 139 dominance hierarchies with more frequent counter-aggression from subordinates towards
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41 140 dominants, high proportions of post-conflict affiliation, less grooming kin bias, and denser,
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43 141 less centralized or modular grooming social networks (Balasubramaniam et al., 2012a;
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45 142 Berman & Thierry, 2010; de Waal & Luttrell, 1989; Sueur et al., 2011b; Thierry, 2007;
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47 143 Thierry et al., 2008). Some versions of the covariation hypothesis posit that a species that
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49 144 shows a single behavioral trait associated with a particular social style will display all other
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51 145 traits (Castles et al., 1996; Petit et al., 1997). However, this extent of covariation has not
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54 146 always been found. Rather, most studies (but see Thierry et al. 2008) thus far have revealed
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3 147 marked differences between species at the extreme ends of the social style scale (grade-1
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5 148 and grade-4 macaques, e.g. Sueur et al., 2011b), but found inconsistencies among macaques
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7 149 in intermediate grades (reviewed in Balasubramaniam et al., 2012b).
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10 In the present study, we expand on the above findings by assessing phylogenetic
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12 151 signals and covariation in dominance and grooming social network traits across 10 species
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14 152 of macaques representing all four social style grades, and groups from both captive and
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16 153 free-living conditions. In accordance with the predictions of socioecological models, we
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18 154 also examine whether sociodemographic factors, specifically group size and current living
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20 155 condition (Kasper & Voelkl, 2009; Pasquaretta et al., 2014), influence social network traits
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22 156 in addition to, or instead of, social style or phylogenetic closeness. Broadly, socioecological
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24 157 models differ from phylogenetic explanations by positing that social structure is relatively
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26 158 more labile to changes in current conditions, and that such changes are independent of
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28 159 phylogenetic relatedness (Koenig et al., 2013; Sterck et al., 1997; van Schaik, 1989).
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30 160 Specifically, some versions of the model predict that among free-living primates, larger
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32 161 group size should lead to the evolution of more despotic social network structures,
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34 162 characterized by steeper, asymmetric dominance hierarchies, and highly centralized,
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36 163 modular grooming networks with less dense connections/ redundant ties. This may be
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38 164 because larger groups are likely to display heightened levels of contest competition for
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40 165 resources (Koenig et al., 2013; Sterck et al., 1997; van Schaik, 1989) and/or increased
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42 166 temporal constraints (Berman & Thierry, 2010; Dunbar, 1992; Korstjens et al., 2010). On
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44 167 the other hand, smaller groups may be expected to show greater within-group social
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46 168 tolerance characterized by more reversals in dominance interactions, and de-centralized
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48 169 grooming networks that show greater density/ redundancy of ties. Such effects may also be
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3 170 influenced by the spatial constraints imposed by captive housing that may result in more
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5 171 frequent social interactions among individuals with a potentially wider range of partners
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8 172 (Duboscq et al., 2013; McCowan et al., 2008).
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10 173 Following the pioneering applications of social network analysis on macaque social
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12 174 structure by Sade (1972), comparative studies of nonhuman primate social structure have
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14 175 increasingly used social network approaches to compare various types of societies (Griffin
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16 176 & Nunn, 2012; Kasper & Voelkl, 2009; Pasquaretta et al., 2014; Sueur et al., 2011b). SNA
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18 177 tools improve on earlier methods by constructing aspects of higher-order group structure
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20 178 from a combination of both direct interactions and indirect or secondary connections among
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22 179 group members, and by identifying consistent patterns of interaction among sub-sets of
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24 180 individuals (Brent et al., 2011; Croft et al., 2008; Farine & Whitehead, 2015; Kasper &
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26 181 Voelkl, 2009; Krause et al., 2007; Lusseau & Newman, 2004; McCowan et al., 2008;
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28 182 Newman, 2004; Sueur et al., 2011a; Wey et al., 2008). Yet in comparison to applied animal
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30 183 behavioral research (e.g. infectious disease transmission (reviewed in Drewe & Perkins, 2015),
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32 184 quantifying group social stability (reviewed in McCowan et al., 2008)), SNA has been used less
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34 185 extensively to examine the evolutionary bases for variation in primate social structure (see Kasper
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36 186 & Voelkl, 2009; Griffin & Nunn, 2012; Sueur et al., 2011b).
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42 187 We first ask whether aspects of female dominance and grooming networks show
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44 188 strong phylogenetic signals (Q1) and whether grooming networks covary with dominance
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46 189 networks (Q2) and/or hypothesized social style grades across macaques (Q3). In
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48 190 accordance with the covariation and social style hypotheses, we predict that macaque
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50 191 species that have the most transitive, decided and/or certain dominance relationships will
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52 192 also show (a) the greatest tendencies for high-ranking individuals to occupy more central
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54 193 positions in more modular grooming networks, and (b) networks that are more modular
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3 194 with sparser, less redundant ties. In comparison, those with the least transitive and/or
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5 195 uncertain dominance relationships are expected to show the opposite characteristics.
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8 196 Further, we predict that transitions from more despotic to more tolerant social styles will be
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10 197 correlated with systematic decreases in the centralization of grooming among dominants
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12 198 and modularity, and increases in network density or redundancy of ties. Finally, we also
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14 199 examine (Q4) the potential impact of sociodemographic factors on networks and patterns of
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16 200 covariation. Specifically, we predict that group size will be positively associated with the
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18 201 centralization of grooming among dominants and with grooming modularity, and
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20 202 negatively associated with the density/ redundancy of ties in grooming network clusters.
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22 203 We also explore the effects of living condition on such relationships, and the impact of a
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24 204 third sociodemographic characteristic -- female-to-male sex ratio -- on such covariation.
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29 **Methods:**
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32 206 This research adhered to the American Society of Primatologists principles for the
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34 207 ethical treatment of primates. We first assembled behavioral and phylogenetic datasets from
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36 208 various sources – published literature, our own unpublished data, and personal donations
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38 209 from other researchers (Table 1). Below we describe these data, the computation of social
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40 210 network measures, and statistical analyses.
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43 *Datasets – macaque social behaviors and phylogenetic trees:*
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46 212 To compute dominance network measures, we assembled a total of 38 behavioral
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48 213 datasets on dyadic aggressive interactions among adult female macaques (individuals ≥ 3.5
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50 214 - 5 years of age, depending on species-typical ages of maturity) from groups living in
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52 215 captive and free-living (free-ranging and wild) conditions (Table 1). These encompassed 20
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54 216 populations representing 10 macaque species from all four social style grades. Except for
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3 217 stumptailed macaques (*M. arctoides*) and bonnet macaques (*M. radiata*), we acquired at
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5 218 least two datasets for each species; these were either from different social groups or from
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8 219 the same social group during different stable study-periods. To compute grooming network
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10 220 measures, we obtained data from 34 (out of the 38) datasets from nine species (Table 1).

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12 221 The datasets had been collected using different types of sampling approaches, and
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15 222 varied in sampling effort per subject (Table 1). The majority (aggression: 33/ 38, or 87%;
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17 223 grooming: 25/34, or 74%) had been collected using focal-animal and/or all-occurrences
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19
20 224 sampling methods (Altmann, 1974; see citations provided in Table 1). For these datasets,
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22 225 all subjects within a dataset had been observed for roughly equal amounts of time (see
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24 226 corresponding citations; information available on request). A minority used either scan
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27 227 sampling (aggression: 2/38, or 5%; grooming: 7/34, or 20%) or *ad-libitum* sampling along
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30 228 with focal animal sampling (aggression: 3/38, or 8%; grooming: 2/34, or 6%). The scan
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32 229 sampling datasets were included based on a previous study on Japanese macaques revealing
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34 230 that for a given number of scans, this approach yields identical amounts of behavioral data
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36 231 to focal sampling for the same duration (in minutes) as the number of scans (Romano et al.,
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38 232 2016). Datasets that used *ad libitum* sampling were included after ensuring that they had
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41 233 been (a) used in previous comparative studies (Balasubramaniam et al., 2012a; Schino &
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43 234 Aureli, 2008), and (b) conducted for overall durations that were comparable to those of the
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46 235 focal- or all-occurrences sampled datasets (6 – 12 months).

