



**HAL**  
open science

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

Krishna Balasubramaniam, Brianne Beisner, Carol Berman, Arianna de Marco, Julie Duboscq, Sabina Koirala, Bonaventura Majolo, Andrew Macintosh, Richard Mcfarland, Sandra Molesti, et al.

### ► To cite this version:

Krishna Balasubramaniam, Brianne Beisner, Carol Berman, Arianna de Marco, Julie Duboscq, et al.. The influence of phylogeny, social style, and sociodemographic factors on macaque social network structure. *American Journal of Primatology*, 2018, Special Section on Chimpanzee Health and Conservation in the Anthropocene, 80 (1), pp.e22727. 10.1002/ajp.22727 . hal-01715327

**HAL Id: hal-01715327**

**<https://hal.science/hal-01715327>**

Submitted on 30 Jul 2020

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



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

Journal:	<i>American Journal of Primatology</i>
Manuscript ID	AJP-17-0061.R2
Wiley - Manuscript type:	Research Article
Date Submitted by the Author:	n/a
Complete List of Authors:	<p>Balasubramaniam, Krishna; University of California Davis School of Veterinary Medicine          Beisner, Brianne; University of California Davis School of Veterinary Medicine, Population Health and Reproduction; California National Primate Research Center          Berman, Carol; University at Buffalo - The State University of New York, Anthropology; University at Buffalo - The State University of New York, Evolution Ecology and Behavior          De Marco, Arianna; Fondazione Ethokios          Duboscq, Julie; Kyoto Daigaku Reichorui Kenkyujo; Kyoto University Wildlife Research Center          Koirala, Sabina; Small Mammal Conservation and Research Foundation (SMCRF)          Majolo, Bonaventura; University of Lincoln, School of Psychology          MacIntosh, Andrew; Kyoto University Primate Research Institute, Ecology and Social Behavior; Kyoto University Wildlife Research Center          McFarland, Richard; University of Wisconsin-Madison, Anthropology          Molesti, Sandra; Universite Toulouse Jean Jaures          Ogawa, Hideshi; Chukyo University, School of International Liberal Studies          Petit, Odile; Ethologie Cognitive et Sociale, Centre National de la Recherche Scientifique          Schino, Gabriele; Istituto di Scienze e Tecnologie della Cognizione, Consiglio Nazionale delle Ricerche          SOSA, Sebastian; Sun-Yat sen University          Sueur, Cédric; Universite de Strasbourg, Centre National de la Recherche Scientifique          Thierry, Bernard; Université de Strasbourg, Centre National de la Recherche Scientifique          de Waal, Frans; Emory University, Psychology          McCowan, Brenda; University of California Davis School of Veterinary Medicine, Population Health and Reproduction; California National Primate Research Center</p>
Keywords:	Social networks, Phylogenetic signals, Social style, Group size, Macaques

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

SCHOLARONE™  
Manuscripts

For Peer Review

1  
2  
3 1 The influence of phylogeny, social style, and sociodemographic factors on macaque social  
4  
5 2 network structure  
6  
7

8 3 Balasubramaniam, K. N.<sup>a</sup>, Beisner, B. A.<sup>a,b</sup>, Berman, C. M.<sup>c</sup>, De Marco, A.<sup>d</sup>, Duboscq, J.<sup>e, f</sup>,  
9  
10 4 Koirala, S.<sup>g</sup>, Majolo, B.<sup>h</sup>, MacIntosh, A. J. J.<sup>e, f</sup>, McFarland, R.<sup>i</sup>, Molesti, S.<sup>j</sup>, Ogawa, H.<sup>k</sup>,  
11  
12 5 Petit, O.<sup>l</sup>, Schino, G.<sup>m</sup>, Sosa, S.<sup>n</sup>, Sueur, C.<sup>o</sup>, Thierry, B.<sup>o</sup>, de Waal, F. B. M.<sup>p</sup> & McCowan,  
13  
14 6 B.<sup>a, b</sup>.  
15  
16

17  
18 <sup>a</sup>Department of Population Health & Reproduction, School of Veterinary Medicine, UC  
19 Davis, Davis, CA, USA; <sup>b</sup>California National Primate Research Center, University of  
20 California Davis, Davis, CA, USA; <sup>c</sup>Department of Anthropology, Graduate Program in  
21 Evolution, Ecology and Behavior, University at Buffalo, Buffalo, NY, USA; <sup>d</sup>Fondazione  
22 Ethokios, Radicondoli, Italy; <sup>e</sup>Wildlife Research Center, Kyoto University, Inuyama,  
23 Japan; <sup>f</sup>Primate Research Institute, Kyoto University, Inuyama, Japan; <sup>g</sup>Small Mammal  
24 Conservation and Research Foundation (SMCRF), Kathamandu, Nepal; <sup>h</sup>School of  
25 Psychology, University of Lincoln, Lincoln, UK; <sup>i</sup>Department of Anthropology, University  
26 of Wisconsin-Madison, 1180 Observatory Drive, Madison, WI, USA; <sup>j</sup>Université Toulouse  
27 Jean Jaurès, Toulouse, France <sup>k</sup>School of International Liberal Studies, Chukyo University,  
28 Toyota, Japan; <sup>l</sup>Ethologie Cognitive et Sociale, Centre National de la Recherche  
29 Scientifique, Strasbourg, France; <sup>m</sup>Istituto di Scienze e Tecnologie della Cognizione,  
30 Consiglio Nazionale delle Ricerche, Rome, Italy; <sup>n</sup>Anthropology Department, Sun-Yat sen  
31 University, Guang Zhou, China; <sup>o</sup>Centre National de la Recherche Scientifique, Université  
32 de Strasbourg, Institut Pluridisciplinaire Hubert Curien, Strasbourg, France; <sup>p</sup>Psychology  
33 Department, Emory University, Atlanta, GA, USA  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

24  
25 Short title: Phylogeny, sociodemography, and networks

26 Corresponding author:

27 Dr. Krishna N. Balasubramaniam

28 Department of Population Health & Reproduction, School of Veterinary Medicine

29 University of California at Davis, Davis CA 95616 USA

30 E-mail: [krishnanatarajan@ucdavis.edu](mailto:krishnanatarajan@ucdavis.edu)

31 Phone: 513-417-4538

**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

1  
2  
3 55 phylogenetically conserved across macaque species than grooming networks, which were  
4  
5 56 more labile to sociodemographic factors. Such findings narrow down the processes that  
6  
7 57 influence interspecific variation in two core aspects of macaque social structure. Future  
8  
9 58 directions should include using phylogeographic approaches, and addressing challenges in  
10  
11 59 examining the effects of socioecological factors on primate social structure.  
12  
13  
14

15 **Key words:**

16  
17  
18 61 Social networks, phylogenetic signals, social style, group size, macaques  
19

20 **Introduction:**

21  
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.  
25  
26 65 competitive, affiliative, cooperative) and relationships among group members (Hinde,  
27  
28 66 1976; Kappeler & Van Schaik, 2002). Several factors have been found to govern social  
29  
30 67 structure, including but not restricted to kinship, age similarity, sex and dominance status  
31  
32 68 (Hinde, 1976; Kappeler & Van Schaik, 2002). However, our understanding of the  
33  
34 69 evolutionary and ecological factors that produce diverse social structures remains limited.  
35  
36 70 Specifically, the extent to which such social structure has been influenced by species'  
37  
38 71 ancestral relationships versus variation in current conditions remains debated (Clutton-  
39  
40 72 Brock & Janson, 2012; Kasper & Voelkl, 2009; Koenig et al., 2013; Thierry, 2004). Here,  
41  
42 73 we use Social Network Analysis to assess whether variation in aspects of social structure  
43  
44 74 across multiple species of macaques (genus: *Macaca*) is related to species' phylogenetic  
45  
46 75 relatedness (Blomberg et al., 2003; Thierry, 2004), and hypothesized tendencies for social  
47  
48 76 traits to co-evolve with each other in suites or packages (de Waal & Luttrell, 1989; Thierry,  
49  
50 77 2007). We also investigate the extent to which such covariation may be influenced by  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 78 group-specific sociodemographic characteristics (Kasper & Voelkl, 2009; Sterck et al.,  
4  
5 79 1997; Sueur et al., 2011b)  
6  
7

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).  
11  
12 82 According to this framework, aspects of sociality are expected to show phylogenetic  
13  
14 83 signals, i.e. to exhibit greater similarity in social structure among more closely-related than  
15  
16 84 distantly-related species (Blomberg et al., 2003). Ecological adaptation is not ruled out but  
17  
18 85 rather hypothesized to occur minimally, or in response to novel, drastic environmental  
19  
20 86 changes (Blomberg et al., 2003; Chan, 1996; Matsumura, 1999). In the past, proponents of  
21  
22 87 phylogenetic signals often referred to them as outcomes of phylogenetic constraints or  
23  
24 88 phylogenetic inertia (Blomberg et al., 2003). However, more recent theory recognizes that  
25  
26 89 phylogenetic signal refers to the observed patterns of trait similarity, rather than one or  
27  
28 90 more evolutionary processes – e.g. random genetic drift, stabilizing selection, pleiotropy, or  
29  
30 91 low rates of evolution -- by which such patterns may arise (reviewed in Kamilar & Cooper,  
31  
32 92 2015). Rather than attempt to distinguish between possible processes or the rates at which  
33  
34 93 they occur, here we simply aim to identify strong and weak phylogenetic signals in order to  
35  
36 94 determine the extent to which social network structure covaries with macaques'  
37  
38 95 phylogenetic closeness.  
39  
40  
41  
42  
43  
44

45 96 Across animal societies, behavioral traits are more labile to evolutionary change in  
46  
47 97 comparison to morphological and/or physiological characteristics (Blomberg et al., 2003).  
48  
49 98 Primates are no exception, with traits like brain size, body mass and canine dimorphism  
50  
51 99 exhibiting stronger phylogenetic signals than those related to social organization and  
52  
53 100 activity budgets (Kamilar & Cooper, 2015). As such, phylogenetic signals for aspects of  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 101 primate social network traits have been hard to identify. For instance, Kasper and Voelkl  
4  
5 102 (2009) established that several aspects of affiliative social networks – e.g. community sub-  
6  
7 103 group formation or modularity, mean centrality in the connectedness of individuals, and the  
8  
9 104 density of network connections (see Methods for precise definitions) -- all showed greater  
10  
11 105 variation between closely related than between distantly related species, i.e. weak  
12  
13 106 phylogenetic signals and a substantial effect of socioecological or demographic factors on  
14  
15 107 network structure. Similarly, Pasquaretta et al. (2014) found no effect of phylogenetic  
16  
17 108 signals on the efficiency of information flow through affiliative social networks of  
18  
19 109 primates, including humans. Tests for phylogenetic signals in aspects of sociality within  
20  
21 110 specific primate families and genera have also revealed inconsistencies. In the genus  
22  
23 111 *Eulemur*, group size and sex-ratio both strongly correlated with phylogenetic distances  
24  
25 112 (Ossi & Kamilar, 2006). Yet among both baboons (genus: *Papio*) and squirrel monkeys  
26  
27 113 (genus: *Saimiri*), interspecific variation in multiple forms of social organization seem to be  
28  
29 114 strongly linked to ecological factors like food distribution, predation pressure, and  
30  
31 115 intergroup feeding competition (Barton et al., 1996; Boinski, 1999; Henzi & Barrett, 2003).  
32  
33  
34 116         Nevertheless, among all primate genera, phylogenetic signals in social traits have  
35  
36 117 been most consistently detected within the genus *Macaca*. Macaques constitute 23 species  
37  
38 118 of Old World primates, with wide-spread geographic distributions in nature (Cords, 2013).  
39  
40 119 Although all species show a predominantly similar social organization (multi-male, multi-  
41  
42 120 female social groups, female philopatry and male dispersal), they show broad inter- and  
43  
44 121 intraspecific variation in several aspects of female social structure (Thierry, 2007).  
45  
46 122 Specifically, post-conflict affiliation, rates of affiliative contact (Thierry et al., 2008), the  
47  
48 123 steepness of dominance hierarchies (Balasubramaniam et al., 2012a), and asymmetry in  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60



1  
2  
3 124 aggression (Balasubramaniam et al., 2012a; Thierry et al., 2008) all show phylogenetic  
4  
5 125 signals, whereas grooming kin bias shows a weak signal (Thierry et al., 2008). These  
6  
7  
8 126 findings have led some proponents of phylogenetic explanations to posit that core aspects  
9  
10  
11 127 of macaque social structure may also be structurally linked, covarying with each other at  
12  
13 128 the species level (Petit et al., 1997; Thierry et al., 2008). Thierry (2007) has characterized  
14  
15 129 this tendency to covary by assigning macaque species to positions on a four-grade 'social  
16  
17 130 style' scale that is broadly consistent with phylogenetic lineage splits (Thierry, 2007). At  
18  
19  
20 131 one extreme, 'grade-1' species (e.g. rhesus macaques (*Macaca mulatta*), Japanese  
21  
22 132 macaques (*M. fuscata*)) of the Fascicularis lineage are hypothesized to show 'despotic'  
23  
24 133 social structure, characterized by steep and asymmetric dominance hierarchies, low levels  
25  
26  
27 134 of post-conflict affiliation, intense affiliative kin-bias, and highly modular or sub-structured  
28  
29 135 social networks in which grooming is both centralized among dominant individuals and is  
30  
31 136 concentrated among more preferred partners. At the other extreme, 'grade-4' species (e.g.  
32  
33  
34 137 Tonkean macaques (*M. tonkeana*), crested macaques (*M. nigra*)) belonging to the Sulawesi  
35  
36 138 lineage are hypothesized to be more 'tolerant' or 'egalitarian', showing shallower  
37  
38  
39 139 dominance hierarchies with more frequent counter-aggression from subordinates towards  
40  
41 140 dominants, high proportions of post-conflict affiliation, less grooming kin bias, and denser,  
42  
43 141 less centralized or modular grooming social networks (Balasubramaniam et al., 2012a;  
44  
45 142 Berman & Thierry, 2010; de Waal & Luttrell, 1989; Sueur et al., 2011b; Thierry, 2007;  
46  
47  
48 143 Thierry et al., 2008). Some versions of the covariation hypothesis posit that a species that  
49  
50 144 shows a single behavioral trait associated with a particular social style will display all other  
51  
52 145 traits (Castles et al., 1996; Petit et al., 1997). However, this extent of covariation has not  
53  
54  
55 146 always been found. Rather, most studies (but see Thierry et al. 2008) thus far have revealed  
56  
57  
58  
59  
60

