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Effect of behavioural sampling methods on local and global social network metrics: A case-study of three macaque species

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I/We declare we have no competing interests

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5 2 **network metrics: A case-study of three macaque species**
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8 3 Running head **Effect of sampling method on social networks**
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23 **ABSTRACT**

24 Social network analysis (SNA) is a powerful, quantitative tool to measure animals' direct
25 and indirect social connectedness in the context of social groups. However, the extent to
26 which behavioural sampling methods influence SNA metrics remains unclear. To fill this
27 gap, here we compare network indices of grooming, huddling, and aggression calculated
28 from data collected from three macaque species through two sampling methods: focal
29 animal sampling (FAS) and all-occurrences behaviour sampling (ABS). We found that
30 measures of direct connectedness (degree centrality, and network density) were correlated
31 between FAS and ABS for all social behaviours. Eigenvector and betweenness
32 centralities were correlated for grooming and aggression networks across all species. In
33 contrast, for huddling, we found a correlation only for betweenness centrality while
34 eigenvector centralities were correlated only for the tolerant bonnet macaque but not so
35 for the despotic rhesus macaque. Grooming and huddling network modularity and
36 centralization were correlated between FAS and ABS for all but three of the eight groups.
37 In contrast, for aggression network, we found a correlation for network centralization but
38 not modularity between the sampling methodologies. We discuss how our findings
39 provide researchers with new guidelines regarding choosing the appropriate sampling
40 method to estimate social network metrics.

41
42 **Keywords:** Aggression; All-occurrences behaviour sampling; Focal animal sampling;
43 Grooming; Huddling; Social Network Analysis

59 INTRODUCTION

60 Understanding the proximate and ultimate functions of social behaviour has been a central
61 topic across many disciplines from behavioural ecology [1], to psychology [2] and
62 neurobiology [3]. From an ultimate perspective, work conducted in the last two decades has
63 shown that individuals who engage in more frequent and stronger social relationships live
64 longer [4], are better at coping with social and environmental stressors [5], and produce more
65 offspring that are more likely to survive [6]. Interestingly, accumulating evidence suggests that
66 fitness-related benefits can be accrued not only through direct connections (i.e., how many
67 social partners individuals have) but also through *indirect* connections (i.e., how many social
68 partners each social partner has) [7].

69 In the last two decades, social network analysis (SNA) has proven to be a powerful tool
70 in animal behavioural ecology to measure both direct and indirect connections in social animals
71 [8,9]. SNA represents social interactions in terms of nodes (i.e., subjects involved in the
72 interactions) and edges (i.e., connections between nodes), and provides quantitative, data-
73 driven approaches to evaluate biologically relevant measures of animals' connectedness both
74 at local (i.e., individual/node) and global (i.e., group/network) levels [9]. Given these
75 advantages, it is perhaps not surprising that SNA has been used across different contexts to
76 study animal social relationships, including comparisons of animal social structures [1], the
77 social diffusion of information between group members [10], the spread of infectious disease
78 via social interactions [11,12], and in the conservation of wildlife populations [13].
79 Furthermore, a broad range of studies have used SNA to investigate what individual- and
80 group-level sociodemographic and behavioural attributes, such as individuals' sex [4],
81 dominance rank [14], personality [15], and groups' sizes and compositions can potentially
82 influence animals' social interactions and emergent social structure.

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3 83 While it is crucial that observed networks, defined as “analytical representations of a
4
5 84 combined set (or subset) of measures of the true relationships” [8], are as similar as possible to
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8 85 the real networks, namely “the real set of interactions between animals that integrate to form
9
10 86 community dynamics” [8], there is increasing evidence that the correspondence between
11
12 87 observed and real networks depends on the behavioural sampling methods employed and/or on
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14 88 the frequency by which animals perform the behaviour of interest [16,17]. This variation may
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17 89 occur because observers might miss recording some real, meaningful interactions between
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19 90 individuals, depending on the sampling technique used and the frequency of the behaviour
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21 91 performed. Since network elements are inter-dependent [8,9], the absence of one or more real
22
23 92 connections might generate an observed network that is potentially very different from a real
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26 93 network [8].

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28 94 To date, the majority of studies examining the effect of sampling technique on variation
29
30 95 in the structure of social networks has largely relied on simulations [16–18]. This work has
31
32 96 suggested that a minimum number of 10-20 observations within a given network might suffice
33
34 97 to construct a reliable network [16–18]. For instance, by generating simulated networks, Farine
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36 98 and Strandburgh-Peshkin [19] showed that a minimum of 20 samples is necessary in order to
37
38 99 have an accurate estimate of the edge weight (i.e., the rate of interaction or association between
39
40 100 two nodes) within a network. Similarly, Davis et al. [16] used proximity data generated by
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42 101 fitting high-resolution GPS collars on free-ranging baboons (*Papio anubis*) to simulate an
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44 102 increase in sampling effort made through two observational methods, focal animal sampling
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46 103 and group scanning. The authors showed that a minimum of 10 samples per individual was
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48 104 necessary in order for the estimated network to be similar to the complete network. In this
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50 105 context, it is pivotal, however, to use real biological data to test whether the reliability of
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52 106 network measures depends on the sampling technique used, as sometimes simulations do not
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54 107 accurately reflect true, biological data [e.g., 20]. Moreover, using real datasets can also better
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3 108 inform researchers on how to best design their methodologies to generate reliable social
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5 109 networks. Notwithstanding, only few studies to date have compared different sampling
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7 110 techniques using actual observations, rather than simulations. McCarthy et al. [21], for
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9 111 instance, compared network measures calculated using data recorded through camera traps and
10
11 112 focal observations among wild chimpanzees (*Pan troglodytes*). The authors found a strong
12
13 113 correlation in network centrality indices between the two data sets, but found differences in
14
15 114 network density and modularity. Conversely, Canteloup et al. [22] found a strong correlation
16
17 115 in both grooming and play networks between data collected via *ad libitum* sampling and those
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19 116 recorded through focal animal sampling among vervet monkeys (*Chlorocebus pygerythrus*).
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22 117 More recently, Gelardi et al. [23] found strong similarities between social networks calculated
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24 118 from direct observations and through wearable proximity sensors. Collectively, these data
25
26 119 suggest that different sampling methods yield similar network metrics, at least for local indices
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28 120 while differences may emerge for global indices.
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33 121 While the studies reviewed above have been crucial to understand to what extent
34
35 122 different sampling techniques can lead to differences in social network metrics, they also
36
37 123 lacked a comparative component as they focused either on single animal species or on a single
38
39 124 type of behaviour. Many group-living animal taxa, however, show both intra- and inter-species
40
41 125 differences in group cohesion and social organization, that are largely influenced by ecological
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43 126 factors [24–26]. Moreover, the frequency and directionality of social interactions may vary
44
45 127 broadly across behavioural types and socio-ecological contexts. For example, groups or species
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47 128 may show greater ‘despotism’ in their social structures, characterized by greater frequency and
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49 129 unidirectionality (from dominants towards subordinates) of agonistic interactions, but lower
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51 130 frequencies of prosocial behaviours that are also more preferentially directed towards sub-sets
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53 131 of preferred prosocial partners such as close kin [27]. Conversely, groups/species that show a
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55 132 more egalitarian/tolerant social system may be expected to show the opposite characteristics
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3 133 [27]. Crucially, it remains unclear to what extent different sampling techniques can produce
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5 134 similar network measurements across different groups/species that display different social
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8 135 systems. In order to fill this gap, our study aims to compare both local and global network
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10 136 measures of three different social networks (aggression, grooming, and huddling) collected
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12 137 through two different sampling techniques, focal animal sampling (FAS) and all-occurrences
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14 138 behaviour sampling (ABS), from three different macaque species, rhesus (*Macaca mulatta*),
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16
17 139 long-tailed (*Macaca fascicularis*) and bonnet macaques (*Macaca radiata*).