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48 236 All datasets included had been collected as part of long-term studies, and during
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50 237 periods when the groups were socially stable in terms of group composition, size,
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53 238 dominance relationships, age-class and/or sex ratios. Out of 38 datasets, the majority (27, or
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55 239 71%) was from free-living groups of macaques. We found significant differences in group
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3 240 size (captive = 28.4 ± 19.1 ; free-living = 48.3 ± 23.9 ; ANOVA: $F_{1, 32} = 6.04$, $p = 0.02$) and
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5 241 sex ratios (captive = 0.50 ± 0.21 ; free-living = 0.33 ± 0.09 ; ANOVA: $F_{1, 32} = 12.07$, $p <$
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7 242 0.01) between captive vs. free-living macaques. Hence, we either conducted separate
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9 243 assessments for only free-living groups (Q1), or directly examined the effect of living
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11 244 condition in our analyses (Q2 - Q4).

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15 245 In order to assess and control for the effects of phylogenetic signals, we extracted a
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17 246 Bayesian consensus tree (Supplementary Figure 1) and a tree-block of 10 trees from
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19 247 *10Ktrees*, an online resource for primate phylogeny based on mitochondrial and nuclear
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21 248 genetic datasets (Arnold et al., 2010). All 11 phylogenies showed proportional branch-
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23 249 lengths, and identical topologies that were also consistent with previously constructed
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25 250 macaque topologies using parametric approaches (e.g. Chatterjee et al., 2009; Tosi et al.,
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27 251 2003). We hence report the results of tests performed using the consensus phylogeny, with
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29 252 those from the tree-block submitted as supplementary material (Supplementary Table 4).

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34 253 *SNA – Dominance and Grooming Measures:*

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36 255 Table 2 provides the definitions and details of the dominance and grooming network
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38 256 traits that we computed. We computed dominance network measures from winner-loser
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40 257 dominance matrices in which non-diagonal cells contained data on the frequencies of
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42 258 dyadic contact and non-contact aggression from animals in the rows to animals in the
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44 259 columns. Acts of bi-directional or counter-aggression were scored twice, once on either
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46 260 side of the diagonal for each interactant. Bidirectional and counter-aggression were
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48 261 included to produce representative measures of dominance network traits, particularly for
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50 262 grade-3 and grade-4 macaque species that typically experience high proportions of such
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52 263 interactions (Balasubramaniam et al., 2012a; Thierry et al., 2008). From each dominance
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3 264 matrix, we computed two traits – triangle transitivity (Shizuka & McDonald, 2012) and
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5 265 dominance certainty (Fujii et al., 2013; Fushing et al., 2011) – that have not been used in
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8 266 previous comparative studies of primate social networks (see Table 2 for definitions).
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10 267 Whereas most methods for describing group level dominance hierarchies consider only
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12 268 dyadic wins and losses from agonistic encounters (e.g., dominance gradient (hierarchical
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15 269 steepness: de Vries et al., 2006), and dominance asymmetry (Directional Consistency
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17 270 Index: de Vries, 1998)), the computation of network-based measures, particularly
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20 271 dominance certainty, uses both direct dominance interactions and indirect pathways of
21
22 272 imputed wins and losses (Fujii et al., 2013; Fushing et al., 2011). Thus, they capture more
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24 273 global aspects of a dominance hierarchy than steepness or DCI, and are less susceptible
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26
27 274 than steepness to error due to the numbers of non-interacting dyads present in the dataset.
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29 275 Specifically, dominance certainty incorporates the presence of non-interacting dyads in its
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31 276 calculation (Table 2) by weighting both the total number of direct wins by an individual ‘A’
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33 277 against an individual ‘D’ ($A \rightarrow D$), as well as imputed wins incurred via the likelihood of
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35 278 traversing longer paths (e.g. $A \rightarrow B \rightarrow C \rightarrow D$) through the dominance network. In doing so,
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37
38 279 the certainty measure characterizes the network-level flow-structure of dominance
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40 280 information, thereby accounting for hidden elements in dominance structure such as
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43 281 avoidance between individuals (Fujii et al., 2013; Fushing et al., 2011) (Table 2).

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46 282 We constructed grooming networks (Figure 1) from weighted, undirected networks,
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48 283 i.e. where individuals represented by *nodes* were connected by *edges* that represent the
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50 284 normalized values of grooming given and received for each pair of nodes. Weighted
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53 285 networks were used to account for the potential impact of differences in observation times
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55 286 across comparative datasets (Griffin & Nunn, 2012; Newman, 2004). Specifically, we
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3 287 calculated three measures – centrality coefficient, Newman’s modularity, and global
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5 288 clustering coefficient -- that were all (a) not collinear (see below), (b) captured biologically
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7 289 different aspects of network structure, and (c) mathematically independent of the number of
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9 290 nodes (or group size: Nunn et al., 2015). First, we calculated *centrality coefficient* as the
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11 291 correlation coefficient between individuals’ dominance statuses (computed using
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13 292 normalized David’s scores computed from dominance matrices: Gammell et al., 2003) see
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15 293 below) and their centralities within grooming networks (as in Sueur et al., 2011b; see Table
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17 294 2 for definitions). For the latter, we used standardized *eigenvector centrality*, i.e. the
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19 295 number and strength of an individuals’ direct and indirect grooming connections indicating
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21 296 each individual’s access to social capital or support (Farine & Whitehead, 2015; Newman,
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23 297 2004; Whitehead, 2008). Eigenvector centrality is among the most biologically meaningful
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25 298 of the centrality measures; it is more indicative of individuals’ social status than measures
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27 299 of *betweenness* and *closeness* centrality in taxa such as primates that have more complete
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29 300 network graphs (Brent et al., 2010; Farine & Whitehead, 2015; Kasper & Voelkl, 2009;
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31 301 McCowan et al., 2008; Sueur et al., 2011a). We also calculated Newman’s eigenvector-
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33 302 based modularity, which is a global measure of network sub-structuring into communities
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35 303 (Newman, 2006; Nunn et al., 2015; see Table 2 for a detailed definition). Finally, as a
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37 304 measure of the density/ redundancy of ties in the network, we calculated the *global*
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39 305 *clustering coefficient*, which is an unweighted measure of how well-connected nodes are to
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41 306 their immediate neighbors (Table 2). Clustering coefficient captures the underlying
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43 307 redundancy of node connectivity at a more local level than alternative measures like
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45 308 network density, making it mathematically independent of the number of nodes (Table 2;
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47 309 Nunn et al., 2015). However, since increased localized clustering may also be a
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3 310 characteristic of more modular networks (Nunn et al., 2015), we confirmed that clustering
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5 311 coefficient was positively correlated with network density measures across our datasets (n
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8 312 = 34, $r = 0.91$, $p < 0.01$). Grooming measures were calculated using the *statnet* (for
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10 313 eigenvector centrality) and *igraph* (for Newman's modularity and global clustering
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12 314 coefficient) R packages (Csardi & Nepusz, 2006; Handcock et al., 2006). Individuals'
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14
15 315 dominance David's scores were calculated from the aggression matrices using the *steepness*
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17 316 R package (de Vries et al., 2006; Leiva & de Vries, 2014).