1  
2  
3 147 marked differences between species at the extreme ends of the social style scale (grade-1  
4  
5 148 and grade-4 macaques, e.g. Sueur et al., 2011b), but found inconsistencies among macaques  
6  
7 149 in intermediate grades (reviewed in Balasubramaniam et al., 2012b).  
8  
9

10 In the present study, we expand on the above findings by assessing phylogenetic  
11  
12 151 signals and covariation in dominance and grooming social network traits across 10 species  
13  
14 152 of macaques representing all four social style grades, and groups from both captive and  
15  
16 153 free-living conditions. In accordance with the predictions of socioecological models, we  
17  
18 154 also examine whether sociodemographic factors, specifically group size and current living  
19  
20 155 condition (Kasper & Voelkl, 2009; Pasquaretta et al., 2014), influence social network traits  
21  
22 156 in addition to, or instead of, social style or phylogenetic closeness. Broadly, socioecological  
23  
24 157 models differ from phylogenetic explanations by positing that social structure is relatively  
25  
26 158 more labile to changes in current conditions, and that such changes are independent of  
27  
28 159 phylogenetic relatedness (Koenig et al., 2013; Sterck et al., 1997; van Schaik, 1989).  
29  
30 160 Specifically, some versions of the model predict that among free-living primates, larger  
31  
32 161 group size should lead to the evolution of more despotic social network structures,  
33  
34 162 characterized by steeper, asymmetric dominance hierarchies, and highly centralized,  
35  
36 163 modular grooming networks with less dense connections/ redundant ties. This may be  
37  
38 164 because larger groups are likely to display heightened levels of contest competition for  
39  
40 165 resources (Koenig et al., 2013; Sterck et al., 1997; van Schaik, 1989) and/or increased  
41  
42 166 temporal constraints (Berman & Thierry, 2010; Dunbar, 1992; Korstjens et al., 2010). On  
43  
44 167 the other hand, smaller groups may be expected to show greater within-group social  
45  
46 168 tolerance characterized by more reversals in dominance interactions, and de-centralized  
47  
48 169 grooming networks that show greater density/ redundancy of ties. Such effects may also be  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 170 influenced by the spatial constraints imposed by captive housing that may result in more  
4  
5 171 frequent social interactions among individuals with a potentially wider range of partners  
6  
7  
8 172 (Duboscq et al., 2013; McCowan et al., 2008).  
9

10 173 Following the pioneering applications of social network analysis on macaque social  
11  
12 174 structure by Sade (1972), comparative studies of nonhuman primate social structure have  
13  
14 175 increasingly used social network approaches to compare various types of societies (Griffin  
15  
16 176 & Nunn, 2012; Kasper & Voelkl, 2009; Pasquaretta et al., 2014; Sueur et al., 2011b). SNA  
17  
18 177 tools improve on earlier methods by constructing aspects of higher-order group structure  
19  
20 178 from a combination of both direct interactions and indirect or secondary connections among  
21  
22 179 group members, and by identifying consistent patterns of interaction among sub-sets of  
23  
24 180 individuals (Brent et al., 2011; Croft et al., 2008; Farine & Whitehead, 2015; Kasper &  
25  
26 181 Voelkl, 2009; Krause et al., 2007; Lusseau & Newman, 2004; McCowan et al., 2008;  
27  
28 182 Newman, 2004; Sueur et al., 2011a; Wey et al., 2008). Yet in comparison to applied animal  
29  
30 183 behavioral research (e.g. infectious disease transmission (reviewed in Drewe & Perkins, 2015),  
31  
32 184 quantifying group social stability (reviewed in McCowan et al., 2008)), SNA has been used less  
33  
34 185 extensively to examine the evolutionary bases for variation in primate social structure (see Kasper  
35  
36 186 & Voelkl, 2009; Griffin & Nunn, 2012; Sueur et al., 2011b).  
37  
38  
39  
40  
41

42 187 We first ask whether aspects of female dominance and grooming networks show  
43  
44 188 strong phylogenetic signals (Q1) and whether grooming networks covary with dominance  
45  
46 189 networks (Q2) and/or hypothesized social style grades across macaques (Q3). In  
47  
48 190 accordance with the covariation and social style hypotheses, we predict that macaque  
49  
50 191 species that have the most transitive, decided and/or certain dominance relationships will  
51  
52 192 also show (a) the greatest tendencies for high-ranking individuals to occupy more central  
53  
54 193 positions in more modular grooming networks, and (b) networks that are more modular  
55  
56  
57  
58  
59  
60

1  
2  
3 194 with sparser, less redundant ties. In comparison, those with the least transitive and/or  
4  
5 195 uncertain dominance relationships are expected to show the opposite characteristics.  
6  
7  
8 196 Further, we predict that transitions from more despotic to more tolerant social styles will be  
9  
10 197 correlated with systematic decreases in the centralization of grooming among dominants  
11  
12 198 and modularity, and increases in network density or redundancy of ties. Finally, we also  
13  
14 199 examine (Q4) the potential impact of sociodemographic factors on networks and patterns of  
15  
16 200 covariation. Specifically, we predict that group size will be positively associated with the  
17  
18 201 centralization of grooming among dominants and with grooming modularity, and  
19  
20 202 negatively associated with the density/ redundancy of ties in grooming network clusters.  
21  
22 203 We also explore the effects of living condition on such relationships, and the impact of a  
23  
24 204 third sociodemographic characteristic -- female-to-male sex ratio -- on such covariation.  
25  
26  
27  
28

29 **Methods:**  
30

31  
32 206 This research adhered to the American Society of Primatologists principles for the  
33  
34 207 ethical treatment of primates. We first assembled behavioral and phylogenetic datasets from  
35  
36 208 various sources – published literature, our own unpublished data, and personal donations  
37  
38 209 from other researchers (Table 1). Below we describe these data, the computation of social  
39  
40 210 network measures, and statistical analyses.  
41  
42

43 *Datasets – macaque social behaviors and phylogenetic trees:*  
44

45  
46 212 To compute dominance network measures, we assembled a total of 38 behavioral  
47  
48 213 datasets on dyadic aggressive interactions among adult female macaques (individuals  $\geq 3.5$   
49  
50 214 - 5 years of age, depending on species-typical ages of maturity) from groups living in  
51  
52 215 captive and free-living (free-ranging and wild) conditions (Table 1). These encompassed 20  
53  
54 216 populations representing 10 macaque species from all four social style grades. Except for  
55  
56  
57  
58  
59  
60

1  
2  
3 217 stumptailed macaques (*M. arctoides*) and bonnet macaques (*M. radiata*), we acquired at  
4  
5 218 least two datasets for each species; these were either from different social groups or from  
6  
7 219 the same social group during different stable study-periods. To compute grooming network  
8  
9 220 measures, we obtained data from 34 (out of the 38) datasets from nine species (Table 1).  
10  
11

12 221 The datasets had been collected using different types of sampling approaches, and  
13  
14 222 varied in sampling effort per subject (Table 1). The majority (aggression: 33/ 38, or 87%;  
15  
16 223 grooming: 25/34, or 74%) had been collected using focal-animal and/or all-occurrences  
17  
18 224 sampling methods (Altmann, 1974; see citations provided in Table 1). For these datasets,  
19  
20 225 all subjects within a dataset had been observed for roughly equal amounts of time (see  
21  
22 226 corresponding citations; information available on request). A minority used either scan  
23  
24 227 sampling (aggression: 2/38, or 5%; grooming: 7/34, or 20%) or *ad-libitum* sampling along  
25  
26 228 with focal animal sampling (aggression: 3/38, or 8%; grooming: 2/34, or 6%). The scan  
27  
28 229 sampling datasets were included based on a previous study on Japanese macaques revealing  
29  
30 230 that for a given number of scans, this approach yields identical amounts of behavioral data  
31  
32 231 to focal sampling for the same duration (in minutes) as the number of scans (Romano et al.,  
33  
34 232 2016). Datasets that used *ad libitum* sampling were included after ensuring that they had  
35  
36 233 been (a) used in previous comparative studies (Balasubramaniam et al., 2012a; Schino &  
37  
38 234 Aureli, 2008), and (b) conducted for overall durations that were comparable to those of the  
39  
40 235 focal- or all-occurrences sampled datasets (6 – 12 months).  
41  
42  
43  
44  
45  
46  
47

48 236 All datasets included had been collected as part of long-term studies, and during  
49  
50 237 periods when the groups were socially stable in terms of group composition, size,  
51  
52 238 dominance relationships, age-class and/or sex ratios. Out of 38 datasets, the majority (27, or  
53  
54 239 71%) was from free-living groups of macaques. We found significant differences in group  
55  
56  
57  
58  
59  
60

1  
2  
3 240 size (captive =  $28.4 \pm 19.1$ ; free-living =  $48.3 \pm 23.9$ ; ANOVA:  $F_{1, 32} = 6.04$ ,  $p = 0.02$ ) and  
4  
5 241 sex ratios (captive =  $0.50 \pm 0.21$ ; free-living =  $0.33 \pm 0.09$ ; ANOVA:  $F_{1, 32} = 12.07$ ,  $p <$   
6  
7 242  $0.01$ ) between captive vs. free-living macaques. Hence, we either conducted separate  
8  
9 243 assessments for only free-living groups (Q1), or directly examined the effect of living  
10  
11 244 condition in our analyses (Q2 - Q4).  
12  
13  
14

15 245 In order to assess and control for the effects of phylogenetic signals, we extracted a  
16  
17 246 Bayesian consensus tree (Supplementary Figure 1) and a tree-block of 10 trees from  
18  
19 247 *10Ktrees*, an online resource for primate phylogeny based on mitochondrial and nuclear  
20  
21 248 genetic datasets (Arnold et al., 2010). All 11 phylogenies showed proportional branch-  
22  
23 249 lengths, and identical topologies that were also consistent with previously constructed  
24  
25 250 macaque topologies using parametric approaches (e.g. Chatterjee et al., 2009; Tosi et al.,  
26  
27 251 2003). We hence report the results of tests performed using the consensus phylogeny, with  
28  
29 252 those from the tree-block submitted as supplementary material (Supplementary Table 4).  
30  
31  
32  
33

### 34 253 *SNA – Dominance and Grooming Measures:*

35 254  
36 255 Table 2 provides the definitions and details of the dominance and grooming network  
37  
38 256 traits that we computed. We computed dominance network measures from winner-loser  
39  
40 257 dominance matrices in which non-diagonal cells contained data on the frequencies of  
41  
42 258 dyadic contact and non-contact aggression from animals in the rows to animals in the  
43  
44 259 columns. Acts of bi-directional or counter-aggression were scored twice, once on either  
45  
46 260 side of the diagonal for each interactant. Bidirectional and counter-aggression were  
47  
48 261 included to produce representative measures of dominance network traits, particularly for  
49  
50 262 grade-3 and grade-4 macaque species that typically experience high proportions of such  
51  
52 263 interactions (Balasubramaniam et al., 2012a; Thierry et al., 2008). From each dominance  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 264 matrix, we computed two traits – triangle transitivity (Shizuka & McDonald, 2012) and  
4  
5 265 dominance certainty (Fujii et al., 2013; Fushing et al., 2011) – that have not been used in  
6  
7  
8 266 previous comparative studies of primate social networks (see Table 2 for definitions).  
9  
10 267 Whereas most methods for describing group level dominance hierarchies consider only  
11  
12 268 dyadic wins and losses from agonistic encounters (e.g., dominance gradient (hierarchical  
13  
14  
15 269 steepness: de Vries et al., 2006), and dominance asymmetry (Directional Consistency  
16  
17 270 Index: de Vries, 1998)), the computation of network-based measures, particularly  
18  
19  
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  
23  
24 273 global aspects of a dominance hierarchy than steepness or DCI, and are less susceptible  
25  
26  
27 274 than steepness to error due to the numbers of non-interacting dyads present in the dataset.  
28  
29 275 Specifically, dominance certainty incorporates the presence of non-interacting dyads in its  
30  
31 276 calculation (Table 2) by weighting both the total number of direct wins by an individual ‘A’  
32  
33 277 against an individual ‘D’ ( $A \rightarrow D$ ), as well as imputed wins incurred via the likelihood of  
34  
35 278 traversing longer paths (e.g.  $A \rightarrow B \rightarrow C \rightarrow D$ ) through the dominance network. In doing so,  
36  
37  
38 279 the certainty measure characterizes the network-level flow-structure of dominance  
39  
40 280 information, thereby accounting for hidden elements in dominance structure such as  
41  
42  
43 281 avoidance between individuals (Fujii et al., 2013; Fushing et al., 2011) (Table 2).