19 140 FAS and ABS are two observational methods that are most commonly used to collect
20
21 141 behavioural data to construct animal social networks [28,29]. FAS allows an observer to focus
22
23 142 their attention on a specific focal subject, thus offering the opportunity to record detailed
24
25 143 information on a wide range of behaviours, both frequent and infrequent, performed by the
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28 144 animal [28]. However, given that, via FAS, an observer focuses only on a single animal subject,
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30 145 an extended period of time is likely to be needed in order to have a big enough sample size to
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32 146 reliably reconstruct the social network of the whole group. Conversely, by observing the whole
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34 147 group, ABS may reduce the number of behaviours the observer can realistically collect, but it
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37 148 offers the advantage of recording interactions involving multiple individuals [28]. Such cost-
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39 149 benefit trade-off between these two sampling techniques is likely to be one of the main criteria
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41 150 behind researchers' decision on which data collection method to use. It would, therefore, be
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43 151 pivotal to examine whether data collected via both methods yield similar network
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45 152 measurements.

49 153 Macaques are a well-suited study model to compare social network indices between
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51 154 different sampling techniques. The genus *Macaca* includes 22 species, that show similar social
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53 155 organizations with female philopatry and male dispersal, but marked inter- and intra-specific
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55 156 variation in their social systems [27]. For instance, while some species, such as bonnet
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58 157 macaques, may be typically characterized by relatively more tolerant social relationships, other
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3 158 species such as rhesus macaques may display relatively more despotic social systems [27].
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5 159 Several other species may fall somewhere in between, with some of them, such as long-tailed
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7 160 macaques, classified closer to the “despotic” end of this spectrum [27]. Such a broad variation
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9 161 of social systems makes macaques well-suited models for our aims pertaining to adopting a
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11 162 comparative approach to assess methodological effects of observational techniques on social
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13 163 networks.
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17 164 Here we constructed social networks for multiple, free-living groups of macaques
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19 165 representing three species that are typically characterized by different social systems. Using
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21 166 data collected via FAS and ABS, we calculated six commonly used network measures: three
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23 167 local metrics (degree, eigenvector, and betweenness) and three global metrics (density,
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25 168 modularity and centralization) [9]. We compared network indices constructed from the two
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27 169 types of data to each other, predicting that if network measures were robust to the type of
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29 170 observation technique regardless of the type of social behaviour considered or the study
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31 171 species, then both local and global network measures from FAS data should correlate with
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33 172 those indices generated using ABS data. Conversely, if the accuracy of SNA metrics is
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35 173 contingent on species-typical social systems, we expect: (a) network measures of affiliative
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37 174 behaviours (grooming and huddling) to be more strongly correlated between observation
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39 175 methods among bonnet macaques than among long-tailed and rhesus macaques; and (b)
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41 176 network measures of aggressive interactions to be more strongly correlated across observation
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43 177 methods among the despotic rhesus and long-tailed macaques than among the more tolerant
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45 178 bonnet macaques. Finally, if observers are likely to record different dyadic interactions with
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47 179 FAS and ABS methods, then we would expect a lack of correlation between the social metrics
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49 180 calculated from FAS data and those calculated from ABS data.
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58 182 **MATERIALS AND METHODS**

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3 183 *Study sites and subjects*
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5 184 The study was conducted on a total of eight social groups of macaques. Rhesus
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8 185 macaques were studied in the city of Shimla, in Northern India (31° 05' N-077° 10' E) between
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10 186 August 2016 and February 2018. Here, we observed a total of 92 rhesus macaques (29 males
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12 187 and 63 females) from three macaque groups in two different locations: one group was observed
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14 188 in Mall Road (hereafter “MG”), and two groups (“HG” and “RG”) were observed at Jakhoo
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16 189 temple (for more details on the study site see [30,31]). Although there were some changes in
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18 190 the number of adult males and females across the three groups during the study period, the
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20 191 majority of the individuals remained in the group for most of the study (i.e., 75% of MG
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22 192 macaques, 79% of RG macaques and 69% of HG macaques remained in the group for at least
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24 193 one year of data collection; Fig. S1).
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28 194 Long-tailed macaques were studied in Kuala Lumpur (Malaysia) between September
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30 195 2016 and February 2018 (3°17' N-101°37' E). Here we observed a total of 79 individuals (24
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32 196 males and 55 females) from three macaque groups in two locations: one group (“Pirate”) was
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34 197 observed at Batu Caves, and two groups (“Entrance” and “Hulk”) were observed at Templer
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36 198 Park (for more details of the study site see [32]). Although these groups were subject to some
37
38 199 demographic changes, the majority of the individuals remained in the group throughout the
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40 200 study period (Pirate: 80%; Entrance: 71%; Hulk: 84%; Fig. S2).
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44 201 Bonnet macaques were observed in Thenmala, within the state of Kerala, in Southern
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46 202 India between July 2017 and May 2018 (8.9° N- 77.0° E). Here the groups were studied in two
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48 203 locations: one (“LG”) was studied at the Thenmala dam while one group (“SG”) was studied
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50 204 at the Ecotourism Recreational Area (for more details of the study site and group composition
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52 see [33]). Overall, we observed a total of 79 bonnet macaques (39 males and 40 females) and,
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54 205 for both groups, composition was subject to very minimal demographic changes, as the
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3 207 majority of the macaques remained in the group throughout the study period (LG: 71%; SG:
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5 208 83%; Fig. S3).
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10 210 *Data collection*
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12 211 Across the three study sites, and with the help of 4-5 field assistants per site, we
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14 212 recorded information on social grooming, huddling, and aggression using both FAS and ABS.
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16 213 We defined grooming as the manipulation of the skin or hair of a conspecifics with the hands
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18 214 in order to remove debris or ectoparasites, and huddling as the ventral-ventral or ventral-dorsal
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20 215 physical contact between individuals, while we classified as aggression any instance of
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22 216 chasing, aggressive grabbing, biting, slapping, or threatening. Data from the field assistants
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24 217 were allowed to contribute to the final data set only after they reached a Cohen reliability index
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26 218 ≥ 0.85 .
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30 219 Through FAS, we followed each adult macaque for 10 minutes recording any social
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32 220 interaction (i.e., grooming, huddling, and aggression) the focal subject was involved in as well
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34 221 as the identity of the conspecific interaction partners of the focal animal. The order by which
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36 222 focal subjects were selected was randomized every day, with the aim of collecting at least two
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38 223 focal sessions per subject per week. ABS was conducted 12 times per week, half of them in the
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40 224 morning and half in the afternoon. Each ABS session lasted for 10 minutes. At the beginning
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42 225 of an ABS session, the observer would record the individuals who were visible at the time.
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44 226 Subsequently, throughout the session, the observer would scan the group from left to right (and
45
46 227 vice versa) to record any new instance of social interaction and the identity of the individuals
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48 228 involved. At the end of this 10-min session, the observer would, again, record the individuals
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50 229 who were present in the group, before searching for a new sub-group and start a new 10-min
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52 230 session. We conducted FASs and ABSs at different times of the day as to avoid recording the
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54 231 same interactions using both methods. Overall, we collected a similar amount of data for both
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3 232 sampling methods (Figs. S4 & S5): for rhesus, we recorded an average of 143.2 and a median
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5 233 of 138 FAS sessions per month (RG: mean = 128.2, median = 139; HG: mean = 118.2, median
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7 = 121.5; MG: mean = 169.2, median = 174), and macaques were sampled via ABS an average
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9 of 166.2 and a median of 165 times per month (HG: mean = 101.2, median = 83; RG: mean =
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11 201.8, median = 166; MG: mean = 194.1, median = 193.5). Similarly, for long-tailed macaques,
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13 we recorded an average of 91.8 and a median of 97 FAS sessions per month (Pirate: mean =
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15 88.7, median = 74; Entrance: mean = 122.2, median = 121; Hulk: mean = 66.4, median = 65.5),
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17 whereas individuals were sampled an average of 88.5 and a median of 66 times per month
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19 through ABS (Pirate: mean = 77.2, median = 79; Entrance: mean = 120.6, median = 95; Hulk:
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21 mean = 71.4, median = 55). Finally, for bonnet macaques, we recorded an average of 219.6
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23 and a median of 207.5 FAS sessions per month (SG: mean = 154.7, median = 159; LG: mean
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25 = 284.5, median = 320), while macaques were sampled an average of 232.7 and a median of
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27 240 times per month via ABS (SG: mean = 183.2, median = 151; LG: mean = 282.3, median
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29 =293).