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20 317 Supplementary Table 1 shows the values of the various network measures computed
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22 318 for each dataset. To avoid potentially pseudoreplicating our results owing to network
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24 319 measures being collinear to each-other, we confirmed that collinearity diagnostics were met
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26
27 320 for both dominance measures (Pearson's r correlation = 0.61; variance inflation factors
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29 321 (VIF) < 2), and grooming measures ($r < 0.78$ for all pairs; generalized variance inflation
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31 322 factors (GVIF) < 3) using the *car* package in R (Fox & Weisberg, 2011). Given the
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33 323 susceptibility of network measures to variation in sampling effort (Croft et al., 2008; Croft
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35 324 et al., 2011; Farine & Whitehead, 2015; Lusseau et al., 2008), we performed diagnostic
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37 325 tests to ascertain that these did not impact our analyses. For each grooming dataset, we
38
39 326 generated 1000 permuted networks using a bootstrapping algorithm (Lusseau et al., 2008),
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41 327 by randomly sampling increasingly smaller subsets (100%, 80%, 60%, 40%, and 20%) of
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43 328 edges from the original network. Plots of percent sampling effort and mean grooming
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45 329 network measure computed across 200 permuted networks under each category of sampling
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47 330 effort revealed asymptotic relationships (Supplementary Figure 2). Further, Wilcoxon rank-
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49 331 sum tests revealed that network measures computed from the original data were not
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51 332 significantly different to those computed from the bootstrapped networks that used smaller
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3 333 subsets of data (80% - 40% sampling effort; but see clustering coefficient at 20% sampling
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5 334 effort: Supplementary Table 2). Finally, we confirmed that across datasets, sampling effort
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8 335 calculated as the mean observation times spent per subject (Table 1) was unrelated to
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10 336 group-level dominance and/or grooming network measures (Supplementary Table 3;
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12 337 Supplementary Figure 3).

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15 338 *Statistical Analyses:*

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17 339 To examine evidence for phylogenetic signals (Q1) in dominance and grooming
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19 340 network traits at the species level, we used the Phytools R package (Revell, 2012). For each
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21 341 trait, we computed Blomberg's Kappa (K) coefficient (Blomberg et al., 2003) as the ratio
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23 342 between the Mean-Squared Errors (or MSE) of the raw, species-means of behavioral traits
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25 343 over the MSEs of traits that have been phylogenetically transformed using tree-specific
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27 344 branch-length information. The K coefficient therefore indicates the strength of the
28
29 345 phylogenetic signal and further, is scaled by a similar ratio of MSEs calculated assuming a
30
31 346 Brownian motion model of evolution where trait change is hypothesized to be directly
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33 347 proportional to the shared evolutionary histories, or branch length distances between taxa
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35 348 (Blomberg et al., 2003; Kamilar & Cooper, 2015). We considered $K > 1$ from the
36
37 349 randomization test as indicative of a "strong" signal that exceeds the amount of signal
38
39 350 expected under a Brownian motion model of evolution (Blomberg et al., 2003). Values of
40
41 351 $0.8 < K < 1$ were considered to be indicative of a "moderate" signal, while values that are
42
43 352 $\ll 0.8$ indicate a weak signal, i.e. greater plasticity due to adaptation to current conditions
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45 353 in a trait (Blomberg et al., 2003). These values were based on previous comparative studies
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47 354 of nonhuman primate behavioral traits that also examined phylogenetic signals among
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49 355 smaller numbers of species (Balasubramaniam et al., 2012a; Thierry et al., 2008). We
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3 356 avoided splitting terminal species' nodes into multiple nodes to represent groups within
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5 357 species. Although doing so offers the potential advantage of increased statistical power, it
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8 358 would also artificially inflate phylogenetic signals (Blomberg et al., 2003; Thierry et al.,
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10 359 2008). Blomberg's K generates identical results to Pagel's Lambda (Pagel, 1997, 1999), an
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12 360 alternative indicator of phylogenetic signal. However, we chose to report K since this
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15 361 statistic is more useful in informing about trait variation relative to Brownian evolution
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17 362 (Kamilar & Cooper, 2015). In addition, we conducted randomization tests to compare the
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20 363 MSE of phylogenetically transformed data to those computed from 1000 randomized
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22 364 datasets generated by scattering the behavioral scores randomly on a phylogeny. In addition
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25 365 to handling the intrinsic dependency of the data, such tests indicate whether any observed
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27 366 phylogenetic signal is greater than that expected by chance. Although they had low
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29 367 statistical power of 20-35% (Blomberg et al., 2003), randomization tests have nonetheless
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31 368 been used in previous studies of similarly small sample sizes (7-10 species:
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33
34 369 Balasubramaniam et al., 2012a; Thierry et al., 2008).

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36 370 To examine whether grooming network traits were linked to dominance traits (Q2)
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38 371 or social style scale (Q3) across species, and to assess the potential impact of
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40 372 sociodemographic factors (Q4) on such covariations, we constructed General Linear
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42 373 Mixed-effects Models (GLMMs: Bates et al., 2016). We implemented an Information-
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44 374 Theoretical approach (Burnham et al., 2011; Grueber et al., 2011) using the *lme4* and
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46 375 *MuMIn* R packages. Given the relatively small number of species, we used neither
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48 376 Phylogenetic Least Squares regression (PGLS: Nunn, 2011), nor permutation-based
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50 377 MCMC models (Croft et al., 2011; Farine & Whitehead, 2015) that are recommended for
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52 378 examining variation in phylogenetic distances and network sampling effort respectively.
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3 379 Instead, we indirectly tested for the effects of phylogeny by assessing covariation with
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5 380 social style grade, since social style and phylogeny have been shown to strongly covary
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8 381 across macaques (Thierry et al., 2000). To rule out the effect of network sampling effort on
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10 382 our results, we replicated our GLMMs using mean network measures computed from
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12 383 permuted datasets of varying degrees of sampling effort (20% - 80% of edges: see above).
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15 384 We first generated 3 global models, one for each grooming network trait treated as
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17 385 the outcome variable. While eigenvector coefficient and Newman's modularity were both
18
19 386 normally distributed (modularity: Shapiro-wilcoxon test: $w = 0.95$, $p = 0.13$), clustering
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21 387 coefficient was arcsine-transformed to meet normality assumptions ($w = 0.98$, $p = 0.65$).
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23 388 As recommended by I-T approaches (Burnham et al., 2011; Grueber et al., 2011), our
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25 389 global models were constructed by the inclusion of just those covariates that catered to
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27 390 testing our specific predictions (Q2-Q4). Specifically, dominance traits (transitivity and
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29 391 dominance certainty), social style category, and sociodemographic factors (group size, sex
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31 392 ratio, and living condition category) were included as fixed effects. Since the effect of
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33 393 group size on grooming networks could be more pronounced among free-living groups
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35 394 (Griffin & Nunn, 2012; Sueur et al., 2011b), we also examined a potential interaction
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37 395 between group size and living condition. Species was set as a random effect to avoid
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39 396 pseudoreplication issues. We next used the *arm* package in R to z standardize ($\mu = 0$, $SD =$
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41 397 1) the predictors in the global model, which is essential for interpreting parameter estimates
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43 398 after model averaging (Gelman et al., 2009). We then used the automated 'dredge' function
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45 399 in the *MuMIn* R package to generate a 'complete' set of 80 models from multiple possible
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47 400 combinations of predictors from the global models (Grueber et al., 2011) (Supplementary
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49 401 Tables 4-6). This included a 'null' or an intercept-only model with just species as a random
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3 402 effect for the sake of comparison. From each full model set, we identified candidate models
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5 403 that included only models whose difference in AICc scores were < 4 from the model with
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8 404 the lowest AICc score (Burnham et al., 2011) (models in bold font in Supplementary Tables
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11 405 4-6). We confirmed that model diagnostics criteria were met for each candidate model, and
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13 406 ruled out multicollinearity issues for models with multiple predictors ($r < 0.8$ for all pairs of
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15 407 predictors; GVIF < 4 for each: the *car* package in R: Fox & Weisberg, 2011). We then
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17 408 determined parameter estimates by model-averaging each set of candidate models using the
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19 409 zero-averaging approach (Burnham & Anderson, 2002; Grueber et al., 2011). Since this
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21 410 approach weakens the effect sizes of predictors that only appear in a minority of models, it
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23 411 is more useful (than the natural averaging method) in cases where the aim is to determine
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25 412 which (among multiple) factors have the strongest effect on a response variable (Grueber et
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27 413 al., 2011; Nakagawa & Freckleton, 2010). For all parameter interpretations, we set the
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29 414 alpha level at 0.05.
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33 34 415 **Results:**