44  
45  
46 282 We constructed grooming networks (Figure 1) from weighted, undirected networks,  
47  
48 283 i.e. where individuals represented by *nodes* were connected by *edges* that represent the  
49  
50 284 normalized values of grooming given and received for each pair of nodes. Weighted  
51  
52  
53 285 networks were used to account for the potential impact of differences in observation times  
54  
55 286 across comparative datasets (Griffin & Nunn, 2012; Newman, 2004). Specifically, we  
56  
57  
58  
59  
60

1  
2  
3 287 calculated three measures – centrality coefficient, Newman’s modularity, and global  
4  
5 288 clustering coefficient -- that were all (a) not collinear (see below), (b) captured biologically  
6  
7 289 different aspects of network structure, and (c) mathematically independent of the number of  
8  
9 290 nodes (or group size: Nunn et al., 2015). First, we calculated *centrality coefficient* as the  
10  
11 291 correlation coefficient between individuals’ dominance statuses (computed using  
12  
13 292 normalized David’s scores computed from dominance matrices: Gammell et al., 2003) see  
14  
15 293 below) and their centralities within grooming networks (as in Sueur et al., 2011b; see Table  
16  
17 294 2 for definitions). For the latter, we used standardized *eigenvector centrality*, i.e. the  
18  
19 295 number and strength of an individuals’ direct and indirect grooming connections indicating  
20  
21 296 each individual’s access to social capital or support (Farine & Whitehead, 2015; Newman,  
22  
23 297 2004; Whitehead, 2008). Eigenvector centrality is among the most biologically meaningful  
24  
25 298 of the centrality measures; it is more indicative of individuals’ social status than measures  
26  
27 299 of *betweenness* and *closeness* centrality in taxa such as primates that have more complete  
28  
29 300 network graphs (Brent et al., 2010; Farine & Whitehead, 2015; Kasper & Voelkl, 2009;  
30  
31 301 McCowan et al., 2008; Sueur et al., 2011a). We also calculated Newman’s eigenvector-  
32  
33 302 based modularity, which is a global measure of network sub-structuring into communities  
34  
35 303 (Newman, 2006; Nunn et al., 2015; see Table 2 for a detailed definition). Finally, as a  
36  
37 304 measure of the density/ redundancy of ties in the network, we calculated the *global*  
38  
39 305 *clustering coefficient*, which is an unweighted measure of how well-connected nodes are to  
40  
41 306 their immediate neighbors (Table 2). Clustering coefficient captures the underlying  
42  
43 307 redundancy of node connectivity at a more local level than alternative measures like  
44  
45 308 network density, making it mathematically independent of the number of nodes (Table 2;  
46  
47 309 Nunn et al., 2015). However, since increased localized clustering may also be a  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60



1  
2  
3 310 characteristic of more modular networks (Nunn et al., 2015), we confirmed that clustering  
4  
5 311 coefficient was positively correlated with network density measures across our datasets ( $n$   
6  
7  
8 312 = 34,  $r = 0.91$ ,  $p < 0.01$ ). Grooming measures were calculated using the *statnet* (for  
9  
10 313 eigenvector centrality) and *igraph* (for Newman's modularity and global clustering  
11  
12 314 coefficient) R packages (Csardi & Nepusz, 2006; Handcock et al., 2006). Individuals'  
13  
14  
15 315 dominance David's scores were calculated from the aggression matrices using the *steepness*  
16  
17 316 R package (de Vries et al., 2006; Leiva & de Vries, 2014).

19  
20 317 Supplementary Table 1 shows the values of the various network measures computed  
21  
22 318 for each dataset. To avoid potentially pseudoreplicating our results owing to network  
23  
24 319 measures being collinear to each-other, we confirmed that collinearity diagnostics were met  
25  
26  
27 320 for both dominance measures (Pearson's  $r$  correlation = 0.61; variance inflation factors  
28  
29 321 (VIF) < 2), and grooming measures ( $r < 0.78$  for all pairs; generalized variance inflation  
30  
31 322 factors (GVIF) < 3) using the *car* package in R (Fox & Weisberg, 2011). Given the  
32  
33 323 susceptibility of network measures to variation in sampling effort (Croft et al., 2008; Croft  
34  
35 324 et al., 2011; Farine & Whitehead, 2015; Lusseau et al., 2008), we performed diagnostic  
36  
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),  
40  
41 327 by randomly sampling increasingly smaller subsets (100%, 80%, 60%, 40%, and 20%) of  
42  
43 328 edges from the original network. Plots of percent sampling effort and mean grooming  
44  
45 329 network measure computed across 200 permuted networks under each category of sampling  
46  
47 330 effort revealed asymptotic relationships (Supplementary Figure 2). Further, Wilcoxon rank-  
48  
49 331 sum tests revealed that network measures computed from the original data were not  
50  
51 332 significantly different to those computed from the bootstrapped networks that used smaller  
52  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 333 subsets of data (80% - 40% sampling effort; but see clustering coefficient at 20% sampling  
4  
5 334 effort: Supplementary Table 2). Finally, we confirmed that across datasets, sampling effort  
6  
7  
8 335 calculated as the mean observation times spent per subject (Table 1) was unrelated to  
9  
10 336 group-level dominance and/or grooming network measures (Supplementary Table 3;  
11  
12 337 Supplementary Figure 3).

13  
14  
15 338 *Statistical Analyses:*

16  
17 339 To examine evidence for phylogenetic signals (Q1) in dominance and grooming  
18  
19 340 network traits at the species level, we used the Phytools R package (Revell, 2012). For each  
20  
21 341 trait, we computed Blomberg's Kappa (K) coefficient (Blomberg et al., 2003) as the ratio  
22  
23 342 between the Mean-Squared Errors (or MSE) of the raw, species-means of behavioral traits  
24  
25 343 over the MSEs of traits that have been phylogenetically transformed using tree-specific  
26  
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  
32  
33 347 proportional to the shared evolutionary histories, or branch length distances between taxa  
34  
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  
44  
45 353 in a trait (Blomberg et al., 2003). These values were based on previous comparative studies  
46  
47 354 of nonhuman primate behavioral traits that also examined phylogenetic signals among  
48  
49 355 smaller numbers of species (Balasubramaniam et al., 2012a; Thierry et al., 2008). We  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 356 avoided splitting terminal species' nodes into multiple nodes to represent groups within  
4  
5 357 species. Although doing so offers the potential advantage of increased statistical power, it  
6  
7 358 would also artificially inflate phylogenetic signals (Blomberg et al., 2003; Thierry et al.,  
8  
9 359 2008). Blomberg's K generates identical results to Pagel's Lambda (Pagel, 1997, 1999), an  
10  
11 360 alternative indicator of phylogenetic signal. However, we chose to report K since this  
12  
13 361 statistic is more useful in informing about trait variation relative to Brownian evolution  
14  
15 362 (Kamilar & Cooper, 2015). In addition, we conducted randomization tests to compare the  
16  
17 363 MSE of phylogenetically transformed data to those computed from 1000 randomized  
18  
19 364 datasets generated by scattering the behavioral scores randomly on a phylogeny. In addition  
20  
21 365 to handling the intrinsic dependency of the data, such tests indicate whether any observed  
22  
23 366 phylogenetic signal is greater than that expected by chance. Although they had low  
24  
25 367 statistical power of 20-35% (Blomberg et al., 2003), randomization tests have nonetheless  
26  
27 368 been used in previous studies of similarly small sample sizes (7-10 species:  
28  
29 369 Balasubramaniam et al., 2012a; Thierry et al., 2008).

30  
31  
32  
33  
34  
35  
36 370 To examine whether grooming network traits were linked to dominance traits (Q2)  
37  
38 371 or social style scale (Q3) across species, and to assess the potential impact of  
39  
40 372 sociodemographic factors (Q4) on such covariations, we constructed General Linear  
41  
42 373 Mixed-effects Models (GLMMs: Bates et al., 2016). We implemented an Information-  
43  
44 374 Theoretical approach (Burnham et al., 2011; Grueber et al., 2011) using the *lme4* and  
45  
46 375 *MuMIn* R packages. Given the relatively small number of species, we used neither  
47  
48 376 Phylogenetic Least Squares regression (PGLS: Nunn, 2011), nor permutation-based  
49  
50 377 MCMC models (Croft et al., 2011; Farine & Whitehead, 2015) that are recommended for  
51  
52 378 examining variation in phylogenetic distances and network sampling effort respectively.  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 379 Instead, we indirectly tested for the effects of phylogeny by assessing covariation with  
4  
5 380 social style grade, since social style and phylogeny have been shown to strongly covary  
6  
7  
8 381 across macaques (Thierry et al., 2000). To rule out the effect of network sampling effort on  
9  
10 382 our results, we replicated our GLMMs using mean network measures computed from  
11  
12 383 permuted datasets of varying degrees of sampling effort (20% - 80% of edges: see above).  
13  
14

15 384 We first generated 3 global models, one for each grooming network trait treated as  
16  
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  
20  
21 387 coefficient was arcsine-transformed to meet normality assumptions ( $w = 0.98$ ,  $p = 0.65$ ).  
22  
23 388 As recommended by I-T approaches (Burnham et al., 2011; Grueber et al., 2011), our  
24  
25 389 global models were constructed by the inclusion of just those covariates that catered to  
26  
27 390 testing our specific predictions (Q2-Q4). Specifically, dominance traits (transitivity and  
28  
29 391 dominance certainty), social style category, and sociodemographic factors (group size, sex  
30  
31 392 ratio, and living condition category) were included as fixed effects. Since the effect of  
32  
33 393 group size on grooming networks could be more pronounced among free-living groups  
34  
35 394 (Griffin & Nunn, 2012; Sueur et al., 2011b), we also examined a potential interaction  
36  
37 395 between group size and living condition. Species was set as a random effect to avoid  
38  
39 396 pseudoreplication issues. We next used the *arm* package in R to z standardize ( $\mu = 0$ ,  $SD =$   
40  
41 397  $1$ ) the predictors in the global model, which is essential for interpreting parameter estimates  
42  
43 398 after model averaging (Gelman et al., 2009). We then used the automated 'dredge' function  
44  
45 399 in the *MuMIn* R package to generate a 'complete' set of 80 models from multiple possible  
46  
47 400 combinations of predictors from the global models (Grueber et al., 2011) (Supplementary  
48  
49 401 Tables 4-6). This included a 'null' or an intercept-only model with just species as a random  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 402 effect for the sake of comparison. From each full model set, we identified candidate models  
4  
5 403 that included only models whose difference in AICc scores were  $< 4$  from the model with  
6  
7  
8 404 the lowest AICc score (Burnham et al., 2011) (models in bold font in Supplementary Tables  
9  
10  
11 405 4-6). We confirmed that model diagnostics criteria were met for each candidate model, and  
12  
13 406 ruled out multicollinearity issues for models with multiple predictors ( $r < 0.8$  for all pairs of  
14  
15 407 predictors; GVIF  $< 4$  for each: the *car* package in R: Fox & Weisberg, 2011). We then  
16  
17 408 determined parameter estimates by model-averaging each set of candidate models using the  
18  
19 409 zero-averaging approach (Burnham & Anderson, 2002; Grueber et al., 2011). Since this  
20  
21 410 approach weakens the effect sizes of predictors that only appear in a minority of models, it  
22  
23 411 is more useful (than the natural averaging method) in cases where the aim is to determine  
24  
25 412 which (among multiple) factors have the strongest effect on a response variable (Grueber et  
26  
27 413 al., 2011; Nakagawa & Freckleton, 2010). For all parameter interpretations, we set the  
28  
29 414 alpha level at 0.05.  
30  
31  
32

### 33 34 415 **Results:**

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

37  
38  
39 417 Mean species-level scores of both dominance network traits -- transitivity and  
40  
41 418 dominance certainty -- showed moderate phylogenetic signals (Table 3). When we repeated  
42  
43 419 the analyses including only free-living groups (27 datasets across 7 species), the results  
44  
45 420 showed a strong phylogenetic signal for dominance traits (K statistics  $\gg 1$ : Table 3). In  
46  
47 421 comparison, grooming traits -- especially eigenvector and clustering coefficient -- showed  
48  
49 422 weak phylogenetic signals (Table 3). Although Newman's modularity showed a moderate  
50  
51 423 signal as indicated by the K statistic, randomization tests neither reached significance nor  
52  
53 424 showed a non-significant trend for this trait (Table 3). Given the relatively small number of  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 425 species, our tests of phylogenetic signals lacked power (~ 20-35%). Yet, results from the  
4  
5 426 randomization significance tests were mostly consistent with our estimations of the strength  
6  
7 427 of the signals from the K statistic (Table 3). Moreover, they were also robust to  
8  
9 428 phylogenetic branch length variation, with results from the consensus phylogeny being  
10  
11 429 largely consistent with those across 10 phylogenetic trees extracted from the *10KTrees*  
12  
13 430 website (Supplementary Table 3).