246

247 *Social network analysis*

248 We used the data on social interactions recorded via both FAS and ABS to construct
249 social networks. Since long-tailed macaques were observed huddling only rarely (Table S1),
250 we excluded huddling interactions for this species from the analysis. In order to take into
251 account the fact that individuals might have been present in the group for different lengths of
252 time, due to new individuals joining the group or some individuals disappearing from the
253 group, we calculated interaction frequencies by dividing the number of dyadic social
254 interactions by either the amount of time (for FAS) or the number of sessions (for ABS) in
255 which both members of the dyad were present in the group. We then used the *sna* and *igraph*
256 packages in R to calculate three local and three global metrics. At local level we measured: 1)

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3 257 *degree centrality* which reflects the number of edges that are connected to a node and thus
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5 258 represents the number of direct connections each subject has [9]; 2) *eigenvector centrality*,
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7 259 which is the sum of centralities of a node's neighbours, thereby representing the social support
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10 260 or social capital of an individual through being connected to animals who are in turn well
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12 261 connected themselves [9,34]; and 3) *betweenness centrality*, that is the number of shortest paths
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14 262 that flow through a node, indicating to what extent an individual connects subgroups, or may
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16 263 act as a 'hub' for information flow through the network [9]. These network measures were
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18 264 rescaled in order to take into account the different group sizes, and so ranged between 0 and 1.
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20 265 At global level, we measured: 1) *density* which is the number of edges divided by the total
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22 266 possible number of edges, and so assesses to what extent animals in the network are highly
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24 267 connected to each other [9]; 2) *modularity*, which is measured as the difference between the
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26 268 observed proportion of edges that fall within subgroups and the expected value of the same
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28 269 quantity if edges are assigned randomly and reflects to what degree a network can be
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30 270 subdivided into clusters of animals that more closely interact with each other than they do with
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32 271 animals in other clusters [35]; and 3) *eigenvector centralization*, which is the difference
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34 272 between the eigenvector centrality of the node with the highest eigenvector centrality of the
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36 273 group and the eigenvector centrality of the other group members, and represents to what extent
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38 274 few individuals tend to be more central within a social network [36]. While degree and density
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40 275 were computed as unweighted measures, without taking into account the frequency of each
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42 276 dyadic interaction, eigenvector, betweenness, modularity and centralization were calculated as
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44 277 weighted measures.
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54 279 *Data analysis*

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56 280 We first tested the robustness of each social network. We used two approaches to assess
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58 281 network robustness: we first assessed, for each data collection method and for each social
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3 282 behaviour, the variation in mean value of all three local network measures as well as the
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5 283 variation of all three global measures over time with monthly increases of data collected. We
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7 284 expected the curves to become progressively “flatter” because, if the networks were becoming
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9 285 more and more stable over time, monthly variation in network measures would become smaller
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11 286 and smaller as observers recorded fewer and fewer new edges between nodes. Second, we
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13 287 followed previous approaches [19,22,37], and used bootstrapping to estimate network
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15 288 uncertainty, which reflects the (un)certainty with which network metrics were estimated. For
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17 289 each monthly data and for each social behaviour examined, the identity of the recipient was
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19 290 randomly reshuffled and social network metrics were re-calculated. This procedure was
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21 291 repeated 1000 times, eventually generating a distribution of possible values. From this
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23 292 distribution, we extracted the 95% confidence interval and subtracted the maximum and
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25 293 minimum value of this range in order to calculate the uncertainty index. We then assessed, for
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27 294 both sampling methods, the monthly variation of this uncertainty index, expecting this value to
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29 295 decline as more observations were recorded and networks would become more certain.
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35 296 In order to assess whether local network measures calculated from FAS and ABS data
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37 297 were correlated, we ran Generalized Linear Mixed Model (GLMM) analyses with Beta error
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39 298 structure through the R function *glmmTMB*. In this model, ABS network measures were set as
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41 299 outcome variables in separate models, giving us a total of nine GLMMs. As predictors, we
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43 300 included FAS network measures, and species ID to account for their potential effects on
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45 301 network measures. We selected a Beta error structure for the GLMM models because the
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47 302 outcome variable could only range between 0 and 1 [38]. Finally, group identity was entered
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49 303 as a random factor in order to control for the non-independence of individuals from the same
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51 304 group. To assess whether network measures calculated using the two different methodologies
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53 305 were positively correlated for all species, or only for some species, we compared the Akaike
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55 306 Information Criterion (AIC) value of the null model (i.e., the model that included only the
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3 307 outcome variable and the random factor), with the model that included the predictors only as
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5 308 main effects, and the model that included the interaction between the FAS network measures
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7 309 and the species. We used the *influence_mixed* and *infIndexPlot* functions to check the presence
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9 310 of influential observations. The “performance” package in R was used to both calculate the
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11 311 effect size (R^2) of the GLMM model and verify that all GLMM models met the necessary
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13 312 assumptions of model validity (i.e., distribution of residuals, residuals plotted against fitted
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15 313 values). Given that network measures are not independent as an individual’s network metric
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17 314 depends on other individuals’ network positions, researchers typically use permutation to test
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19 315 the statistical significance of regression models [8,39]. However, recent simulations have
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21 316 suggested that permutation methods do not control for non-independence of the data and that
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23 317 GLMMs can already provide robust results [40]. Because no consensus has yet been reached
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25 318 on the best statistical approach when using regression models for social network data, in the
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27 319 main text we present the results of the GLMM analysis without permutation, while in the
28
29 320 supplementary materials we present the results of the permutation analysis, in which we
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31 321 compared the estimates generated from the observed data with a distribution of estimates
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33 322 calculated from random networks [41]. To this end, for each best GLMM model, we conducted
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35 323 a post-network node-swapping randomization which generated 1000 networks from the ABS
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37 324 data by randomly shuffling the identity of the network nodes, and then re-ran the GLMM
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39 325 analysis for each of these 1000 networks. This produced a distribution of estimates from these
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41 326 models and we calculated one-tailed p-values by comparing the number of the random
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43 327 estimates that were higher than the observed estimate.
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51 328 Finally, we used Pearson’s correlation test to assess whether global measures calculated
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53 329 from FAS data significantly correlated with the measures calculated from ABS data.
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3 330 R-codes and data are available in our data repository
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5 331 ([https://figshare.com/projects/Effect_of_behavioural_sampling_methods_on_local_and_glob](https://figshare.com/projects/Effect_of_behavioural_sampling_methods_on_local_and_global_social_network_metrics_A_case-study_of_three_macaque_species/166205)
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7 332 [al_social_network_metrics_A_case-study_of_three_macaque_species/166205](https://figshare.com/projects/Effect_of_behavioural_sampling_methods_on_local_and_global_social_network_metrics_A_case-study_of_three_macaque_species/166205)).
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12 334 *Ethical note*