35 36 416 *(Q1) Tests for phylogenetic signals:*

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38 417 Mean species-level scores of both dominance network traits -- transitivity and
39
40 418 dominance certainty -- showed moderate phylogenetic signals (Table 3). When we repeated
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42 419 the analyses including only free-living groups (27 datasets across 7 species), the results
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44 420 showed a strong phylogenetic signal for dominance traits (K statistics $\gg 1$: Table 3). In
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46 421 comparison, grooming traits -- especially eigenvector and clustering coefficient -- showed
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48 422 weak phylogenetic signals (Table 3). Although Newman's modularity showed a moderate
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50 423 signal as indicated by the K statistic, randomization tests neither reached significance nor
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52 424 showed a non-significant trend for this trait (Table 3). Given the relatively small number of
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3 425 species, our tests of phylogenetic signals lacked power (~ 20-35%). Yet, results from the
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5 426 randomization significance tests were mostly consistent with our estimations of the strength
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7 427 of the signals from the K statistic (Table 3). Moreover, they were also robust to
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9 428 phylogenetic branch length variation, with results from the consensus phylogeny being
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11 429 largely consistent with those across 10 phylogenetic trees extracted from the *10KTrees*
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13 430 website (Supplementary Table 3).

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15 431 *(Q2-4) The effect of dominance traits, social style, and sociodemographic factors on*
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17 432 *grooming traits:*

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20 433 Table 4 shows the model-averaged coefficients and parameter estimates from
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22 434 candidate GLMM sets shortlisted using our dAICc criterion, from the complete model sets
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24 435 for grooming Newman's modularity and clustering coefficient. Our criterion shortlisted 8
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26 436 models for modularity, and 7 for clustering coefficient. Neither candidate model set
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28 437 included the 'random effect only' model, which had a dAICc > 12 from the candidate sets
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30 438 (Supplementary Table 6, 7). Model averaged coefficients revealed that group size strongly
31
32 439 influenced modularity and clustering coefficient in predicted directions. Larger groups
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34 440 showed more modular, but less dense clusters or redundant ties than smaller groups, which
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36 441 showed the opposite characteristics (Table 4; Figure 2). Further, group size was both
37
38 442 present, and the most important predictor in all candidate models for both modularity and
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40 443 clustering coefficient (Table 4). We also detected a significant effect of living condition,
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42 444 with captive groups showing less modular networks and greater density/ redundancy of
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44 445 cluster ties than free-living groups (Table 4; Figure 2). However, there was no interaction
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46 446 between group size and living condition (Table 4), suggesting that the effect of group size
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48 447 were independent of living condition. Sex ratio also showed no effect. Finally, neither
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3 448 dominance traits nor social style grade strongly influenced these grooming network traits in
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5 449 predicted directions (Table 4). In fact, social style did not make the candidate models for
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8 450 modularity.
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10 451 In contrast to Newman's modularity and clustering coefficient, candidate model
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12 452 selection for grooming eigenvector centrality coefficient failed to eliminate the 'random
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14 453 effect only' model (Supplementary Table 5). Zero-based model averaging revealed that
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17 454 none of the predictors had a strong effect on these indices (Supplementary Table 8).
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20 455 Finally, replications of our GLMMs using network measures computed from
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22 456 permuted datasets revealed that our findings, particularly for group size, were highly
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24 457 consistent across varying degrees of sampling effort. As per findings from the complete
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27 458 data, group size showed positive associations with modularity, and negative associations
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29 459 with clustering coefficient for all degrees of sampling effort (e.g. at 60% and 20% effort:
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31 460 Supplementary Tables 9, 10). On the other hand, the effect of living condition on grooming
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33 461 clustering coefficient weakened at lower sampling effort (Supplementary Tables 9, 10).
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35 462 **Discussion:**

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38 463 In group-living animals, the evolutionary origins of variation in aspects of social
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40 464 structure remain much debated. Here we used a social network approach to examine the
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42 465 impact of phylogenetic relatedness, specifically phylogenetic signals and trait covariation,
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44 466 as well as sociodemographic factors like group size and living condition on interspecific
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47 467 variation in higher-order aspects of dominance and grooming social structure across
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49 468 macaques. We found that while dominance social network traits showed strong
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51 469 phylogenetic signals, grooming network traits showed weak signals and were not strongly
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53 470 covariant with social style or with dominance traits. Rather, two aspects of grooming
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3 471 network structure – modularity and clustering coefficient – were strongly influenced by
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5 472 group size independently of current living condition. Below we discuss our findings in
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7 473 depth, and offer avenues for future comparative assessments of primate social network
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9 474 structure.