14  
15 431 *(Q2-4) The effect of dominance traits, social style, and sociodemographic factors on*  
16  
17 432 *grooming traits:*

18  
19  
20 433 Table 4 shows the model-averaged coefficients and parameter estimates from  
21  
22 434 candidate GLMM sets shortlisted using our dAICc criterion, from the complete model sets  
23  
24 435 for grooming Newman's modularity and clustering coefficient. Our criterion shortlisted 8  
25  
26 436 models for modularity, and 7 for clustering coefficient. Neither candidate model set  
27  
28 437 included the 'random effect only' model, which had a dAICc > 12 from the candidate sets  
29  
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  
33  
34 440 showed more modular, but less dense clusters or redundant ties than smaller groups, which  
35  
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  
39  
40 443 clustering coefficient (Table 4). We also detected a significant effect of living condition,  
41  
42 444 with captive groups showing less modular networks and greater density/ redundancy of  
43  
44 445 cluster ties than free-living groups (Table 4; Figure 2). However, there was no interaction  
45  
46 446 between group size and living condition (Table 4), suggesting that the effect of group size  
47  
48 447 were independent of living condition. Sex ratio also showed no effect. Finally, neither  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 448 dominance traits nor social style grade strongly influenced these grooming network traits in  
4  
5 449 predicted directions (Table 4). In fact, social style did not make the candidate models for  
6  
7  
8 450 modularity.  
9

10 451 In contrast to Newman's modularity and clustering coefficient, candidate model  
11  
12 452 selection for grooming eigenvector centrality coefficient failed to eliminate the 'random  
13  
14 453 effect only' model (Supplementary Table 5). Zero-based model averaging revealed that  
15  
16  
17 454 none of the predictors had a strong effect on these indices (Supplementary Table 8).  
18

19  
20 455 Finally, replications of our GLMMs using network measures computed from  
21  
22 456 permuted datasets revealed that our findings, particularly for group size, were highly  
23  
24 457 consistent across varying degrees of sampling effort. As per findings from the complete  
25  
26  
27 458 data, group size showed positive associations with modularity, and negative associations  
28  
29 459 with clustering coefficient for all degrees of sampling effort (e.g. at 60% and 20% effort:  
30  
31 460 Supplementary Tables 9, 10). On the other hand, the effect of living condition on grooming  
32  
33 461 clustering coefficient weakened at lower sampling effort (Supplementary Tables 9, 10).  
34

### 35 462 **Discussion:**

36  
37  
38 463 In group-living animals, the evolutionary origins of variation in aspects of social  
39  
40 464 structure remain much debated. Here we used a social network approach to examine the  
41  
42 465 impact of phylogenetic relatedness, specifically phylogenetic signals and trait covariation,  
43  
44 466 as well as sociodemographic factors like group size and living condition on interspecific  
45  
46  
47 467 variation in higher-order aspects of dominance and grooming social structure across  
48  
49 468 macaques. We found that while dominance social network traits showed strong  
50  
51 469 phylogenetic signals, grooming network traits showed weak signals and were not strongly  
52  
53 470 covariant with social style or with dominance traits. Rather, two aspects of grooming  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 471 network structure – modularity and clustering coefficient – were strongly influenced by  
4  
5 472 group size independently of current living condition. Below we discuss our findings in  
6  
7 473 depth, and offer avenues for future comparative assessments of primate social network  
8  
9 474 structure.

10  
11  
12 475 Previous studies among macaques have established strong phylogenetic signals in  
13  
14 476 some aspects of social structure (e.g. dominance steepness and counter-aggression:  
15  
16 477 Balasubramaniam et al., 2012a), but moderate-to-weak signals in others (e.g. kin-bias:  
17  
18 478 Thierry et al., 2008). Consistent with this pattern, we found moderate to strong  
19  
20 479 phylogenetic signals for aspects of female dominance network traits, but moderate or weak  
21  
22 480 signals for grooming networks. Specifically, both transitivity and dominance certainty  
23  
24 481 exhibited degrees of signal that are close in strength to what is expected under a Brownian  
25  
26 482 motion model of evolution (Blomberg et al., 2003). In other words, the covariance between  
27  
28 483 dominance trait values of adjacent taxa strongly proportional to their shared evolutionary  
29  
30 484 histories indicated by their phylogenetic branch length distances (Kamilar & Cooper,  
31  
32 485 2015). This finding extends earlier findings of strong phylogenetic signals on group-level  
33  
34 486 aspects of dominance structure that were based on dyadic interactions (e.g., hierarchical  
35  
36 487 steepness, counter-aggression: Balasubramaniam et al., 2012a) to broader patterns of triadic  
37  
38 488 motifs (transitivity) and network-wide flow patterns (dominance certainty). It also extends  
39  
40 489 it to indirect connections that reflect the higher-order structure of the flow of dominance  
41  
42 490 information through pathways that connect both interacting and non-interacting individuals  
43  
44 491 (dominance certainty: Fujii et al., 2013; Fushing et al., 2011). Phylogenetic signals were  
45  
46 492 even stronger when we analyzed only free-living groups of macaques, despite a reduction  
47  
48 493 in sample size from 10 to 7 species (Blomberg et al., 2003). This may be due to the  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60



1  
2  
3 494 differences in living conditions between groups of closely related species. In captivity,  
4  
5 495 spatial constraints and/or management strategies may force animals to interact that might  
6  
7 496 otherwise avoid one another after one or two decided outcomes (Duboscq et al., 2013;  
8  
9 497 McCowan et al., 2008). This may result in greater than expected degrees of reversals in  
10  
11 498 agonistic success and hence, greater uncertainty in dominance relationships. Unfortunately,  
12  
13 499 limited datasets prevented an analysis of phylogenetic signals among captive groups alone  
14  
15 500 (11 out of 38 datasets: 5 species). Nevertheless, the detection of strong phylogenetic signals  
16  
17 501 among free-living macaques (27 out of 38 datasets: 7 species) builds on previous studies  
18  
19 502 that have either included both captive and free living groups (Balasubramaniam et al.,  
20  
21 503 2012a) or only captive groups (Thierry et al., 2008). Since previous comparative studies  
22  
23 504 across primates have shown a general lack of correspondence between phylogeny and  
24  
25 505 socioecology (Koenig et al., 2013; Ménard, 2004; Okamoto & Matsumura, 2002), it is  
26  
27 506 unlikely that the observed phylogenetic signals in dominance traits are ‘artifacts’ of  
28  
29 507 correlations between phylogeny and current socioecological factors. Further, the signals  
30  
31 508 were detected despite the fact that a fraction of the free-living groups in our dataset were  
32  
33 509 exposed to food provisioning by humans (Table 1), although predation pressure, another  
34  
35 510 socioecological factor (van Schaik, 1989), was anecdotally either uniformly low or absent  
36  
37 511 across the study populations. Taken together, our findings suggest that phylogeny predicts a  
38  
39 512 major component of the interspecific variance in dominance structure among free-living  
40  
41 513 macaques. Nevertheless, these findings do not entirely rule out an adaptive component. For  
42  
43 514 instance, the concept of social reaction norms proposes that aspects of social structure may  
44  
45 515 change dynamically by responding to socioecological and environmental factors, but within  
46  
47 516 the limits posed by a species- or phylogenetic lineage-typical range of responses that may  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 517 in turn be linked to phylogenetic closeness (Berman & Thierry, 2010). Moreover,  
4  
5 518 phylogenetic signals, rather than being linked to ancestral genetic splits, may be outcomes  
6  
7  
8 519 of adaptations by ancestral species dispersing into historically similar environments  
9  
10 520 (Kamilar & Cooper, 2015). We suggest that future assessments of the bases of phylogenetic  
11  
12 521 signals in social network traits focus on phylogeographic approaches (Lemey et al., 2009;  
13  
14 522 Ree & Smith, 2008). Specifically, a comparison of the reconstructed social networks and  
15  
16 523 geographic ranges of ancestral primate taxa may provide better insights into whether  
17  
18 524 phylogenetic signals in primate social networks are indeed ‘artifacts’ of adaptive responses  
19  
20 525 in their evolutionary past.  
21  
22  
23

24 526 In comparison to dominance traits, grooming networks, particularly eigenvector and  
25  
26 527 clustering coefficients, showed moderate (modularity) or weak (eigenvector and clustering  
27  
28 528 coefficient) phylogenetic signals. Further, grooming traits did not covary with dominance  
29  
30 529 traits in the directions predicted. A possible explanation is that covariation between social  
31  
32 530 network traits is not always linear (but see Thierry et al.’s (2008) findings on covariation  
33  
34 531 between traits associated with conciliatory tendencies across macaques). Further, it may be  
35  
36 532 discernible at levels of organization other than species, for instance, across phylogenetic  
37  
38 533 lineages (Thierry, 2000). Yet the lack of a strong effect of species-typical social style on  
39  
40 534 grooming networks may be seen as evidence to refute this argument given that social style  
41  
42 535 and phylogeny are correlated (Thierry et al., 2000). A more likely explanation is that  
43  
44 536 grooming traits may come under the additional influence of current socioecological and/or  
45  
46 537 sociodemographic factors.  
47  
48  
49  
50  
51

52  
53 538 Among all the primate genera, macaques are presently unique in the extent to which  
54  
55 539 interspecific variation in social traits is consistent with phylogeny, and covariant with social  
56  
57  
58  
59  
60

1  
2  
3 540 style (Balasubramaniam et al., 2012a; Sueur et al., 2011b; Thierry et al., 2008; Thierry et  
4  
5 541 al., 2000). Yet we found that group size had a stronger influence on grooming modularity  
6  
7 542 and clustering coefficient than either dominance traits or social styles. Specifically, larger  
8  
9 543 groups of macaques showed more modular grooming networks, as well as less density/  
10  
11 544 redundancy in connections among localized, triadic clusters.  
12  
13  
14

15 545 It is conceivable that the effect of group size on grooming traits may have been an  
16  
17 546 artifact of intergroup differences in (1) living condition (McCowan et al., 2008; Duboscq et  
18  
19 547 al., 2013) and/or (2) chance interactions (Griffin & Nunn, 2012; Nunn et al., 2015). In our  
20  
21 548 dataset, for instance, captive groups were both significantly smaller (see Methods) and, as  
22  
23 549 expected due to spatial constraints, showed less modular grooming networks with more  
24  
25 550 densely connected clusters (see Results) than free-living groups. Yet we found no effect of  
26  
27 551 an interaction between group size and living condition on grooming traits, suggesting that  
28  
29 552 the effect of group size on grooming traits was independent of the effect of living condition.  
30  
31 553 Moreover, the permuted datasets revealed that both the grooming traits themselves, and the  
32  
33 554 strong relationships between group size and grooming traits, were robust to variation in  
34  
35 555 sampling effort. Together, these findings suggest that the effect of group size on grooming  
36  
37 556 traits, rather than being artefactual, may more likely have socioecological underpinnings.  
38  
39 557 Specifically, one school of thought is that living in larger groups may heighten levels of  
40  
41 558 within-group contest competition (or WGC) for resources (Koenig et al., 2013; Sterck et  
42  
43 559 al., 1997; van Schaik, 1989). This may lead to despotic, nepotistic primate societies  
44  
45 560 characterized by both steep and transitive dominance structure (Majolo et al., 2009), and  
46  
47 561 more modular, sparsely connected grooming community structures (the social bottleneck  
48  
49 562 hypothesis: Griffin & Nunn, 2012). In comparison, smaller groups may show weaker WGC  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 563 and the opposite characteristics that are indicative of greater social tolerance. An alternative  
4  
5 564 perspective is that individuals in large groups may face spatial or time constraints on their  
6  
7  
8 565 abilities to interact consistently with all other group members (Berman & Thierry, 2010;  
9  
10 566 Dunbar, 1992; Korstjens et al., 2010; Puga & Sueur, 2017). This may in turn result in  
11  
12 567 modular or clustered but sparser social networks in larger groups, in which individuals may  
13  
14  
15 568 come into contact with each other less frequently (Griffin & Nunn, 2012). Given the lack of  
16  
17 569 a clear association between group size and dominance networks in our dataset (e.g. Group  
18  
19 570 size vs. dominance certainty:  $n = 38$ ,  $r = 0.02$ ,  $p = 0.88$ ), our findings point to a  
20  
21 571 spatiotemporal rather than a resource-competition based explanation. Yet final conclusions  
22  
23 572 await the expansion of our dataset to include additional groups and species, and comparable  
24  
25 573 operational measures of resource distribution (see below).  
26  
27

28  
29 574 Unlike grooming modularity and clustering coefficient, grooming centrality  
30  
31 575 coefficient was not influenced by dominance traits, social style, or sociodemographic  
32  
33 576 factors. One reason for this lack of concordance could be due to the way this index was  
34  
35 577 computed. For instance, the exclusion of males from our grooming networks, unlike in  
36  
37 578 Sueur et al.'s (2011b) study, may have masked skew in grooming centrality towards  
38  
39 579 dominants. In despotic macaques, high-ranking males may be among the most attractive  
40  
41 580 grooming partners for females who may gain benefits such as access to social support  
42  
43 581 and/or resources (Schino, 2001; Silk et al., 2003; Sueur et al., 2011b). It is possible that  
44  
45 582 female dominance status could be related to centralization in the grooming network that is  
46  
47 583 based on *specific types* of grooming connections rather than their overall connectedness.  
48  
49 584 These could be grooming connections with non-kin, grooming that is directed up the  
50  
51 585 hierarchy in exchange for access to rank-related benefits such as resource tolerance and  
52  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 586 support in conflicts, and/or grooming that is reciprocated in the short or long-term  
4  
5 587 (reviewed in Henzi & Barrett, 1999). Should comparative data be available, such  
6  
7  
8 588 assessments may generate centralization indices that better reflect female social structure.  
9