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14 335 All applicable international, national, and/or institutional guidelines for the care and use of
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16 336 animals were followed. All procedures performed in this study were in accordance with the
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18 337 ethical standards of the Institutional Animal Care and Use Committee of the University of
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20 338 California, Davis, and complied with the legal requirements of India and Malaysia.
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25
26 340 **RESULTS**

27
28 341 *Network robustness*

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30 342 Table S1 summarizes the total number and frequencies of social interactions recorded
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32 343 for all three species and for both sampling methods, while visual representations of social
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34 344 networks calculated from both FAS and ABS for all three behaviours examined can be found
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36 345 in the supplementary material (Figs. S6-S13). Plotting monthly variation in network metrics
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38 346 (both mean local and global metrics) and their uncertainty values with monthly increases of
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40 347 data recorded across the three species revealed a progressive flattening of the curves for both
41
42 348 FAS and ABS data (Fig. 1 and Figs. S14-S24). Although network density was expected to
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44 349 either remain the same or increase over time, our analysis showed occasional reductions in
45
46 350 network density values. These are likely due to small changes in demographics (e.g., if an
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48 351 individual disappeared from the group, the connections this individual had with other group
49
50 352 members will have disappeared too). For both FAS and ABS, mean individual metrics flattened
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52 353 and uncertainty values dropped (suggesting more accuracy in the measurement) relatively early
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54 354 in data collection, although it required substantially more effort to achieve this when data were
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3 355 collected through FAS than when they were collected via ABS. More specifically, when data
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5 356 were collected via FAS, it took at least 50 hours of observations to reach no or minimal
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7 357 fluctuations of local metrics and their uncertainty with progressive increase in observation time
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9 358 (Figs. 1 & S14-S15). Conversely, when data were recorded through ABS, it took less than 10
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11 359 hours to reach the same result (Figs. S16-S18). Furthermore, similar to the local network
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13 360 metrics, our analysis of global metrics and their uncertainty values shows a progressive
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15 361 flattening of the curves. However, we found more fluctuation over time of global metrics
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17 362 compared to local indices with larger fluctuations for data collected through ABS than those
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19 363 collected through FAS (Figs. S19-S24). Furthermore, interestingly, it appears that it takes
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21 364 longer to reach a stability in global metrics compared to local metrics for both sampling
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23 365 methods. In fact, it took at least 100 hours of observation time with FAS and 15 hours of
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25 366 observation time with ABS to achieve minimal fluctuation in global metrics. Collectively, the
26
27 367 fact that our analysis shows that variation in both local and global metrics with progressive
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29 368 increase in observation time reaches a plateau and that uncertainty levels decrease suggest that
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31 369 the social networks measures in this study are accurate and robust.

370 **FIGURE 1 HERE**

371 *Grooming network analysis*

372 The analysis of the grooming network showed a significant effect of the interaction
373 between FAS data and species on ABS network metrics for both degree and betweenness
374 (Tables 1 & S2). While all three species showed a positive relationship between FAS and ABS
375 networks, this relationship was stronger for long-tailed macaques than for the other two species
376 (Fig. 2). Conversely, we found a significant main effect of FAS eigenvector on ABS
377 eigenvector (Tables 1 & S2). In other words, the macaques who were more central in the
378 grooming network (through both direct and indirect connections) as measured by the FAS data,

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3 379 were also more central in the grooming network as estimated by ABS data, across all three
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5 380 species.

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8 381 For global measures, we found a significant correlation between FAS and ABS data for
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10 382 both grooming density ($r(6) = 0.79$; $p = 0.02$) and modularity ($r(6) = 0.76$; $p = 0.03$, Fig. 2),
11
12 383 but not centralization ($r(6) = 0.59$; $p = 0.11$, Fig. 2). A close look at the centralization values
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14 384 shows that these values were particularly different between sampling methods in one rhesus
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16 385 (RG) and two long-tailed macaque groups (Hulk and Entrance). In fact, when these data points
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18 386 were removed, we found a significant correlation between ABS and FAS centralization values
19
20 387 ($r(3) = 0.91$; $p = 0.03$).

23
24 388 Collectively, this analysis showed that grooming network density and modularity were
25
26 389 both highly consistent (correlated) across sampling methods for all three macaque species,
27
28 390 whereas we did not find evidence that grooming network centralization was correlated between
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30 391 ABS and FAS. This lack of correlation is likely driven by one rhesus and two long-tailed
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32 392 macaque groups.

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38 394 **TABLE 1 HERE**

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42 396 **FIGURE 2 HERE**

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45 397 *Huddling network analysis*

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47 398 The analysis of huddling network at local level showed that, for both degree and eigenvector
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49 399 centrality, the interaction between FAS data and species was better fit compared to the null
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51 400 model and the model which included only the main effects terms (Tables 2 & S5). Exploring
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53 401 this interaction term further revealed that, for both rhesus and bonnet macaques, FAS degree
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55 402 positively predicted the corresponding ABS centrality measures, but that the relationship was
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57 403 stronger for bonnet macaques compared to rhesus macaques (Fig. 3), which supports our
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3 404 prediction. Conversely, for huddling network eigenvector, there was a positive relationship
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5 405 between FAS and ABS data for bonnet, while a negative relationship for rhesus macaques (Fig.
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7 406 3). Finally, for betweenness centrality, the model that included only the main effect was a
8
9 407 significantly better fit compared to the model that included the interaction term (Table S5). As
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11 408 predicted, this model showed a positive relationship between FAS and ABS betweenness
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13 409 (Table 2).

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17 410 Global analysis revealed a significant correlation between ABS and FAS data for both
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19 411 network density ($r(3) = 0.89$; $p = 0.04$) and modularity ($r(3) = 0.93$; $p = 0.02$, Fig. 3). In contrast,
20
21 412 we did not find a significant correlation between the two sampling methods for network
22
23 413 centralization ($r(3) = 0.57$; $p = 0.32$). Again, data from the RG group appeared to be an outlier.
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25 414 When this group was excluded, there was a significant correlation between ABS and FAS
26
27 415 huddling network centralization values ($r(2) = 0.97$; $p = 0.03$, Fig. 3).