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12 475 Previous studies among macaques have established strong phylogenetic signals in
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14 476 some aspects of social structure (e.g. dominance steepness and counter-aggression:
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16 477 Balasubramaniam et al., 2012a), but moderate-to-weak signals in others (e.g. kin-bias:
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18 478 Thierry et al., 2008). Consistent with this pattern, we found moderate to strong
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20 479 phylogenetic signals for aspects of female dominance network traits, but moderate or weak
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22 480 signals for grooming networks. Specifically, both transitivity and dominance certainty
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24 481 exhibited degrees of signal that are close in strength to what is expected under a Brownian
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26 482 motion model of evolution (Blomberg et al., 2003). In other words, the covariance between
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28 483 dominance trait values of adjacent taxa strongly proportional to their shared evolutionary
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30 484 histories indicated by their phylogenetic branch length distances (Kamilar & Cooper,
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32 485 2015). This finding extends earlier findings of strong phylogenetic signals on group-level
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34 486 aspects of dominance structure that were based on dyadic interactions (e.g., hierarchical
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36 487 steepness, counter-aggression: Balasubramaniam et al., 2012a) to broader patterns of triadic
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38 488 motifs (transitivity) and network-wide flow patterns (dominance certainty). It also extends
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40 489 it to indirect connections that reflect the higher-order structure of the flow of dominance
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42 490 information through pathways that connect both interacting and non-interacting individuals
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44 491 (dominance certainty: Fujii et al., 2013; Fushing et al., 2011). Phylogenetic signals were
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46 492 even stronger when we analyzed only free-living groups of macaques, despite a reduction
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48 493 in sample size from 10 to 7 species (Blomberg et al., 2003). This may be due to the
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3 494 differences in living conditions between groups of closely related species. In captivity,
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5 495 spatial constraints and/or management strategies may force animals to interact that might
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7 496 otherwise avoid one another after one or two decided outcomes (Duboscq et al., 2013;
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9 497 McCowan et al., 2008). This may result in greater than expected degrees of reversals in
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11 498 agonistic success and hence, greater uncertainty in dominance relationships. Unfortunately,
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13 499 limited datasets prevented an analysis of phylogenetic signals among captive groups alone
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15 500 (11 out of 38 datasets: 5 species). Nevertheless, the detection of strong phylogenetic signals
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17 501 among free-living macaques (27 out of 38 datasets: 7 species) builds on previous studies
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19 502 that have either included both captive and free living groups (Balasubramaniam et al.,
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21 503 2012a) or only captive groups (Thierry et al., 2008). Since previous comparative studies
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23 504 across primates have shown a general lack of correspondence between phylogeny and
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25 505 socioecology (Koenig et al., 2013; Ménard, 2004; Okamoto & Matsumura, 2002), it is
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27 506 unlikely that the observed phylogenetic signals in dominance traits are ‘artifacts’ of
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29 507 correlations between phylogeny and current socioecological factors. Further, the signals
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31 508 were detected despite the fact that a fraction of the free-living groups in our dataset were
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33 509 exposed to food provisioning by humans (Table 1), although predation pressure, another
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35 510 socioecological factor (van Schaik, 1989), was anecdotally either uniformly low or absent
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37 511 across the study populations. Taken together, our findings suggest that phylogeny predicts a
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39 512 major component of the interspecific variance in dominance structure among free-living
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41 513 macaques. Nevertheless, these findings do not entirely rule out an adaptive component. For
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43 514 instance, the concept of social reaction norms proposes that aspects of social structure may
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45 515 change dynamically by responding to socioecological and environmental factors, but within
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47 516 the limits posed by a species- or phylogenetic lineage-typical range of responses that may
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3 517 in turn be linked to phylogenetic closeness (Berman & Thierry, 2010). Moreover,
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5 518 phylogenetic signals, rather than being linked to ancestral genetic splits, may be outcomes
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8 519 of adaptations by ancestral species dispersing into historically similar environments
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10 520 (Kamilar & Cooper, 2015). We suggest that future assessments of the bases of phylogenetic
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12 521 signals in social network traits focus on phylogeographic approaches (Lemey et al., 2009;
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14 522 Ree & Smith, 2008). Specifically, a comparison of the reconstructed social networks and
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16 523 geographic ranges of ancestral primate taxa may provide better insights into whether
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18 524 phylogenetic signals in primate social networks are indeed ‘artifacts’ of adaptive responses
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20 525 in their evolutionary past.
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24 526 In comparison to dominance traits, grooming networks, particularly eigenvector and
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26 527 clustering coefficients, showed moderate (modularity) or weak (eigenvector and clustering
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28 528 coefficient) phylogenetic signals. Further, grooming traits did not covary with dominance
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30 529 traits in the directions predicted. A possible explanation is that covariation between social
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32 530 network traits is not always linear (but see Thierry et al.’s (2008) findings on covariation
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34 531 between traits associated with conciliatory tendencies across macaques). Further, it may be
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36 532 discernible at levels of organization other than species, for instance, across phylogenetic
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38 533 lineages (Thierry, 2000). Yet the lack of a strong effect of species-typical social style on
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40 534 grooming networks may be seen as evidence to refute this argument given that social style
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42 535 and phylogeny are correlated (Thierry et al., 2000). A more likely explanation is that
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44 536 grooming traits may come under the additional influence of current socioecological and/or
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46 537 sociodemographic factors.
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53 538 Among all the primate genera, macaques are presently unique in the extent to which
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55 539 interspecific variation in social traits is consistent with phylogeny, and covariant with social
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3 540 style (Balasubramaniam et al., 2012a; Sueur et al., 2011b; Thierry et al., 2008; Thierry et
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5 541 al., 2000). Yet we found that group size had a stronger influence on grooming modularity
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7 542 and clustering coefficient than either dominance traits or social styles. Specifically, larger
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9 543 groups of macaques showed more modular grooming networks, as well as less density/
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11 544 redundancy in connections among localized, triadic clusters.
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15 545 It is conceivable that the effect of group size on grooming traits may have been an
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17 546 artifact of intergroup differences in (1) living condition (McCowan et al., 2008; Duboscq et
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19 547 al., 2013) and/or (2) chance interactions (Griffin & Nunn, 2012; Nunn et al., 2015). In our
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21 548 dataset, for instance, captive groups were both significantly smaller (see Methods) and, as
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23 549 expected due to spatial constraints, showed less modular grooming networks with more
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25 550 densely connected clusters (see Results) than free-living groups. Yet we found no effect of
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27 551 an interaction between group size and living condition on grooming traits, suggesting that
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29 552 the effect of group size on grooming traits was independent of the effect of living condition.
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31 553 Moreover, the permuted datasets revealed that both the grooming traits themselves, and the
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33 554 strong relationships between group size and grooming traits, were robust to variation in
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35 555 sampling effort. Together, these findings suggest that the effect of group size on grooming
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37 556 traits, rather than being artefactual, may more likely have socioecological underpinnings.
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39 557 Specifically, one school of thought is that living in larger groups may heighten levels of
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41 558 within-group contest competition (or WGC) for resources (Koenig et al., 2013; Sterck et
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43 559 al., 1997; van Schaik, 1989). This may lead to despotic, nepotistic primate societies
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45 560 characterized by both steep and transitive dominance structure (Majolo et al., 2009), and
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47 561 more modular, sparsely connected grooming community structures (the social bottleneck
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49 562 hypothesis: Griffin & Nunn, 2012). In comparison, smaller groups may show weaker WGC
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3 563 and the opposite characteristics that are indicative of greater social tolerance. An alternative
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5 564 perspective is that individuals in large groups may face spatial or time constraints on their
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8 565 abilities to interact consistently with all other group members (Berman & Thierry, 2010;
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10 566 Dunbar, 1992; Korstjens et al., 2010; Puga & Sueur, 2017). This may in turn result in
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12 567 modular or clustered but sparser social networks in larger groups, in which individuals may
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15 568 come into contact with each other less frequently (Griffin & Nunn, 2012). Given the lack of
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17 569 a clear association between group size and dominance networks in our dataset (e.g. Group
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19 570 size vs. dominance certainty: $n = 38$, $r = 0.02$, $p = 0.88$), our findings point to a
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21 571 spatiotemporal rather than a resource-competition based explanation. Yet final conclusions
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23 572 await the expansion of our dataset to include additional groups and species, and comparable
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25 573 operational measures of resource distribution (see below).
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29 574 Unlike grooming modularity and clustering coefficient, grooming centrality
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31 575 coefficient was not influenced by dominance traits, social style, or sociodemographic
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33 576 factors. One reason for this lack of concordance could be due to the way this index was
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35 577 computed. For instance, the exclusion of males from our grooming networks, unlike in
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37 578 Sueur et al.'s (2011b) study, may have masked skew in grooming centrality towards
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39 579 dominants. In despotic macaques, high-ranking males may be among the most attractive
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41 580 grooming partners for females who may gain benefits such as access to social support
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43 581 and/or resources (Schino, 2001; Silk et al., 2003; Sueur et al., 2011b). It is possible that
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45 582 female dominance status could be related to centralization in the grooming network that is
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47 583 based on *specific types* of grooming connections rather than their overall connectedness.
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49 584 These could be grooming connections with non-kin, grooming that is directed up the
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51 585 hierarchy in exchange for access to rank-related benefits such as resource tolerance and
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3 586 support in conflicts, and/or grooming that is reciprocated in the short or long-term
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5 587 (reviewed in Henzi & Barrett, 1999). Should comparative data be available, such
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7
8 588 assessments may generate centralization indices that better reflect female social structure.
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10 589 Alternatively, it is conceivable that intergroup variation in centrality coefficients
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12 590 may be influenced by additional socioecological variables (Griffin & Nunn, 2012; Sterck et
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14 591 al., 1997), and/or intraspecific variation (Borgeaud et al., 2016; Romano et al., 2016).
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16
17 592 Yet assessments of the socioecological bases of variation in sociality have proved to be
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19 593 complicated. For instance, we currently lack a consistent operational measure of resource
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21 594 abundance and distribution that may be used in comparative contexts across a wide range of
22
23 595 taxa (Clutton-Brock & Janson, 2012). Another challenge is assessing the effects of
24
25 596 infectious disease risk on social networks. For instance, increased parasite infection risk
26
27 597 may lead to the evolution of more modular networks because individuals engage fewer
28
29 598 social partners (Griffin & Nunn, 2012; Nunn et al., 2015). At the same time, possessing
30
31 599 more partners can also reduce infection risk via socially buffering individuals against
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33 600 susceptibility to infectious agents (Balasubramaniam et al., 2016; Duboscq et al., 2016;
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35 601 Young et al., 2014). Third, the spatial distribution of females may also influence male
36
37 602 reproductive tactics, i.e. the extent to which males show reproductive skew by
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39 603 monopolizing mating opportunities which may in turn influence female social networks
40
41 604 (Schülke & Ostner, 2008, 2013). More definitive conclusions await the ability to draw
42
43 605 interspecies links between reproductive skew and female social networks, and indeed male-
44
45 606 male social relationships. Finally, in comparison to interspecific variation, few comparative
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47 607 studies have assessed the evolutionary origins of inter-individual or intergroup variation
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49 608 (Clutton-Brock & Janson, 2012). In addition to impacting group-level outcomes, selection
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3 609 pressures may act on the spatial orientation, behavioral strategies, and personalities of
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5 610 individuals, any or all of which may in turn affect social networks (Borgeaud et al., 2016;
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8 611 Capitanio, 1999; Krause et al., 2010; Lusseau & Newman, 2004; Puga & Sueur, 2017; Sih
9
10 612 et al., 2004). Although beyond the scope of this study, adopting similar comparative,
11
12 613 evolutionary approaches to assess the influence of intraspecific variation in spatial and
13
14 614 social strategies on social network structure may be a logical next step.
15
16