10 589 Alternatively, it is conceivable that intergroup variation in centrality coefficients  
11  
12 590 may be influenced by additional socioecological variables (Griffin & Nunn, 2012; Sterck et  
13  
14 591 al., 1997), and/or intraspecific variation (Borgeaud et al., 2016; Romano et al., 2016).  
15  
16 592 Yet assessments of the socioecological bases of variation in sociality have proved to be  
17  
18 593 complicated. For instance, we currently lack a consistent operational measure of resource  
19  
20 594 abundance and distribution that may be used in comparative contexts across a wide range of  
21  
22 595 taxa (Clutton-Brock & Janson, 2012). Another challenge is assessing the effects of  
23  
24 596 infectious disease risk on social networks. For instance, increased parasite infection risk  
25  
26 597 may lead to the evolution of more modular networks because individuals engage fewer  
27  
28 598 social partners (Griffin & Nunn, 2012; Nunn et al., 2015). At the same time, possessing  
29  
30 599 more partners can also reduce infection risk via socially buffering individuals against  
31  
32 600 susceptibility to infectious agents (Balasubramaniam et al., 2016; Duboscq et al., 2016;  
33  
34 601 Young et al., 2014). Third, the spatial distribution of females may also influence male  
35  
36 602 reproductive tactics, i.e. the extent to which males show reproductive skew by  
37  
38 603 monopolizing mating opportunities which may in turn influence female social networks  
39  
40 604 (Schülke & Ostner, 2008, 2013). More definitive conclusions await the ability to draw  
41  
42 605 interspecies links between reproductive skew and female social networks, and indeed male-  
43  
44 606 male social relationships. Finally, in comparison to interspecific variation, few comparative  
45  
46 607 studies have assessed the evolutionary origins of inter-individual or intergroup variation  
47  
48 608 (Clutton-Brock & Janson, 2012). In addition to impacting group-level outcomes, selection  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 609 pressures may act on the spatial orientation, behavioral strategies, and personalities of  
4  
5  
6 610 individuals, any or all of which may in turn affect social networks (Borgeaud et al., 2016;  
7  
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  
17  
18 **Acknowledgements:**

19  
20 616 We thank C. Young, C. Desportes, L. Marechal, P. Fedurek, J. Micheletta, Y.  
21  
22 617 Februanti, V. Romano, R. O'Hagan, T. Suzumura, A. Takahashi, E. Polizzi di Sorrentino,  
23  
24 618 B. Tiddi, M. S. Chaitra, R. Cozzolino, C. Demaria, F. Dessi-Fulgheri, S. Geminiani, M. L.  
25  
26 619 Gong, M. Haque, S. Hardie, C. S. Ionica, K. Jones, N. F. Koyama, M. Li, J. Sloan, R.  
27  
28 620 Ventura, and L. Zhang for their participation in collecting the datasets used in the study.  
29  
30 621 We acknowledge Matthew Cooper, Irwin Bernstein, Antje Engelhardt, and Marina  
31  
32 622 Butovskaya for sharing their data. We are grateful to the following people: Muhammad  
33  
34 623 Agil, Mewa Singh, Jinhua Li, Suchinda Malaivijitnond, Yuzuru Hamada, Mukesh Kumar  
35  
36 624 Chalise, Mohamed Qarro and Ellen Merz, and organizations: the Cooperative Research  
37  
38 625 Program of Kyoto University's Wildlife Research Centre, the Caribbean Primate Research  
39  
40 626 Center, the Macaca Nigra Project, the Haut Commissariat aux Eaux et Forêts et à la Lutte  
41  
42 627 Contre la Désertification of Morocco, the Rome Zoo (Bioparco), the Huangshan Monkey  
43  
44 628 Management Centre, University of Strasbourg Institute for Advanced Studies (USIAS), and  
45  
46 629 the Barbary Macaque Project, for facilitating the collection of these datasets. Finally, we  
47  
48 630 wish to thank Dr. Heish Fushing and Kevin Fujii for their input regarding the computation  
49  
50 631 of dominance network traits and the generation of permuted network datasets. Authors  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 632 KNB, BAB and BJM were supported by the University of California at Davis, the National  
4  
5 633 Institute of Health (NIH: R01-HD068335), and the National Science Foundation (NSF:  
6  
7  
8 634 NSF-V451CNH). The International Animal Care and Use Committee of the University of  
9  
10 635 California at Davis approved the research.

11  
12  
13 636 **References:**

14  
15 637 Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, 49, 227-  
16  
17 638 266.

18  
19 639 Arnold, C., Matthews, L. J., & Nunn, C. L. (2010). The *10kTrees* website: a new online resource  
20  
21 640 for primate phylogeny. *Evolutionary Anthropology*, 19, 114-118.

22  
23  
24 641 Balasubramaniam, K. N., Beisner, B. A., Vandeleest, J., Atwill, E. R., & McCowan, B. (2016).

25  
26 642 Social buffering and contact transmission: network connections have beneficial and  
27  
28 643 detrimental effects on Shigella infection risk among captive rhesus macaques. *PeerJ*,  
29  
30 644 4:e2630. doi:<https://doi.org/10.7717/peerj.2630>

31  
32  
33 645 Balasubramaniam, K. N., Berman, C. M., Ogawa, H., & Li, J. (2011). Using Biological Markets  
34  
35 646 Principles to Examine Patterns of Grooming Exchange in *Macaca thibetana*. *American*  
36  
37 647 *Journal of Primatology*, 73(12), 1269-1279. doi:10.1002/ajp.20999

38  
39  
40 648 Balasubramaniam, K. N., Dittmar, K., Berman, C. M., Butovskaya, M., Cooper, M. A., Majolo, B., . .  
41  
42 649 . de Waal, F. B. M. (2012a). Hierarchical steepness and phylogenetic models:  
43  
44 650 phylogenetic signals in *Macaca*. *Animal Behaviour*, 83, 1207-1218.

45  
46 651 Balasubramaniam, K. N., Dittmar, K., Berman, C. M., Butovskaya, M., Cooper, M. A., Majolo, B., . .  
47  
48 652 . De Waal, F. B. M. (2012b). Hierarchical steepness, counter-aggression, and macaque  
49  
50 653 social style scale. *American Journal of Primatology*, 74, 915-925.

51  
52  
53 654 Balasubramaniam, K. N., Dunayer, E. S., Gilhooly, L. J., Rosenfield, K. A., & Berman, C. M. (2014).  
54  
55 655 Group size, contest competition, and social structure in Cayo Santiago rhesus  
56  
57 656 macaques. *Behaviour*, 151, 1759-1798.

- 1  
2  
3 657 Barton, R. A., Bryne, R. W., & Whiten, A. (1996). Ecology, feeding competition and social  
4  
5 658 structure in baboons. *Behavioral Ecology and Sociobiology*, *38*, 321-329.  
6  
7  
8 659 Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., . . . Green, P.  
9  
10 660 (2016). Linear mixed-effects models using 'eigen' and S4. Retrieved from  
11  
12 661 <https://github.com/lme4/lme4/> <http://lme4.r-forge.r-project.org/>  
13  
14 662 Berman, C. M., & Thierry, B. (2010). Variation in kin bias: species differences and time  
15  
16 663 constraints in macaques. *147*(13), 1863-1887. doi:doi:10.1163/000579510X539691  
17  
18 664 Blomberg, S. P., Garland, T., & Ives, A. (2003). Testing for Phylogenetic Signal in Comparative  
19  
20 665 Data: Behavioral Traits are more Labile. *Evolution*, *57*, 717-745.  
21  
22 666 Boinski, S. (1999). The social organizations of squirrel monkeys: implications for ecological  
23  
24 667 models of social evolution. *Evolutionary Anthropology*, *8*, 101-112.  
25  
26 668 Borgeaud, C., Sosa, S., Bshary, R., Sueur, C., & van de Waal, E. (2016). Intergroup Variation of  
27  
28 669 Social Relationships in Wild Vervet Monkeys: A Dynamic Network Approach. *Front.*  
29  
30 670 *Psychol.*, *7*: 915. doi:10.3389/fpsyg.2016.00915  
31  
32 671 Brent, L. J. N., Lehmann, J., & Ramos-Fernandez, G. (2011). Social Network Analysis in the  
33  
34 672 Study of Nonhuman Primates: A Historical Perspective. *American Journal of*  
35  
36 673 *Primatology*, *73*(8), 720-730. doi:10.1002/ajp.20949  
37  
38 674 Brent, L. J. N., Semple, S., Dubuc, C., Heistermann, M., & MacLarnon, A. (2010). Social capital  
39  
40 675 and physiological stress levels in adult female rhesus macaques. *Physiology &*  
41  
42 676 *Behavior*, *102*, 76-83.  
43  
44 677 Burnham, K. P., & Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical*  
45  
46 678 *Information-Theoretic Approach*, 2nd edn. Berlin: Springer.  
47  
48 679 Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel  
49  
50 680 inference in behavioral ecology: some background, observations, and comparisons.  
51  
52 681 *Behavioral Ecology and Sociobiology*, *65*, 23-35.  
53  
54  
55  
56  
57  
58  
59  
60



- 1  
2  
3 682 Butovskaya, M., Kozintsev, A., & Welker, C. (1995). Grooming and social rank by birth: the case  
4  
5 683 of *Macaca fascicularis*. *Folia Primatologica*, 65, 30-33.  
6  
7  
8 684 Capitano, J. P. (1999). Personality dimensions in adult male rhesus macaques: prediction of  
9  
10 685 behaviors across time and situation. *American Journal of Primatology*, 47, 299-320.  
11  
12 686 Castles, D. L., Aureli, F., & de Waal, F. B. M. (1996). Variation in conciliatory tendency and  
13  
14 687 relationship quality across groups of pigtailed macaques. *Animal Behaviour*, 52, 389-  
15  
16 688 403.  
17  
18  
19 689 Chan, L. K. W. (1996). Phylogenetic interpretations of primate socioecology: with special  
20  
21 690 reference to social and ecological diversity in *Macaca*. In E. P. Martins (Ed.),  
22  
23 691 *Phylogenies and the Comparative Method in Animal Behaviour* (pp. 324-360). Oxford:  
24  
25 692 Oxford University Press.  
26  
27  
28 693 Chatterjee, H. J., Ho, S. Y. W., Barnes, I., & Groves, C. (2009). Estimating the Phylogeny and  
29  
30 694 Divergence Times of Primates Using a Supermatrix Approach. *BMC Evol. Biol.*, 9, 259-  
31  
32 695 277.  
33  
34 696 Clutton-Brock, T. H., & Janson, C. H. (2012). Primate socioecology at the crossroads: past,  
35  
36 697 present, and future. *Evolutionary Anthropology*, 21, 136-150. doi:10.1002/evan.21316  
37  
38  
39 698 Cooper, M. A., Aureli, F., & Singh, M. (2007). Sex Differences in Reconciliation and Post-Conflict  
40  
41 699 Anxiety in Bonnet Macaques. *Ethology*, 113, 26-38.  
42  
43 700 Cooper, M. A., & Bernstein, I. S. (2008). Evaluating Dominance Styles in Assamese and Rhesus  
44  
45 701 Macaques. *Int. J. of Primatol.*, 29, 225-243.  
46  
47  
48 702 Cords, M. (2013). The behavior, ecology, and social evolution of Cercopithecine monkeys. In J.  
49  
50 703 C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit, & J. B. Silk (Eds.), *The Evolution of*  
51  
52 704 *Primate Societies* (pp. 91-112). Chicago and London: The University of Chicago Press.  
53  
54  
55 705 Croft, D. P., James, R., & Krause, J. (2008). *Exploring Animal Social Networks*. Princeton:  
56  
57 706 Princeton University Press.  
58  
59  
60