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30 416 Collectively, these results suggest that FAS and ABS yield similar, consistent network
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32 417 metrics for all local network metrics. At the global level, these methods yield consistent metrics
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34 418 for network density and modularity, while for network centralization ABS and FAS sampling
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36 419 methods produced similar values for all but one group.
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42 421 **TABLE 2 HERE**

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46 423 **FIGURE 3 HERE**

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51 425 *Aggression network analysis*

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53 426 The analysis of aggression network showed that, across all three local measures, the
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55 427 models that included the predictors as main effects only had a better fit compared to the models
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57 428 that included the interaction between FAS network and species (Tables 3 & S6). For all three
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3 429 measures, there was a positive relationship between FAS and ABS data across all three species
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5 430 (degree: $\beta \pm SE = 23.80 \pm 2.02$, $z = 11.77$, $p < 0.001$; eigenvector: $\beta \pm SE = 8.85 \pm 2.18$, $z =$
6
7 431 4.07 , $p < 0.001$; betweenness: $\beta \pm SE = 11.17 \pm 1.78$, $z = 6.29$, $p < 0.001$; Table 3; Fig. 4),
8
9 432 suggesting that individuals that displayed higher aggression network degree, eigenvector and
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11 433 betweenness centrality values when data were collected through FAS, exhibited similar
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13 434 centrality values when data were collected through ABS.
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17 435 At global level, we found a significant correlation between FAS and ABS data for both
18
19 436 aggression network density ($r(6) = 0.90$; $p = 0.002$) and centralization ($r(6) = 0.78$; $p = 0.02$;
20
21 437 Fig. 4). In contrast, we found no evidence that aggression network modularity was significantly
22
23 438 correlated between the two sampling methods ($r(6) = 0.02$; $p = 0.95$).
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26 439 Collectively, our results showed that, for aggressive interactions, FAS data produce
27
28 440 similar network measures as those produced by ABS data for all local network indices (i.e.,
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30 441 degree, eigenvector and betweenness) and for two of the three global metrics examined (i.e.,
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32 442 density and centralization), while aggression modularity was not correlated between the two
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34 443 sampling methods.
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40 445 **TABLE 3 HERE**

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45 447 **FIGURE 4 HERE**

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49 449 Tables 4 and 5 provide a summary of the results.
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54 451 **TABLE 4 HERE**

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58 453 **TABLE 5 HERE**
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3 454 **DISCUSSION**
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5 455 The overarching goal of our study was to investigate whether two commonly used data
6 456 collection methods, FAS and ABS, produce similar social network measures. To this end, we
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8 457 compared three local (degree, eigenvector and betweenness) and three global (density,
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10 458 modularity and centralization) network indices for three social behaviours (aggression,
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12 459 grooming, and huddling) in three macaque species (rhesus, long-tailed and bonnet) that display
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15 460 different levels of species-typical social structures.
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19 461 Previous simulation-based work suggested that researchers would need to collect at
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21 462 least 15-20 interactions per dyad in order to construct a reliable social network [16–18]. For
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23 463 large groups containing many individuals and potential interactions, this would mean having
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25 464 to collect thousands of observations [16]. In contrast, our analysis examining variation in local
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27 465 and global metrics over time revealed that it took no more than a total of 50 hours for data
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29 466 collected through FAS, and 10 hours for data collected through ABS, to reach a stable network
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31 467 with minimal or no fluctuation of local network metric values with progressive increases in
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33 468 observation time. This was true across all group sizes, from the small rhesus macaque MG
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35 469 group, with 24 adults, to the large bonnet macaque group LG, with 60 individuals. This
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37 470 discrepancy is likely due to the fact that, while previous research was largely based on
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39 471 simulations [17,18], our study relied on actual behavioural observations. One possible reason
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41 472 why it takes less effort than expected to construct and estimate reliable social network measures
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43 473 could be that, in the attempt to establish or maintain long-term social relationships within their
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45 474 groups such as social bonds [6] or dominance ranks [42], animals direct social behaviours, such
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47 475 as grooming, huddling and aggression, towards specific group members. This means that with
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49 476 only few hours of observations, individuals' network position would become apparent.
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51 477 Crucially, this means that species characterized by sparser and less kin-directed social
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53 478 interactions might require a greater sampling effort to generate a reliable social network [18].
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3 479 Interestingly, it takes more observation hours (at least 100) to reach a stability in global
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5 480 compared to local metrics, probably because global network metrics are more sensitive to
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7 481 missing edges compared to local network metrics [16] and so a larger number of observations
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9
10 482 are needed to record all or most dyadic interactions, including the more infrequent ones.

11
12 483 Our comparison of the network metrics calculated from the two sampling methods
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14 484 revealed that, for grooming and aggression networks, all three local network centrality
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16 485 measures were significantly, positively correlated across the two behavioural sampling
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18 486 methods, and for all three macaque species. This suggested that methodological differences in
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21 487 behavioural data collection did not seem to impact node degree, eigenvector and betweenness
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23 488 centrality measures, regardless of species-typical social structure or social styles. In contrast,
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25 489 for huddling networks, only degree and betweenness centralities were correlated between the
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28 490 two sampling methods for both bonnet and rhesus macaques, while eigenvector centrality
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30 491 measures were correlated between the two sampling methods only for the tolerant bonnet
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33 492 macaques but not for the despotic rhesus macaques.

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35 493 The analysis and comparisons of global metrics revealed that correlations between
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37 494 metrics calculated using the two sampling methods depended both on the species, the type of
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39 495 behaviour and network metric examined. In particular, for grooming behaviour, we found a
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41 496 positive correlation for grooming network density and modularity while grooming network
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43 497 centralization was correlated between FAS and ABS data only if three groups (one rhesus and
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45 498 two long-tailed macaque groups) were excluded from the analysis. Similarly, we found that
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47 499 FAS huddling network metrics correlated with the respective ABS global network metrics for
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49 500 density and modularity but not for centralization. Yet, when one rhesus macaque group was
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51 501 excluded from the analysis, we did find a correlation in huddling centralization between the
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54 502 two sampling methods. Finally, for aggression networks, we found a positive correlation
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3 503 between the two sampling methods only for network density and centralization but not for
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5 504 network modularity.

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8 505 Collectively, our study shows that, for all social behaviours examined and for all the
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10 506 macaque species investigated, network attributes that measure *direct* interactions, namely
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12 507 degree (at local level) and density (at global level) were strongly correlated between the two
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14 508 sampling techniques. This indicates that researchers who are interested in assessing how many
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16 509 direct interactions each animal has and/or how many edges are present in the group, can employ
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18 510 either sampling technique regardless of the social behaviour examined or the degree of specie-
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20 511 specific sociality. However, despite the fact that ABS and FAS data produce comparable social
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22 512 network measures of direct interactions, the usefulness of SNA lies in its ability to provide
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24 513 measurements of animals' *indirect* connections [7,43]. In this regard, our study showed that
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26 514 the correspondence between FAS and ABS network metrics largely depends on the social
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28 515 behaviour examined, and group- or species-typical characteristics such as social organization
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30 516 and emergent social structure or social style. More specifically, we found that for those social
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32 517 behaviours performed at high frequency, namely social grooming and aggression for all three
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34 518 species, and huddling for bonnet macaques, there was a strong positive relationship in
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36 519 eigenvector and betweenness centrality values calculated from both sampling methods. This
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38 520 suggests that both sampling methods yield similar local network metrics that reflect indirect
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40 521 connections regardless of group- or species-typical social style. In this context, ABS seems to
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42 522 be the most cost-effective sampling method as it requires less effort to collect more dyadic
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44 523 interactions.