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900 Table 1: Macaque datasets analyzed in the study

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

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3	<i>thibetana</i>	2	Mt. Huangshan, China	Balasubramaniam et al. (2011)	42	9	47	Free-living ^d
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5	<i>thibetana</i>	2	Mt. Huangshan, China	Balasubramaniam et al. (2011)	42	9	38	Free-living ^d
6								
7	<i>thibetana</i>	2	Mt. Huangshan, China	Balasubramaniam et al. (2011)	52	10	11	Free-living ^d
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9	<i>thibetana</i>	2	Mt. Huangshan, China	Balasubramaniam et al. (2011)	49	10	12	Free-living ^d
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11	<i>thibetana</i>	2	Mt. Huangshan, China	Balasubramaniam et al. (2011)	37	10	20	Free-living ^d
12								
13	<i>arctoides</i> ^a	3	Yerkes Primate Center, USA	de Waal & Luttrell (1989)	14	12	225 (NA)	Captive
14								
15	<i>radiata</i>	3	Mysore, India	Cooper et al. (2007)	41-49	13	-	Free-living ^d
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17	<i>sylvanus</i>	3	Middle Atlas Mountains, Morocco	McFarland & Majolo (2011)	19	8	32	Free-living
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19	<i>sylvanus</i>	3	Middle Atlas Mountains, Morocco	McFarland & Majolo (2011)	29	10	10	Free-living
20								
21	<i>sylvanus</i>	3	Middle Atlas Mountains, Morocco	Molesti & Majolo (2013)	18	7	-(12)	Free-living
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23	<i>sylvanus</i>	3	Rocamadour, France	Sosa (2014)	55	24	14	Free-living ^d
24								
25	<i>sylvanus</i>	3	Rocamadour, France	Sosa (2014)	55	24	8	Free-living ^d
26								
27	<i>sylvanus</i>	3	Rocamadour, France	Sosa (2014)	55	24	12	Free-living ^d
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29	<i>nigra</i>	4	Tangkoko Reserve, Indonesia	Duboscq et al. (2013)	50	18	24	Free-living
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31	<i>nigra</i>	4	Tangkoko Reserve, Indonesia	Duboscq et al. (2013)	80	21	45	Free-living
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33	<i>nigra</i>	4	Tangkoko Reserve, Indonesia	Duboscq et al. (2013)	80	21	43	Free-living
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35	<i>nigra</i>	4	Tangkoko Reserve, Indonesia	Duboscq et al. (2013)	80	24	22	Free-living
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37	<i>tonkeana</i>	4	Primate Center, Strasbourg, France	Thierry (1985); Demaria & Thierry (2001)	16	9	104 (8)	Captive
38								
39	<i>tonkeana</i>	4	Orangerie Zoo, Strasbourg, France	De Marco et al. (2010)	21	7	110 (5)	Captive
40								
41	<i>tonkeana</i>	4	Primate Center, Strasbourg, France	Thierry (1985); Demaria & Thierry (2001)	29	11	87 (6)	Captive
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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**

<u>Trait</u>	<u>Description</u>	<u>Data Source</u>	<u>Code Source</u>
Dominance			
Triangle transitivity	A transitive triangle is 3 individuals connected in the following manner: <i>a</i> wins its encounters with <i>b</i> , <i>b</i> with <i>c</i> , and <i>a</i> with <i>c</i> (Snijders, 2012). Group-level triangle transitivity is number of such “triangles” divided by all possible triangles within a group	Aggression network matrix	<i>Perc</i> R package (Fujii et al. 2015)
Dominance certainty	Based on a tally of all directed network paths between <i>a</i> and <i>b</i> , dyadic dominance certainty is the degree of consistency in direction of all dominance paths. It reflects the probability that <i>a</i> will win against <i>b</i> . Group-level dominance certainty is the mean of the row-wise averages of just the win-probabilities for each individual	Aggression network matrix	<i>Perc</i> 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	<i>Statnet</i> 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	<i>Igraph</i> 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 <i>potential</i> triplets.	Groom network string	<i>Igraph</i> R package (Csardi & Nepusz, 2006)

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3 917 **Table 3: Results of tests for phylogenetic signals among macaque dominance and**
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6 918 **grooming social network traits. K: Blomberg's Kappa coefficient; P: significance from**
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8 919 **Randomization tests (Blomberg et al. 2003)**
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<u>Behavioral Metric</u>	<u>All Datasets (10 species)</u>		<u>Free-living Groups (7 species)</u>	
	K	P	K	P
	<u>Dominance Metrics</u>			
Transitivity	0.892	0.081(*)	1.704	0.022*
Dominance Certainty	0.893	0.078(*)	1.634	0.023*
	<u>Grooming Network Metrics</u>			
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

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Bold font: K values (> 1) indicate strong phylogenetic signals

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* P < 0.05; (*) 0.05 < P < 0.1

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Phylogenetic tree used was the Bayesian MCMC consensus tree from the 10krees website (Arnold et al. 2010)

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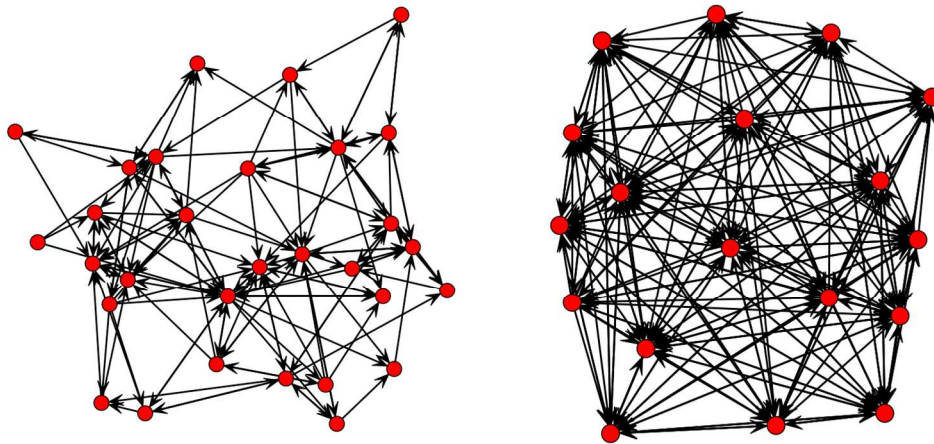
927 **Table 4: Summary of zero-averaged coefficients from the candidate models for**
 928 **Newman's modularity and clustering coefficient of grooming networks.**