- 1  
2  
3 707 Croft, D. P., Madden, J. R., Franks, D. W., & James, R. (2011). Hypothesis testing in animal social  
4  
5 708 networks. *Journal of Animal Ecology*, 26, 502-507.  
6  
7 709 Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research,  
8  
9 710 Interjournal.  
10  
11 711 De Marco, A., Cozzolino, R., Dessi-Fulgheri, F., & Thierry, B. (2010). Conflicts induce affiliative  
12  
13 712 interactions among bystanders in a tolerant species of macaque (*Macaca tonkeana*).  
14  
15 713 *Animal Behaviour*, 80, 197-203.  
16  
17 714 de Vries, H. (1998). Finding a dominance order most consistent with a linear hierarchy: a new  
18  
19 715 procedure and review. *Animal Behaviour*, 55, 827-843.  
20  
21 716 de Vries, H., Stevens, J. M. G., & Vervaecke, H. (2006). Measuring and testing the steepness of  
22  
23 717 dominance hierarchies. *Animal Behaviour*, 71, 585-592.  
24  
25 718 de Waal, F. B. M., & Luttrell, L. M. (1989). Towards a Comparative Ecology of the Genus  
26  
27 719 *Macaca*: Different Dominance Styles in Rhesus and Stumptailed Macaques. *Am. J. of*  
28  
29 720 *Primatol.*, 19, 83-109.  
30  
31 721 Demaria, C., & Thierry, B. (2001). A Comparative Study of Reconciliation in Rhesus and  
32  
33 722 Tonkean Macaques. *Behaviour*, 138, 397-410.  
34  
35 723 Duboscq, J., Micheletta, J., Agil, M., Hodges, K., Thierry, B., & Engelhardt, A. (2013). Social  
36  
37 724 tolerance in wild female crested macaques (*Macaca nigra*) in Tangkoko-Batuangus  
38  
39 725 nature reserve, Sulawesi, Indonesia. *Am. J. Primatol.*, 75, 361-375.  
40  
41 726 Duboscq, J., Romano, V., Sueur, C., & MacIntosh, A. J. J. (2016). Network centrality and  
42  
43 727 seasonality interact to predict lice load in a social primate. *Scientific Reports*, 6, 22095.  
44  
45 728 doi:10.1038/srep22095  
46  
47 729 Dunbar, R. I. M. (1992). Time: a hidden constraint on the behavioural ecology of baboons.  
48  
49 730 *Behavioral Ecology and Sociobiology*, 31, 35-49.  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 731 Farine, D. R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal social  
4  
5 732 network analysis. *Journal of Animal Ecology*, *84*, 1144-1163.  
6  
7 733 Fox, J., & Weisberg, S. (2011). *An R Companion to Applied Regression*. Sage: Second Edition.  
8  
9 734 Fujii, K., Fushing, H., Beisner, B. A., & McCowan, B. (2013). Computing power structures in  
10  
11 735 directed biosocial networks: flow percolation and imputed conductance. *Technical*  
12  
13 736 *Report. Department of Statistics, UC Davis*.  
14  
15 737 Fushing, H., McAssey, M. P., Beisner, B., & McCowan, B. (2011). Ranking network of a captive  
16  
17 738 rhesus macaque society: a sophisticated corporative kingdom. *PLoS ONE*, *6*, e17817.  
18  
19 739 Gammell, M. P., de Vries, H., Jennings, D. J., Carlin, C. M., & Hayden, T. J. (2003). David's Score: A  
20  
21 740 More Appropriate Dominance Ranking Method than Clutton-Brock et al.'s Index.  
22  
23 741 *Animal Behaviour*, *66*, 601-605.  
24  
25 742 Gelman, A., Su, Y. S., Yajima, M., Hill, J., Pittau, M. G., & Kerm, J. (2009). arm: data analysis using  
26  
27 743 regression and multilevel/hierarchical models. *R package, version 9.01*.  
28  
29 744 Griffin, R. H., & Nunn, C. L. (2012). Community structure and the spread of infectious disease  
30  
31 745 in primate social networks. *Evolutionary Ecology*, *26*(4), 779-800.  
32  
33 746 doi:10.1007/s10682-011-9526-2  
34  
35 747 Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in  
36  
37 748 ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology*, *24*,  
38  
39 749 699-711.  
40  
41 750 Handcock, M., Hunter, D., Butts, C., Goodreau, S., & Morris, M. (2006). Statnet: An R package  
42  
43 751 for the statistical analysis and simulation of social networks. University of  
44  
45 752 Washington: <http://www.csde.washington.edu/statnet>.  
46  
47 753 Henzi, S. P., & Barrett, L. (1999). The value of grooming to female primates. *Primates*, *40*(1),  
48  
49 754 47-59.  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 755 Henzi, S. P., & Barrett, L. (2003). Evolutionary ecology, sexual conflict, and behavioral  
4  
5 756 differentiation among baboon populations. *Evolutionary Anthropology*, *12*, 217-230.  
6  
7 757 Hinde, R. A. (1976). Interactions, Relationships and Social Structure. *Man*, *11*, 1-17.  
8  
9 758 Kamilar, J., & Cooper, N. (2015). Phylogenetic signal in primate behaviour, ecology and life  
10  
11 759 history. *Philos. Trans. R. Soc. B*, *368*, 20120341.  
12  
13 760 Kappeler, P. M., & Van Schaik, C. P. (2002). Evolution of Primate Social Systems. *Int. J. of*  
14  
15 761 *Primatol.*, *23*, 707-740.  
16  
17 762 Kasper, C., & Voelkl, B. (2009). A social network analysis of primate groups. *Primates*, *50*, 343-  
18  
19 763 256.  
20  
21 764 Koenig, A., Scarry, C. J., Wheeler, B. C., & Borries, C. (2013). Variation in grouping patterns,  
22  
23 765 mating systems and social structure: what socio-ecological models attempt to explain.  
24  
25 766 *Philosophical Transactions of the Royal Society B-Biological Sciences*, *368*, 20120348.  
26  
27 767 doi:10.1098/rstb.2012.0348  
28  
29 768 Korstjens, A. H., Lehmann, J., & Dunbar, R. I. M. (2010). Resting time as an ecological constraint  
30  
31 769 on primate biogeography. *Animal Behaviour*, *79*(2), 361-374.  
32  
33 770 doi:<http://dx.doi.org/10.1016/j.anbehav.2009.11.012>  
34  
35 771 Krause, J., Croft, D. P., & James, R. (2007). Social network theory in the behavioural sciences:  
36  
37 772 potential applications. *Behavioral Ecology and Sociobiology*, *62*, 15-27.  
38  
39 773 Krause, J., James, R., & Croft, D. P. (2010). Personality in the context of social networks. *Philos.*  
40  
41 774 *Trans. R. Soc. B*, *365*, 4099-4106.  
42  
43 775 Leiva, D., & de Vries, H. (2014). Testing steepness of dominance hierarchies.  
44  
45 776 Lemey, P., Rambaut, A., Drummond, A. J., & Suchard, M. A. (2009). Bayesian Phylogeography  
46  
47 777 Finds Its Roots. *PLoS Comp Biol*, *5*(9), e1000520. doi:10.1371/journal.pcbi.1000520  
48  
49 778 Lusseau, D., & Newman, M. E. J. (2004). Identifying the role that individual animals play in  
50  
51 779 their social network. *Proc R Soc London B (Suppl)*, *271*, S477-S481.  
52  
53  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 780 Lusseau, D., Whitehead, H., & Gero, S. (2008). Incorporating uncertainty into the study of  
4  
5 781 animal social networks. *Animal Behaviour*, 75, 1809-1815.  
6  
7  
8 782 Majolo, B., Ventura, R., Koyama, N. F., Hardie, S. M., Jones, B. M., Knapp, L. A., & Schino, G.  
9  
10 783 (2009). Analyzing the Effects of Group Size and Food Competition on Japanese  
11  
12 784 Macaque Social Relationships. *Behaviour*, 146, 113-137.  
13  
14 785 Matsumura, S. (1999). The evolution of "egalitarian" and "despotic" social systems among  
15  
16 786 macaques. *Primates*, 40, 23-31.  
17  
18  
19 787 McCowan, B., Anderson, K., Heagarty, A., & Cameron, A. (2008). Utility of social network  
20  
21 788 analysis for primate behavioral management and well-being. *Applied Animal*  
22  
23 789 *Behaviour Science*, 109, 396-405. doi:10.1016/j.applanim.2007.02.009  
24  
25 790 McFarland, R., & Majolo, B. (2011). Exploring the Components, Asymmetry and Distribution of  
26  
27 791 Relationship Quality in Wild Barbary Macaques (*Macaca sylvanus*). *PLoS ONE*, 6,  
28  
29 792 e28826. doi:10.1371/journal.pone.0028826  
30  
31  
32 793 Ménard, N. (2004). Do ecological factors explain variation in social organization? . In B.  
33  
34 794 Thierry, M. Singh, & W. Kaumanns (Eds.), *Macaque Societies: a Model for the Study of*  
35  
36 795 *Social Organization* (pp. 157-185). Cambridge: Cambridge University Press.  
37  
38 796 Molesti, S., & Majolo, B. (2013). Grooming increases self-directed behaviour in wild Barbary  
39  
40 797 macaques, *Macaca sylvanus*. *Animal Behaviour*, 86 169-175.  
41  
42  
43 798 Nakagawa, S., & Freckleton, R. P. (2010). Model averaging, missing data and multiple  
44  
45 799 imputation: a case study for behavioural ecology. *Behavioral Ecology and Sociobiology*,  
46  
47 800 65, 103-116.  
48  
49  
50 801 Newman, M. E. J. (2004). Analysis of weighted networks. *Physical Review E*, 70, 056131.  
51  
52 802 Newman, M. E. J. (2006). Modularity and community structure in networks. *PNAS*, 103, 8577-  
53  
54 803 8582.  
55  
56  
57  
58  
59  
60

- 1  
2  
3 804 Nunn, C. L. (2011). *The Comparative Approach in Evolutionary Anthropology and Biology*.  
4  
5 805 Chicago: Univ of Chicago Press.  
6  
7 806 Nunn, C. L., Jordan, F., McCabe, C. M., Verdolin, J. L., & Fewell, J. H. (2015). Infectious disease  
8  
9 807 and group size: more than just a numbers game. *Philos. Trans. R. Soc. B*, *370*,  
10  
11 808 20140111.  
12  
13 809 Okamoto, K., & Matsumura, S. (2002). Intergroup encounters in wild moor macaques (*Macaca*  
14  
15 810 *maurus*). *Primates*, *43*, 119-125.  
16  
17 811 Ossi, J., & Kamilar, J. M. (2006). Environmental and phylogenetic correlates of Eulemur  
18  
19 812 behavior and ecology (Primates: Lemuridae). *Behavioral Ecology and Sociobiology*, *61*,  
20  
21 813 53-64.  
22  
23 814 Pagel, M. (1997). Inferring evolutionary processes from phylogenies. *Zool. Scripta*, *26*, 331-  
24  
25 815 348. doi:10.1111/j.1463-6409.1997.tb00423.x  
26  
27 816 Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, *401*, 877-  
28  
29 817 884. doi:10.1038/44766  
30  
31 818 Pasquaretta, C., Levé, M., Claidière, N., van de Waal, E., Whiten, A., MacIntosh, A. J. J., . . . Sueur,  
32  
33 819 C. (2014). Social networks in primates: smart and tolerant species have more efficient  
34  
35 820 networks. *Scientific Reports*, *4*, 7600. doi:10.1038/srep07600  
36  
37 821 Petit, O., Abegg, C., & Thierry, B. (1997). A Comparative Study of Aggression and Conciliation  
38  
39 822 in Three Cercopithecae Monkeys (*Macaca fuscata*, *Macaca nigra* and *Papio papio*).  
40  
41 823 *Behaviour*, *134*, 415-432.  
42  
43 824 Pons, P., & Latapy, M. (2004). Computing communities in large networks using random walks.  
44  
45 825 *J Graph Algorithms Appl.*, *10*, 284-293.  
46  
47 826 Puga, I., & Sueur, C. (2017). Emergence of complex social networks from spatial structure and  
48  
49 827 rules of thumb: a modelling approach. *Ecological Complexity*, *31*, 189-200.  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 828 Ree, R. H., & Smith, S. A. (2008). Maximum likelihood inference of geographic range evolution  
4  
5 829 by dispersal, local extinction, and cladogenesis. *Systematic Biology*, 51, 4-14.  
6  
7 830 doi:10.1080/10635150701883881  
8  
9 831 Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other  
10  
11 832 things). *Methods Ecol. Evol.*, 3, 217-233. doi:10.1111/j.2041-210X.2011.00169.x  
12  
13 833 Romano, V., Duboscq, J., Sarabian, C., Thomas, E., Sueur, C., & MacIntosh, A. J. J. (2016).  
14  
15 834 Modeling infection transmission in primate networks to predict centrality-based risk.  
16  
17 835 *American Journal of Primatology*, 78, 767-779.  
18  
19 836 Sade, D. (1972). Sociometrics of *Macaca mulatta* I. Linkages and cliques in grooming matrices.  
20  
21 837 *Folia Primatologica*, 18, 196-223.  
22  
23 838 Schino, G. (2001). Grooming, competition and social rank among female primates: a meta-  
24  
25 839 analysis. *Animal Behaviour*, 62, 265-271.  
26  
27 840 Schino, G., & Aureli, F. (2008). Tradeoffs in primate grooming reciprocation: testing behavioral  
28  
29 841 flexibility and correlated evolution. *Biological Journal of the Linnean Society*, 95, 439-  
30  
31 842 446.  
32  
33 843 Schino, G., di Sorrentino, E. P., & Tiddi, B. (2007). Grooming and Coalitions in Japanese  
34  
35 844 Macaques (*Macaca fuscata*): Partner Choice and Time Frame of Reciprocation. *J. Comp.*  
36  
37 845 *Psychol.*, 121, 181-188.  
38  
39 846 Schülke, O., & Ostner, J. (2008). Male reproductive skew, paternal relatedness, and female  
40  
41 847 social relationships. *Am. J. of Primatol.*, 70, 695-698. doi:10.1002/ajp.20546  
42  
43 848 Schülke, O., & Ostner, J. (2013). Ecological and social influences on sociality *The Evolution of*  
44  
45 849 *Primate Societies* (pp. 195-219). Chicago and London: The University of Chicago Press.  
46  
47 850 Shizuka, D., & Mcdonald, D. B. (2012). A social network perspective on measurements of  
48  
49 851 dominance hierarchies. *Animal Behaviour*, 83, 925-934.  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 852 Sih, A., Bell, A., & Chadwick Johnson, J. (2004). Behavioral syndromes: an ecological and  
4  
5 853 evolutionary overview. *Trends in Ecology and Evolution*, *19*, 372-378.  
6  
7  
8 854 Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant  
9  
10 855 survival. *Science*, *302*, 1231-1234.  
11  
12 856 Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social  
13  
14 857 relationships in non-human primates. *Behavioral Ecology and Sociobiology*, *41*, 291-  
15  
16 858 309.  
17  
18  
19 859 Sueur, C., Jacobs, A., Amblard, F., Petit, O., & King, A. J. (2011a). How can social network  
20  
21 860 analysis improve the study of primate behavior? *American Journal of Primatology*, *73*,  
22  
23 861 703-719.  
24  
25 862 Sueur, C., Petit, O., De Marco, A., Jacobs, A. T., Watanabe, K., & Thierry, B. (2011b). A  
26  
27 863 comparative network analysis of social style in macaques. *Animal Behaviour*, *82*(4),  
28  
29 864 845-852. doi:10.1016/j.anbehav.2011.07.020  
30  
31  
32 865 Thierry, B. (1985). Patterns of Agonistic Interactions in Three Species of Macaque (*Macaca*  
33  
34 866 *mulatta*, *M. fascicularis*, *M. tonkeana*). *Aggressive Behavior*, *11*, 223-233.  
35  
36 867 Thierry, B. (2000). Covariation of conflict management patterns across macaque species. In F.  
37  
38 868 Aureli & F. B. M. deWaal (Eds.), *In: Natural Conflict Resolution* (pp. 106-128). Berkley,  
39  
40 869 CA: University of California Press.  
41  
42  
43 870 Thierry, B. (2004). Social Epigenesis. In B. Thierry, M. Singh, & W. Kaumanns (Eds.), *Macaque*  
44  
45 871 *Societies: A Model for the Study of Social Organization* (pp. 267-290). Cambridge:  
46  
47 872 Cambridge University Press.  
48  
49 873 Thierry, B. (2007). Unity in diversity: lessons from macaque societies. *Evolutionary*  
50  
51 874 *Anthropology*, *16*, 224-238. doi:10.1002/evan.20147  
52  
53  
54  
55  
56  
57  
58  
59  
60