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47 524 While our findings indicate that either sampling method can be used to construct
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49 525 reliable social networks from frequently occurring social behaviours, they also suggest that
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51 526 network measures calculated from *infrequent behaviours* are especially vulnerable to the type
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53 527 of sampling method used. In fact, for huddling interactions, we found that eigenvector
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3 528 centrality was correlated between the two sampling methods only for the tolerant bonnet
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5 529 macaque, but not so for the despotic rhesus macaques which were observed huddling at much
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8 530 lower frequencies. When or where feasible, we therefore suggest the use of ABS rather than
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10 531 FAS in order to construct reliable social networks from infrequent behaviours as ABS allows
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12 532 researchers to record more dyadic interactions compared to FAS. In fact, via ABS, we collected
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14 533 a frequency of huddling behaviour from rhesus macaques that was nearly 5 times higher
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16
17 534 compared to the frequency of interactions recorded through FAS (see Table S1).

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19 535 For prosocial behaviours (i.e., grooming and huddling), we found that FAS network
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21 536 centralization correlated with ABS network centralization only if one rhesus macaque (RG)
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23 537 and two long-tailed macaque (Hulk and Entrance) groups were excluded from the analysis.
24
25 538 Network centralization reflects the proportion of social interactions that involve one or few
26
27 539 individuals, and, in macaques, variation in this index has been found to be associated with
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29 540 dominance rank and species' degree of tolerance/despotism [36]. In other words, in despotic
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31 541 species such as rhesus macaques, which exhibit marked rank relationships, social grooming
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33 542 tends to be largely directed towards high-ranking individuals, and so these species tend to have
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35 543 a highly centralized network, while in more tolerant macaque species, grooming interactions
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37 544 tend to be more equally distributed across dyads exhibiting, therefore, a less centralized
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39 545 network [36]. Here we suggest that the variation in key demographic components and the
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41 546 degree of social (in)stability of the study groups might explain why, for some macaque groups,
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43 547 network centralizations calculated from both FAS and ABS data were not correlated. In RG,
44
45 548 for instance, some high-ranking individuals, including the dominant female, disappeared from
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47 549 the group during our study period. Similarly, the long-tailed macaque groups experienced
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49 550 several turnovers in the male dominance hierarchy. These demographic changes might have
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51 551 shifted the rank relationships within the study groups influencing the effect of rank on the
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53 552 direction of grooming interactions, affecting, thereby, grooming network centralizations.
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3 553 Finally, we did not find evidence that network modularity was correlated between the
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5 554 two sampling methods. Network modularity reflects the degree to which animals form clusters
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8 555 of social interactions by interacting preferably with partners belonging to their own clusters
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10 556 compared to partners from other clusters. For this reason, this network metric is commonly
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12 557 assessed in prosocial behaviours such as grooming and huddling [44], whereby behaviours tend
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14 558 to be directed to preferred partners based on long-term affiliations dictated by, for instance, the
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16 559 degree of social bonds [6], or kinship [45]. Aggressive interactions, in contrast, tend to be less
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18 560 modular/clustered as they tend to be distributed more dynamically and may be affected by
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20 561 multiple factors, such as food distribution, or seasonality.
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23
24 562 In conclusion, our analysis suggests the use of ABS as a suitable alternative to FAS,
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26 563 particularly if researchers are interested in local network measures, such as degree, eigenvector
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28 564 or betweenness as this seems the most cost-effective method: it allows researchers to collect
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30 565 data on multiple dyads in a shorter amount of time, compared to FAS, while providing similar
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32 566 network metrics as FAS. ABS is likely to be a particularly suitable sampling method for
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34 567 infrequent behaviours such as huddling interactions in despotic species. Finally, we found
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36 568 limited evidence that the degree of despotism/tolerance of a species affects the reliability of the
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38 569 sampling method used to construct social networks. Overall, our results may provide
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40 570 researchers with new guidance on whether to use FAS or ABS to collect their social network
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42 571 data.
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FIGURE CAPTIONS

Figure 1. Monthly variation in individual mean grooming, huddling and aggression degree (top row) and degree uncertainty (bottom row) with progressive monthly increases in focal animal sampling observation time. Each line represents a study group. Rhesus macaque groups: RG, HG, MG; long-tailed macaque groups: Pirate, Hulk, Entrance; bonnet macaque groups: SG, LG.

Figure 2. Scatterplot plotting the three local (top row) and global (bottom row) grooming network metrics calculated from all-occurrences behaviour sampling (ABS) data against those calculated from focal animal sampling (FAS) data.

Figure 3. Scatterplot plotting the three local (top row) and global (bottom row) huddling network metrics calculated from all-occurrences behaviour sampling (ABS) data against those calculated from focal animal sampling (FAS) data.

Figure 4. Scatterplot plotting the three local (top row) and global (bottom row) aggression network metrics calculated from all-occurrences behaviour sampling (ABS) data against those calculated from focal animal sampling (FAS) data.

TABLE CAPTIONS

Table 1. Results of the GLMM analysis testing whether individuals' grooming centrality measures calculated from the focal animal sampling (FAS) data and species identity (rhesus, long-tailed, bonnet) significantly predicted grooming centrality measures calculated from the all-occurrences behaviour sampling (ABS) data. Significant predictors are indicated in bold.

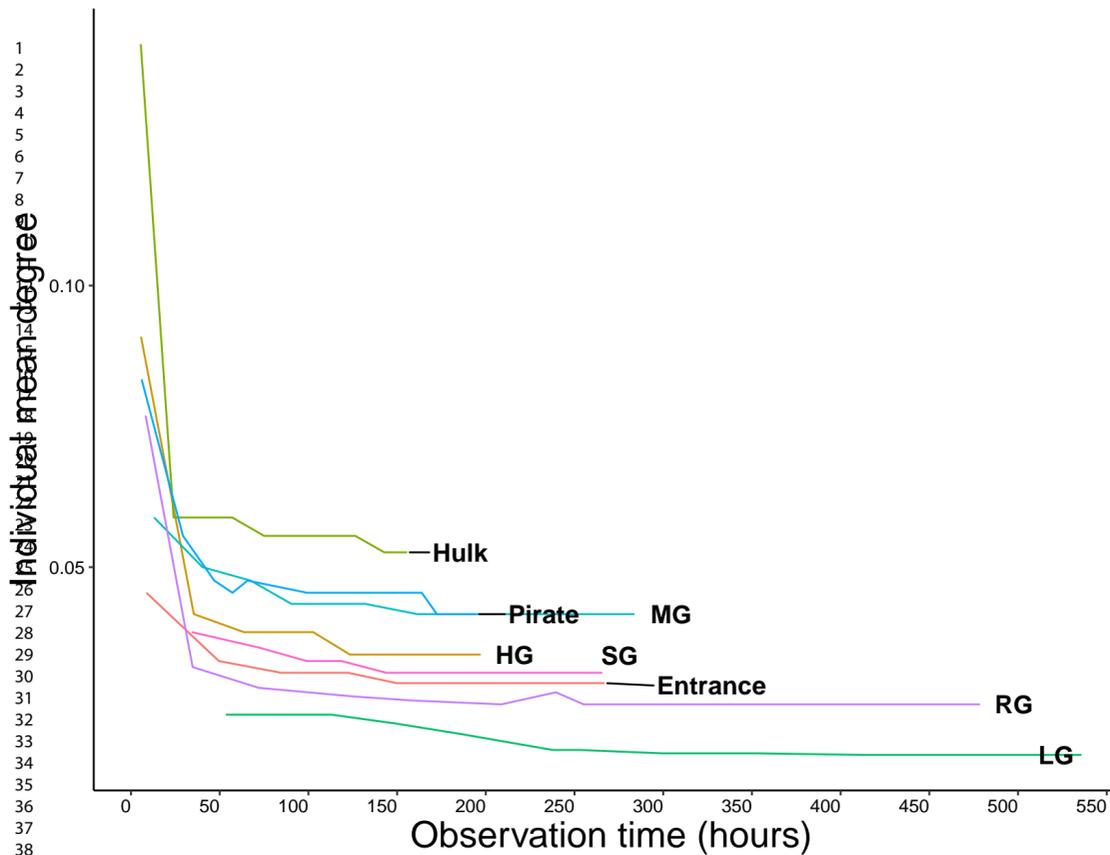
Table 2. Results of the GLMM analysis testing whether individuals' huddling centrality measures calculated from the focal animal sampling (FAS) data and species identity (rhesus and bonnet) predicted centrality calculated from the all-occurrences behaviour sampling (ABS) data. Significant predictors are indicated in bold.