<u>(A) Newman's Modularity (8 candidate models)</u>					
	<u>B</u>	<u>Adj SE</u>	<u>z</u>	<u>Pr (> z)</u>	<u>Importance</u>
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
<u>(B) Clustering Coefficient (7 candidate models)</u>					
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 ≤ 0.05 ** p < 0.01



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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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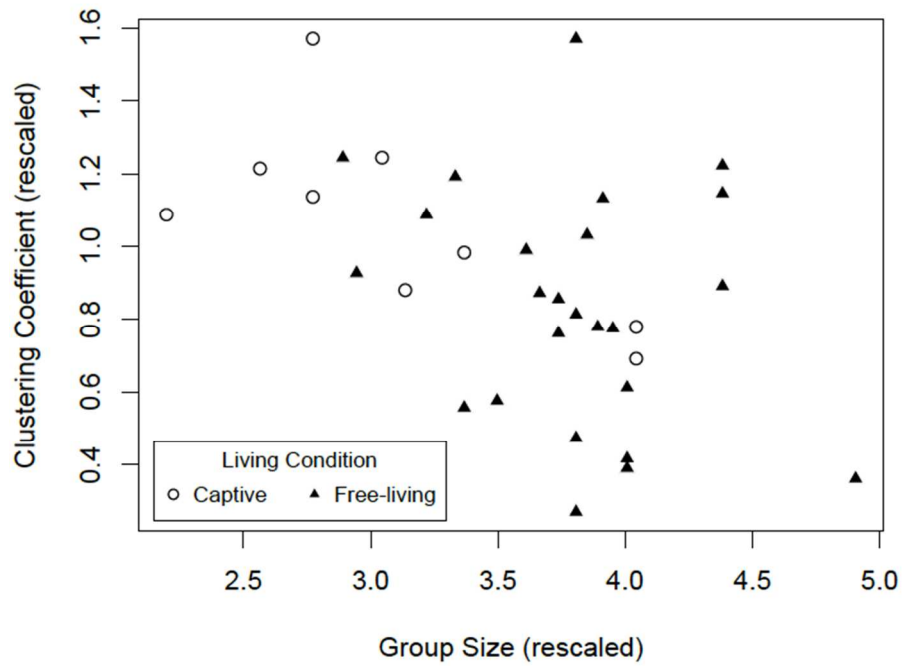
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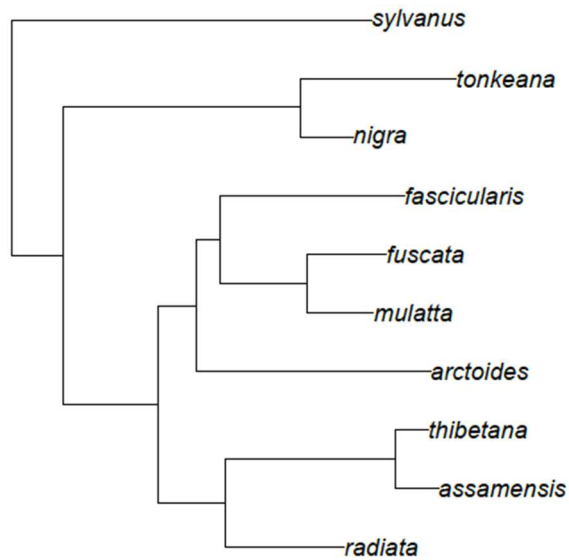
1012 Figure 2: Influence of group size on grooming clustering coefficient across 34 datasets of
 1013 captive and free-living macaque groups representing 9 species

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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

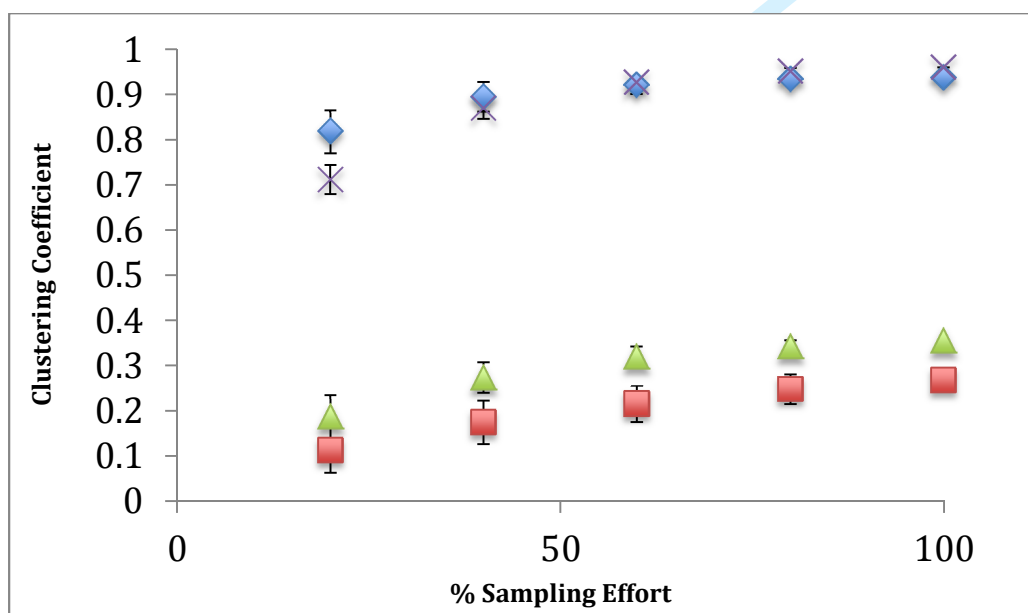
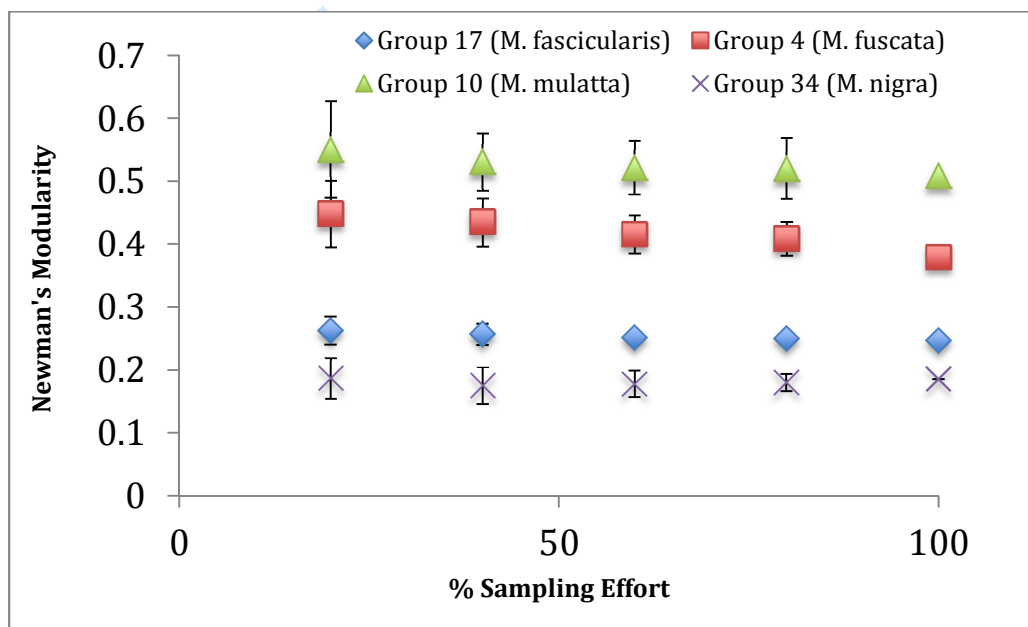
For Peer Review