- 1  
2  
3 875 Thierry, B., Aureli, F., Nunn, C. L., Petit, O., Abegg, C., & de Waal, F. B. M. (2008). A Comparative  
4  
5 876 Study of Conflict Resolution in Macaques: Insights into the Nature of Covariation.  
6  
7 877 *Animal Behaviour*, 75, 847-860.  
8  
9  
10 878 Thierry, B., Iwaniuk, A. N., & Pellis, S. M. (2000). The influence of phylogeny on the social  
11  
12 879 behaviour of macaques (primates: cercopithecidae, genus *Macaca*). *Ethology*, 106,  
13  
14 880 713-728.  
15  
16 881 Tosi, A. J., Morales, J. C., & Melnick, D. J. (2003). Paternal, Maternal, and Biparental Molecular  
17  
18 882 Markers Provide Unique Windows onto the Evolutionary History of Macaque  
19  
20 883 Monkeys. *Evolution*, 57, 1419-1435.  
21  
22  
23 884 van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. In V.  
24  
25 885 Standen & R. A. Foley (Eds.), *Comparative Socioecology* (pp. 195-218): Blackwell  
26  
27 886 Scientific, Oxford.  
28  
29  
30 887 Ventura, R., Majolo, B., Koyama, N. F., Hardie, S. M., & Schino, G. (2006). Reciprocation and  
31  
32 888 Interchange in Wild Japanese Macaques: Grooming, Cofeeding and Agonistic Support.  
33  
34 889 *Am. J. Primatol.*, 68, 1138-1149.  
35  
36  
37 890 Wey, T., Blumstein, D. T., Shen, W., & Jordan, F. (2008). Social network analysis of animal  
38  
39 891 behaviour: a promising tool for the study of sociality. *Animal Behaviour*, 75, 333-344.  
40  
41 892 Whitehead, H. (2008). *Analyzing Animal Societies: Quantitative Methods for Vertebrate Social*  
42  
43 893 *Analysis*. Chicago: University of Chicago Press.  
44  
45 894 Young, C., Majolo, B., Heistermann, M., Schülke, O., & Ostner, J. (2014). Responses to social and  
46  
47 895 environmental stress are attenuated by strong male bonds in wild macaques. *PNAS*,  
48  
49 896 111, 18195-18200.  
50  
51  
52 897  
53  
54 898  
55  
56 899  
57  
58  
59  
60

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<sup>b</sup></u>	<u>Living</u> <u>Condition<sup>c</sup></u>
<i>fuscata</i> <sup>a</sup>	1	Yakushima, Japan	Ventura et al. (2006)	25	8	25 (NA)	Free-living
<i>fuscata</i> <sup>a</sup>	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 <sup>d</sup>
<i>mulatta</i>	1	Cayo Santiago, Puerto Rico	Balasubramaniam et al. (2014)	33	10	16	Free-living <sup>d</sup>
<i>mulatta</i> <sup>a</sup>	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 <sup>d</sup>
<i>assamensis</i>	2	Tham Pla Temple, Thailand	Ogawa (unpub)	47	14	9	Free-living <sup>d</sup>
<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 <sup>d</sup>

1								
2								
3	<i>thibetana</i>	2	Mt. Huangshan, China	Balasubramaniam et al. (2011)	42	9	47	Free-living <sup>d</sup>
4								
5	<i>thibetana</i>	2	Mt. Huangshan, China	Balasubramaniam et al. (2011)	42	9	38	Free-living <sup>d</sup>
6								
7	<i>thibetana</i>	2	Mt. Huangshan, China	Balasubramaniam et al. (2011)	52	10	11	Free-living <sup>d</sup>
8								
9	<i>thibetana</i>	2	Mt. Huangshan, China	Balasubramaniam et al. (2011)	49	10	12	Free-living <sup>d</sup>
10								
11	<i>thibetana</i>	2	Mt. Huangshan, China	Balasubramaniam et al. (2011)	37	10	20	Free-living <sup>d</sup>
12								
13	<i>arctoides</i> <sup>a</sup>	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 <sup>d</sup>
16								
17	<i>sylvanus</i>	3	Middle Atlas Mountains, Morocco	McFarland & Majolo (2011)	19	8	32	Free-living
18								
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
22								
23	<i>sylvanus</i>	3	Rocamadour, France	Sosa (2014)	55	24	14	Free-living <sup>d</sup>
24								
25	<i>sylvanus</i>	3	Rocamadour, France	Sosa (2014)	55	24	8	Free-living <sup>d</sup>
26								
27	<i>sylvanus</i>	3	Rocamadour, France	Sosa (2014)	55	24	12	Free-living <sup>d</sup>
28								
29	<i>nigra</i>	4	Tangkoko Reserve, Indonesia	Duboscq et al. (2013)	50	18	24	Free-living
30								
31	<i>nigra</i>	4	Tangkoko Reserve, Indonesia	Duboscq et al. (2013)	80	21	45	Free-living
32								
33	<i>nigra</i>	4	Tangkoko Reserve, Indonesia	Duboscq et al. (2013)	80	21	43	Free-living
34								
35	<i>nigra</i>	4	Tangkoko Reserve, Indonesia	Duboscq et al. (2013)	80	24	22	Free-living
36								
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
42								
43								
44								
45								
46								
47								
48								
49								

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>
<b>Dominance</b>			
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)
<b>Grooming</b>			
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)

912

913

914

915

916

1  
2  
3 917 **Table 3: Results of tests for phylogenetic signals among macaque dominance and**  
4  
5  
6 918 **grooming social network traits. K: Blomberg's Kappa coefficient; P: significance from**  
7  
8 919 **Randomization tests (Blomberg et al. 2003)**  
9

920

<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(*)	<b>1.704</b>	<b>0.022*</b>
Dominance Certainty	0.893	0.078(*)	<b>1.634</b>	<b>0.023*</b>
	<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

921

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

922

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

923

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

924

925

926

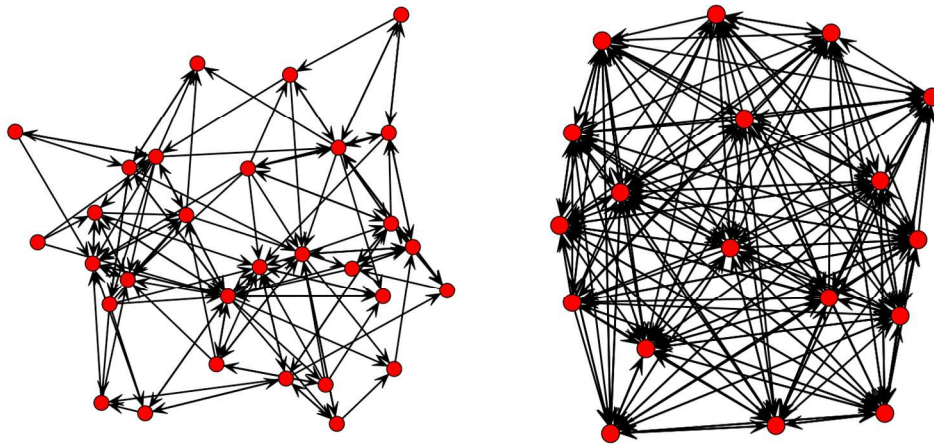
927 **Table 4: Summary of zero-averaged coefficients from the candidate models for**  
 928 **Newman's modularity and clustering coefficient of grooming networks.**

<u>(A) Newman's Modularity (8 candidate models)</u>					
	<u>B</u>	<u>Adj SE</u>	<u>z</u>	<u>Pr (&gt; z )</u>	<u>Importance</u>
Intercept	0.19	0.03	5.82	<0.01**	
Living Condition (Captive vs. Free living)	<b>0.15</b>	<b>0.04</b>	<b>4.16</b>	<b>&lt;0.01**</b>	<b>1</b>
Sex Ratio (proportion of females)	0.04	0.05	0.86	0.39	0.57
Group Size	<b>0.09</b>	<b>0.03</b>	<b>3.27</b>	<b>&lt;0.01**</b>	<b>1</b>
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**	
<b>Living Condition (Captive vs. Free living)</b>	<b>-0.44</b>	<b>0.20</b>	<b>2.25</b>	<b>0.02*</b>	<b>0.93</b>
Dominance Certainty	0.34	0.19	1.75	0.08	0.83
<b>Group Size</b>	<b>-0.21</b>	<b>0.09</b>	<b>2.43</b>	<b>0.02*</b>	<b>1</b>
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 <sup>a</sup> 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