Table 3. Results of the GLMM analysis testing whether individuals' aggression centrality measures calculated from the focal animal sampling (FAS) data and species identity (rhesus, long-tailed, bonnet) significantly predicted aggression centrality calculated from the all-occurrences behaviour sampling (ABS) data. Predictors that are significant are indicated in bold.

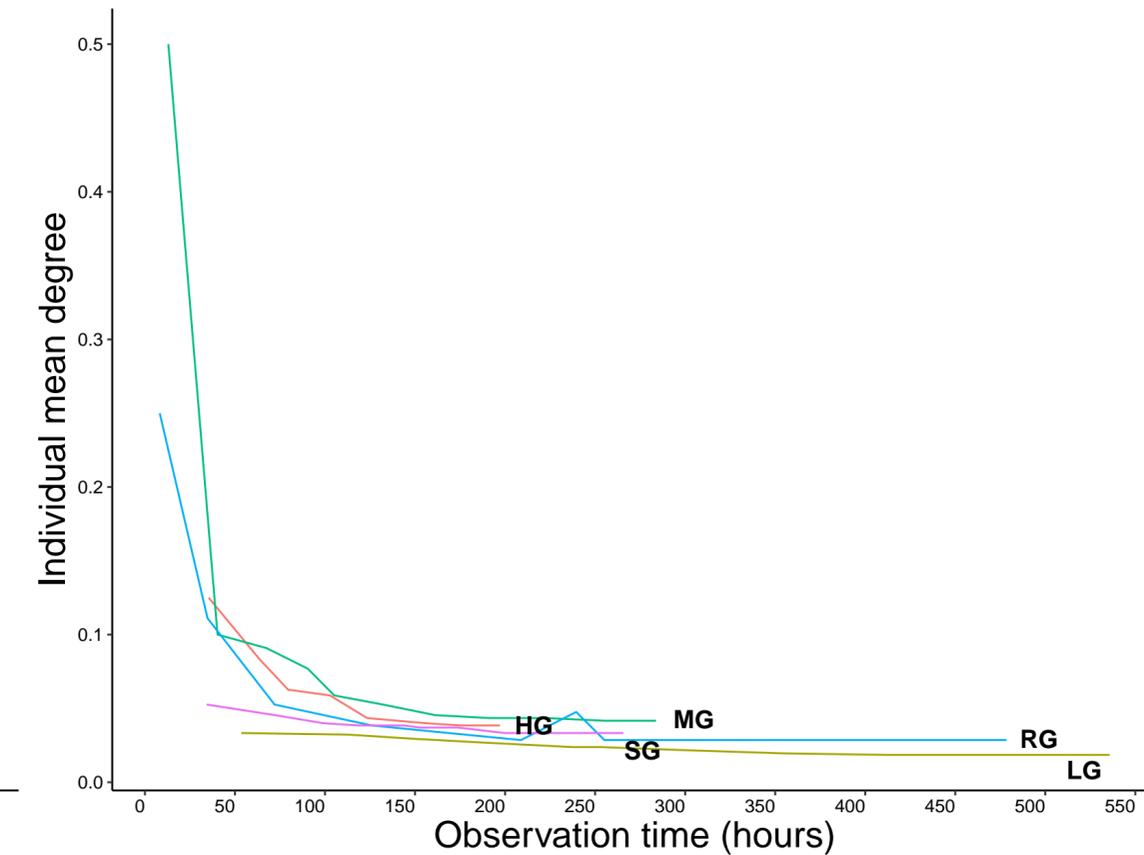
Table 4. Summary of the results of the analysis testing the correlation of local network measures between data collected through focal animal sampling (FAS) and all-occurrences behaviour sampling (ABS).

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2
3 **Table 5.** Summary of the results of the analysis testing the correlation of global network
4 measures between data collected through focal animal sampling (FAS) and all-occurrences
5 behaviour sampling (ABS). Rhesus macaque groups: RG, HG, MG; long-tailed macaque
6 groups: Pirate, Hulk, Entrance; bonnet macaque groups: SG, LG.
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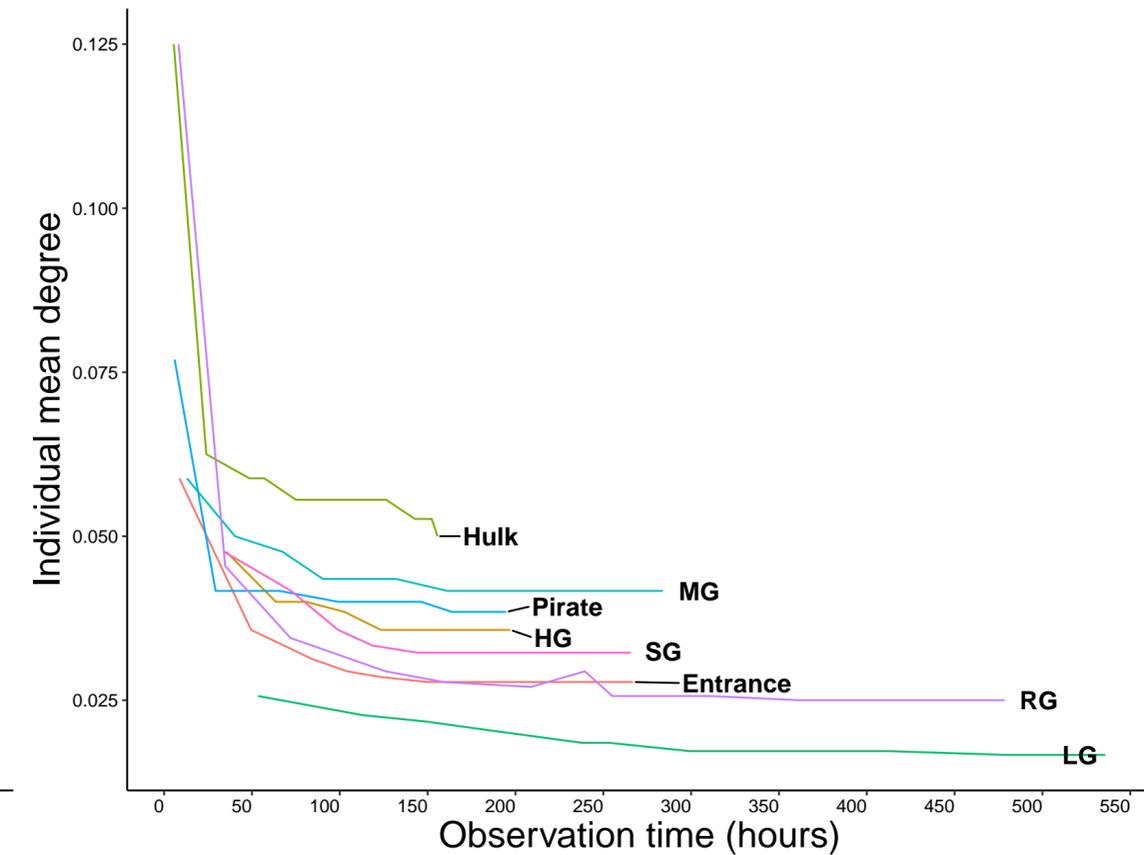
MEAN GROOMING DEGREE – FOCAL