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



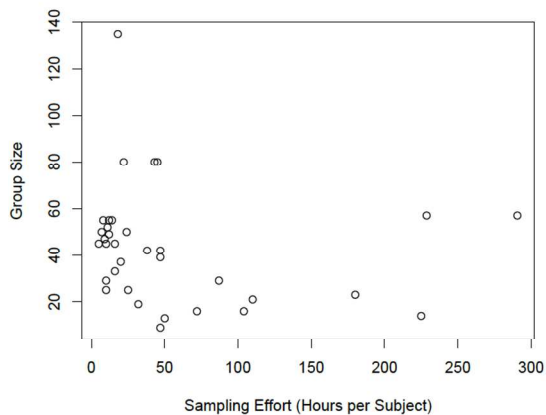
Review

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)

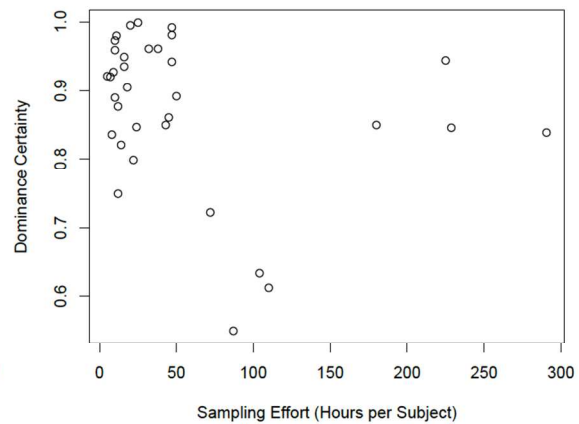


Supplementary Figure 3: Scatterplots between sampling effort and (A) group size, (B) dominance certainty, and (C) grooming Newman's modularity across the datasets. Datasets that used *Ad libitum* sampling (B: 3/38; C: 2/34), and/or were outliers (B: 1/38 dataset sampled for 675 hours per subject; C: 2/34 datasets sampled for 224 and 280 hours per subject respectively) have been omitted

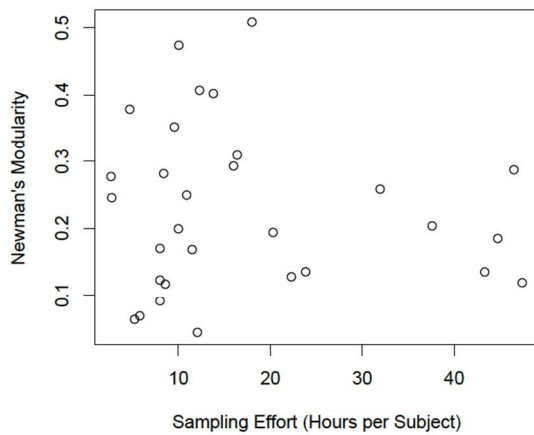
(A)



(B)



(C)



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

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

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

<i>Sampling Effort vs. Dominance Network Measures</i>				
		<u>N¹</u>	<u>Pearson's R</u>	<u>p (p_{crit} = 0.02)</u>
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
<i>Sampling Effort vs. Grooming Network Measures</i>				
		<u>N¹</u>	<u>Pearson's R</u>	<u>p (p_{crit} = 0.01)</u>
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

¹Datasets 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)

<u>Behavioral Metric</u>	<u>All Datasets (10 species)</u>		<u>Free-living Groups (7 species)</u>	
	K (m±sd)	P (m)	K (m±sd)	P (m)
<u>Dominance Metrics</u>				
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*
<u>Grooming Network Metrics</u>				
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.

<u>Model</u>	<u>(Int)</u>	<u>B Coefficients</u>							<u>df</u>	<u>AICc</u>	<u>Δ</u>	<u>w</u>
		LC	SS	DC	SR	GS	T	GS: LC				
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

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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

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

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4	31	0.31	0.17	+					7	-61.00	11.34	0	
5	32	0.30	0.18	+	-0.06	0.07	0.09	0.00	11	-60.90	11.48	0	
6	33	0.30	0.18	+	-0.05		0.07	0.04	10	-60.60	11.81	0	
7	34	0.32	0.23	+	-0.10	0.03			9	-60.30	12.08	0	
8	35	0.31	0.17	+	-0.06		0.07	0.01	10	-60.20	12.17	0	
9	36	0.19			0.07		0.11		5	-60.20	12.21	0	
10	37	0.19					0.12		4	-59.80	12.57	0	
11	38	0.19	0.21		-0.05	0.01			6	-59.30	13.05	0	
12	39	0.19	0.20		-0.05			0.00	6	-59.30	13.09	0	
13	40	0.29	0.15	+			0.07	-0.01	0.04	10	-58.70	13.68	0
14	41	0.32	0.22	+	-0.11			0.02	9	-58.60	13.79	0	
15	42	0.19			0.07	0.05	0.13		6	-58.40	13.99	0	
16	43	0.19	0.18			0.00		-0.01	6	-58.30	14.02	0	
17	44	0.29	0.15	+		0.07	0.10	-0.01	0.01	11	-57.90	14.50	0
18	45	0.19				0.05	0.13		5	-57.90	14.51	0	
19	46	0.31	0.18	+				-0.01	8	-57.80	14.55	0	
20	47	0.19					0.11	0.02	5	-57.70	14.63	0	
21	48	0.32	0.17	+		0.01			8	-57.70	14.71	0	
22	49	0.27		+			0.11		7	-57.60	14.78	0	
23	50	0.19			0.08		0.11	-0.01	6	-57.20	15.19	0	
24	51	0.33	0.23	+	-0.12	0.03		0.02	10	-56.40	15.92	0	
25	52	0.30	0.18	+	-0.06		0.07	0.01	0.04	11	-56.30	16.10	0
26	53	0.30	0.19	+	-0.08	0.07	0.09	0.01	0.00	12	-56.20	16.13	0
27	54	0.19	0.21		-0.06	0.01		0.00	7	-56.00	16.33	0	
28	55	0.19				0.05	0.13	0.03	6	-55.70	16.66	0	
29	56	0.19			0.08	0.05	0.13	-0.01	7	-55.10	17.23	0	
30	57	0.31	0.18	+		0.02		-0.01	9	-54.20	18.15	0	
31	58	0.27		+			0.11	0.02	8	-54.10	18.27	0	
32	59	0.27		+	0.06		0.11		8	-53.40	19.00	0	
33	60	0.27		+		0.04	0.13		8	-53.30	19.05	0	
34	61	0.27		+	0.08	0.06	0.13		9	-49.90	22.50	0	
35	62	0.27		+		0.04	0.12	0.02	9	-49.70	22.65	0	
36	63	0.27		+	0.06		0.11	0.00	9	-49.50	22.82	0	
37	64 [^]	0.19							3	-49.20	23.12	0	
38	65	0.19			0.07				4	-49.00	23.33	0	
39	66	0.19				-0.05			4	-47.70	24.7	0	
40	67	0.19						0.03	4	-47.30	25.03	0	
41	68	0.19			0.07	-0.04			5	-47.10	25.25	0	
42	69	0.29		+					6	-47.10	25.29	0	
43	70	0.19			0.08			0.00	5	-46.20	26.12	0	
44	71	0.29		+		-0.05			7	-46.20	26.2	0	
45	72	0.27		+	0.08	0.06	0.13	0.00	10	-45.70	26.7	0	
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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

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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.

Mod	(Int)	B Coefficients							df	AICc	Δ	w
el		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

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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

For Peer Review

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

<u>(A) Newman's Modularity (8 candidate models)</u>					
	<u>B</u>	<u>Adj SE</u>	<u>z</u>	<u>Pr (> z)</u>	<u>Importance</u>
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
<u>(B) Clustering Coefficient (7 candidate models)</u>					
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

<u>(A) Newman's Modularity (8 candidate models)</u>					
	<u>B</u>	<u>Adj SE</u>	<u>z</u>	<u>Pr (> z)</u>	<u>Importance</u>
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
<u>(B) Clustering Coefficient (7 candidate models)</u>					
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

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