984

985

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

991

992

993

994

995

996

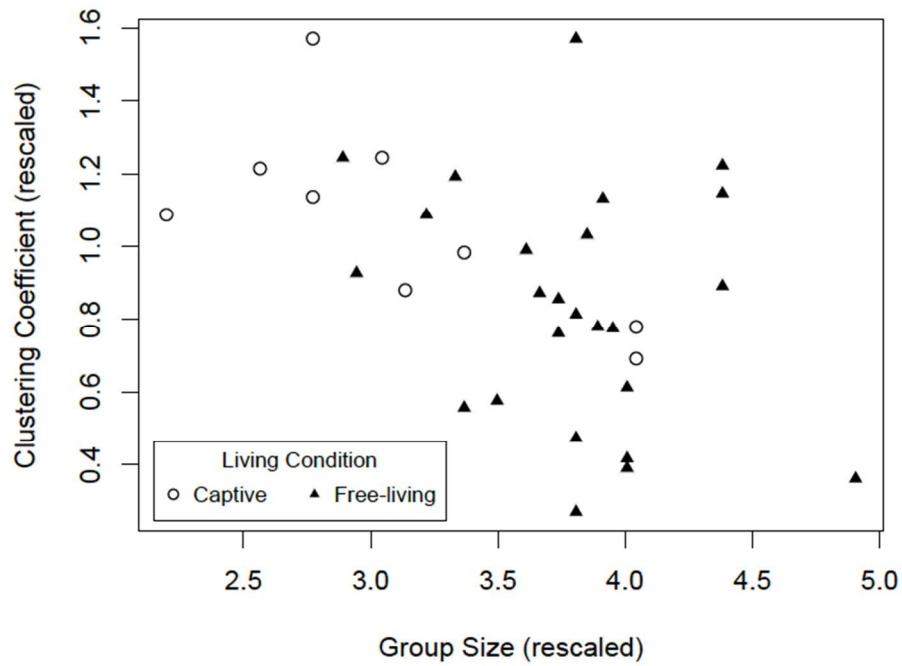
997

998

999

1000

1001



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

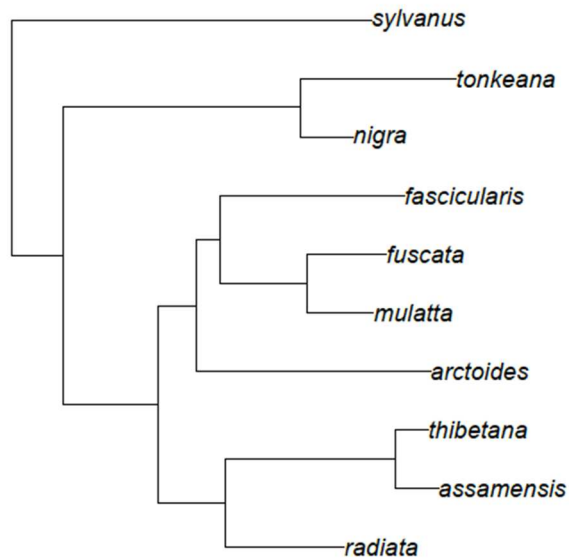


1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

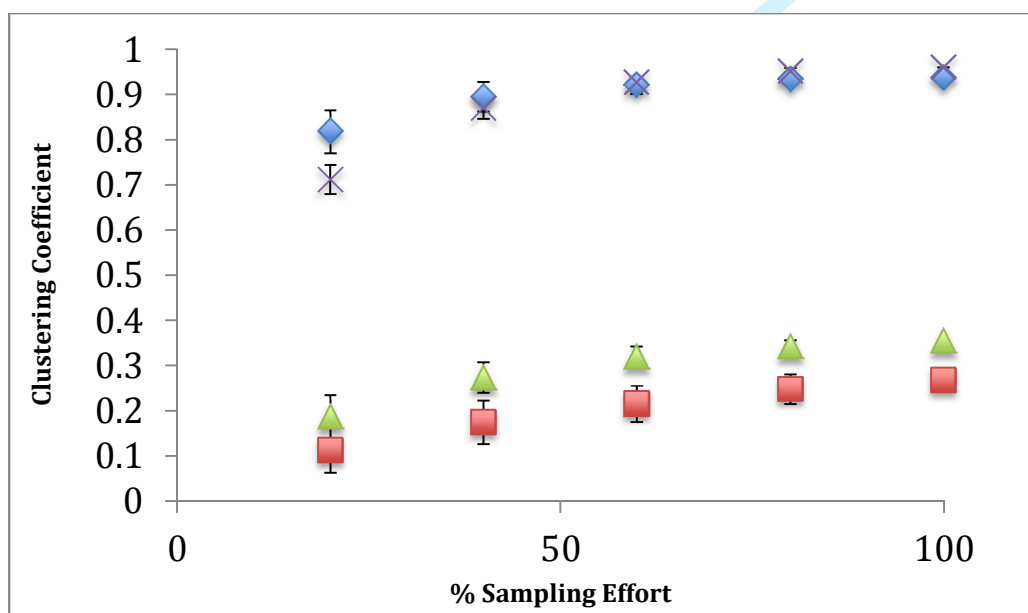
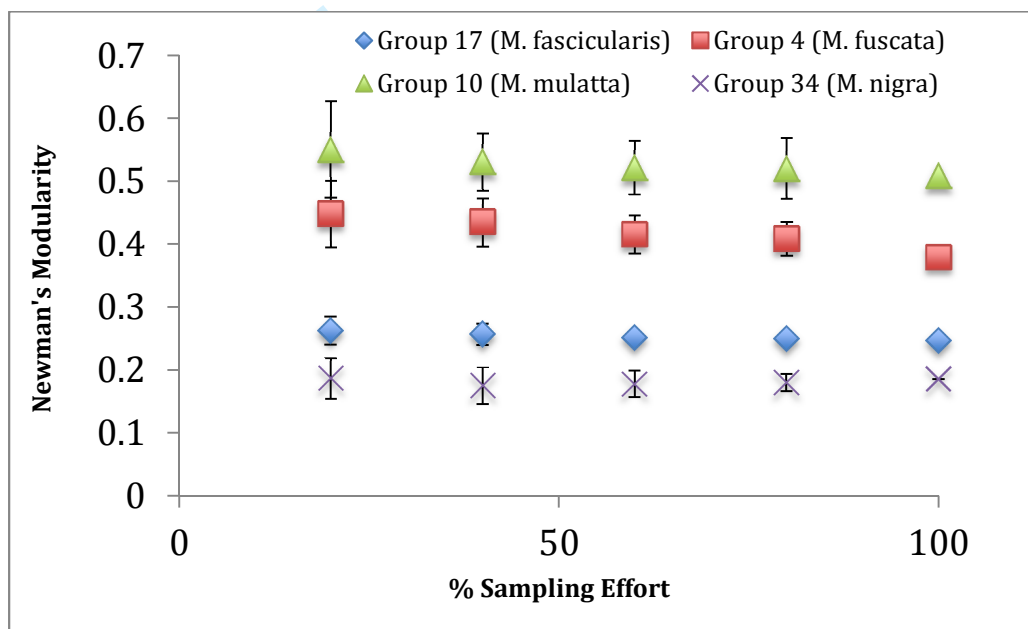
- We assessed the bases for variation in macaque social network structure
- Dominance traits showed phylogenetic signals, but grooming traits were linked to group size
- Social networks are influenced by both ancestral and sociodemographic factors

For Peer Review

1  
2  
3  
4 **Supplementary Figure 1: Consensus tree of phylogenetic relationships among 10**  
5 **species of macaques extracted from the 10ktrees website (Arnold et al., 2010), on**  
6 **which tests of phylogenetic signals were conducted**  
7  
8  
9

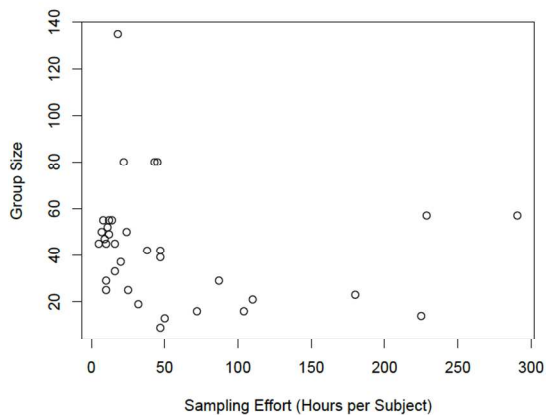


Supplementary Figure 2: Plots of grooming network measures against % sampling effort. Data-points represent means computed from values across 200 networks permuted from a natural dataset, and error bars represent standard deviations. Data-points at 100% sampling effort represent the value of the original 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)

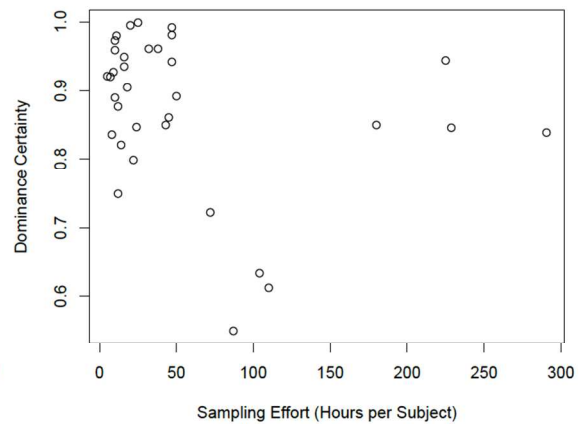


Supplementary Figure 3: Scatterplots between sampling effort and (A) group size, (B) dominance certainty, and (C) grooming Newman's modularity across the datasets. Datasets that used *Ad libitum* sampling (B: 3/38; C: 2/34), and/or were outliers (B: 1/38 dataset sampled for 675 hours per subject; C: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

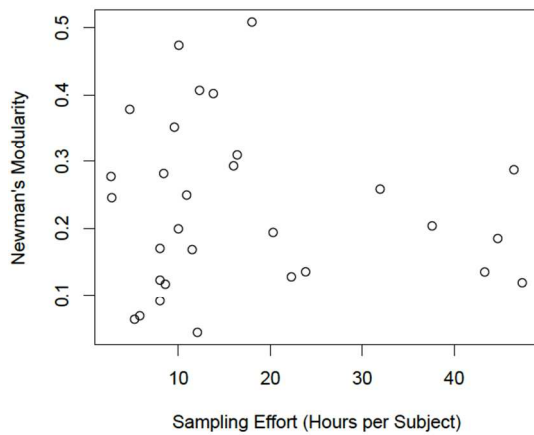
(A)



(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	<b>924 (&lt;0.01*)</b>	<b>893 (&lt;0.01*)</b>	<b>848 (&lt;0.01*)</b>	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>N<sup>1</sup></u>	<u>Pearson's R</u>	<u>p (p<sub>crit</sub> = 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>N<sup>1</sup></u>	<u>Pearson's R</u>	<u>p (p<sub>crit</sub> = 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

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

p<sub>crit</sub>: 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	<b>1.64 ± 0.06</b>	0.03*
Dominance Certainty	0.90 ± 0.08	0.10	<b>1.58 ± 0.07</b>	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.

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

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

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

For Peer Review

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.

<b>Model</b>	<b>(Int)</b>	<b>B Coefficients</b>							<b>df</b>	<b>AICc</b>	<b><math>\Delta</math></b>	<b>w</b>
		LC	SS	DC	SR	GS	T	GS: LC				
<b>1</b>	<b>0.19</b>	<b>0.15</b>			<b>0.07</b>	<b>0.10</b>			<b>6</b>	<b>-72.40</b>	<b>0.00</b>	<b>0.29</b>
<b>2</b>	<b>0.20</b>	<b>0.14</b>				<b>0.08</b>			<b>5</b>	<b>-71.70</b>	<b>0.65</b>	<b>0.21</b>
<b>3</b>	<b>0.19</b>	<b>0.16</b>		<b>-0.03</b>	<b>0.07</b>	<b>0.10</b>			<b>7</b>	<b>-69.60</b>	<b>2.77</b>	<b>0.07</b>
<b>4</b>	<b>0.19</b>	<b>0.15</b>			<b>0.07</b>	<b>0.10</b>	<b>-0.01</b>		<b>7</b>	<b>-69.30</b>	<b>3.06</b>	<b>0.06</b>
<b>5</b>	<b>0.19</b>	<b>0.15</b>			<b>0.07</b>	<b>0.10</b>		<b>0.00</b>	<b>7</b>	<b>-69.10</b>	<b>3.30</b>	<b>0.06</b>
<b>6</b>	<b>0.20</b>	<b>0.16</b>		<b>-0.03</b>		<b>0.08</b>			<b>6</b>	<b>-69.10</b>	<b>3.31</b>	<b>0.06</b>
<b>7</b>	<b>0.19</b>	<b>0.15</b>				<b>0.08</b>		<b>0.04</b>	<b>6</b>	<b>-68.90</b>	<b>3.43</b>	<b>0.05</b>
<b>8</b>	<b>0.20</b>	<b>0.15</b>				<b>0.08</b>	<b>-0.01</b>		<b>6</b>	<b>-68.90</b>	<b>3.46</b>	<b>0.05</b>
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

1													
2													
3													
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 <sup>^</sup>	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	
46													
47													
48													
49													
50													
51													
52													
53													
54													
55													
56													
57													
58													
59													
60													

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

For Peer Review

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.

<b>Mod</b>	<b>(Int)</b>	<b>B Coefficients</b>							<b>df</b>	<b>AICc</b>	<b><math>\Delta</math></b>	<b>w</b>
<b>el</b>		LC	SS	DC	SR	GS	T	GS: LC				
<b>1</b>	<b>0.97</b>	<b>-0.49</b>		<b>0.37</b>		<b>-0.20</b>			<b>6</b>	<b>7.50</b>	<b>0.00</b>	<b>0.28</b>
<b>2</b>	<b>0.94</b>	<b>-0.49</b>		<b>0.41</b>		<b>-0.22</b>		<b>0.23</b>	<b>7</b>	<b>9.70</b>	<b>2.17</b>	<b>0.10</b>
<b>3</b>	<b>0.62</b>	<b>-0.54</b>	+	<b>0.46</b>		<b>-0.19</b>			<b>9</b>	<b>10.00</b>	<b>2.44</b>	<b>0.08</b>
<b>4</b>	<b>0.97</b>	<b>-0.51</b>		<b>0.39</b>	<b>0.07</b>	<b>-0.18</b>			<b>7</b>	<b>10.50</b>	<b>2.95</b>	<b>0.06</b>
<b>5</b>	<b>0.97</b>	<b>-0.49</b>		<b>0.36</b>		<b>-0.20</b>	<b>0.01</b>		<b>7</b>	<b>10.70</b>	<b>3.18</b>	<b>0.06</b>
<b>6</b>	<b>0.97</b>	<b>-0.21</b>				<b>-0.26</b>			<b>5</b>	<b>10.90</b>	<b>3.40</b>	<b>0.05</b>
<b>7</b>	<b>0.97</b>					<b>-0.31</b>			<b>4</b>	<b>11.10</b>	<b>3.61</b>	<b>0.05</b>
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



1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

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 (&gt; z )</u>	<u>Importance</u>
Intercept	0.22	0.04	6.026	<0.01	
<b>Living Condition (Captive vs. Free living)</b>	<b>0.15</b>	<b>0.03</b>	<b>4.64</b>	<b>&lt;0.01**</b>	<b>1</b>
Sex Ratio (proportion of females)	0.07	0.05	1.47	0.14	0.82
<b>Group Size</b>	<b>0.09</b>	<b>0.03</b>	<b>3.40</b>	<b>&lt;0.01**</b>	<b>1</b>
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**	
<b>Group Size</b>	<b>-0.24</b>	<b>0.09</b>	<b>2.59</b>	<b>0.01*</b>	<b>1</b>
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

<sup>a</sup> 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 (&gt; z )</u>	<u>Importance</u>
Intercept	0.25	0.04	6.25	<0.01**	
<b>Living Condition (Captive vs. Free living)</b>	<b>0.14</b>	<b>0.03</b>	<b>4.52</b>	<b>&lt;0.01**</b>	<b>1</b>
Sex Ratio (proportion of females)	0.03	0.04	0.72	0.47	0.82
<b>Group Size</b>	<b>0.10</b>	<b>0.02</b>	<b>4.31</b>	<b>&lt;0.01**</b>	<b>1</b>
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**	
<b>Group Size</b>	<b>-0.20</b>	<b>0.07</b>	<b>2.82</b>	<b>0.00**</b>	<b>1</b>
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

<sup>a</sup> Effect sizes are standardized, comparable values (Gelman et al., 2009)

Data are from 34 groups of 9 macaque species

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