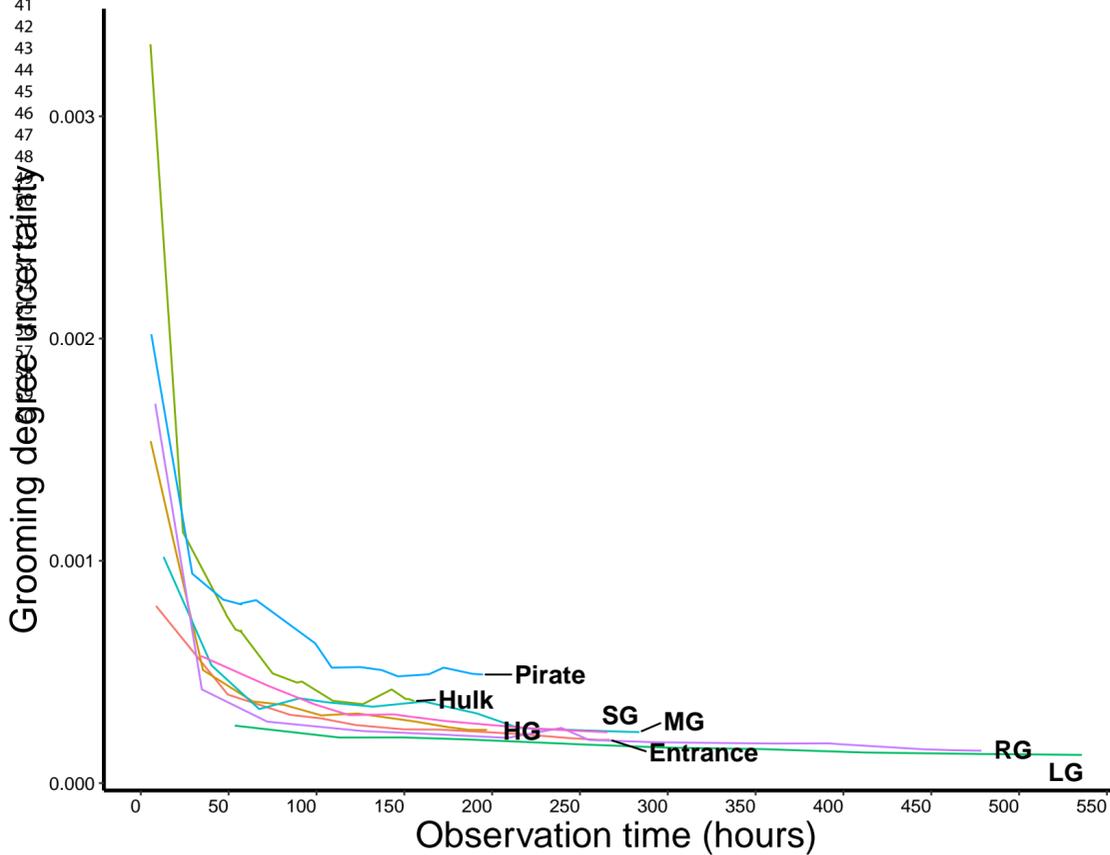
MEAN HUDDLING DEGREE – FOCAL



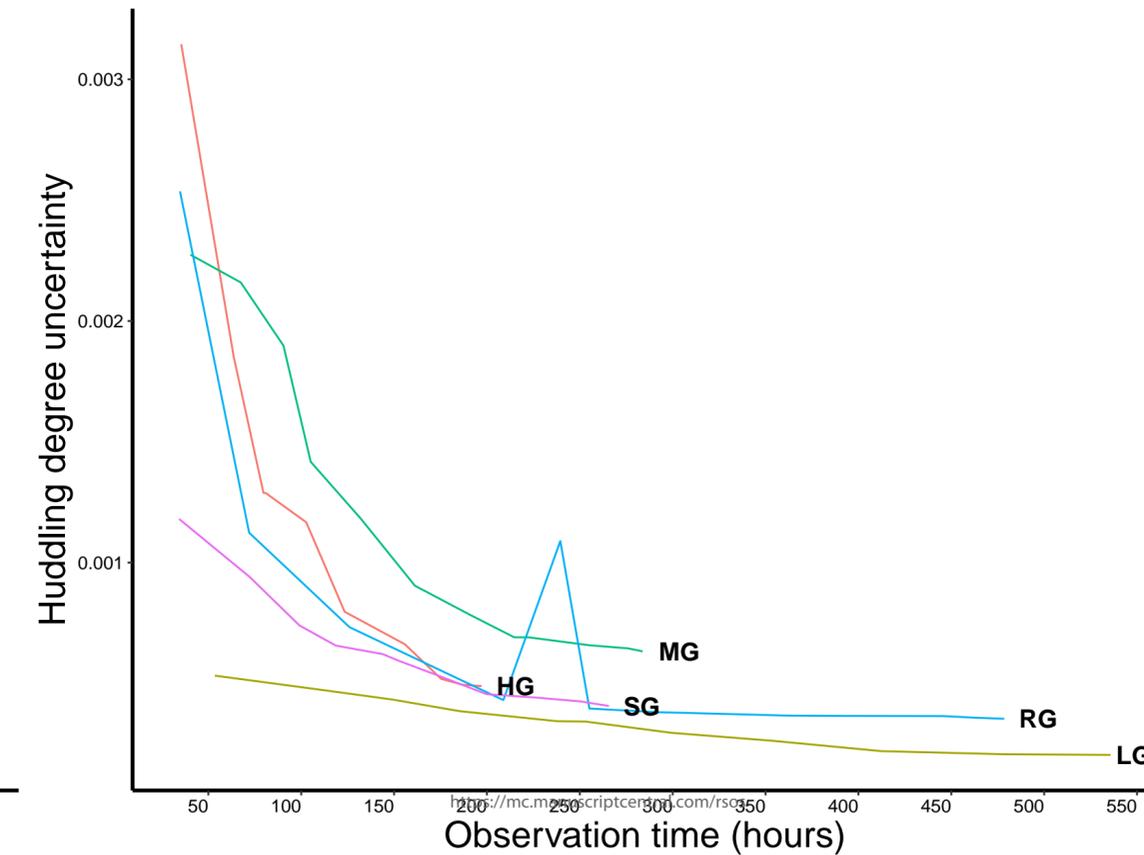
MEAN AGGRESSION DEGREE – FOCAL



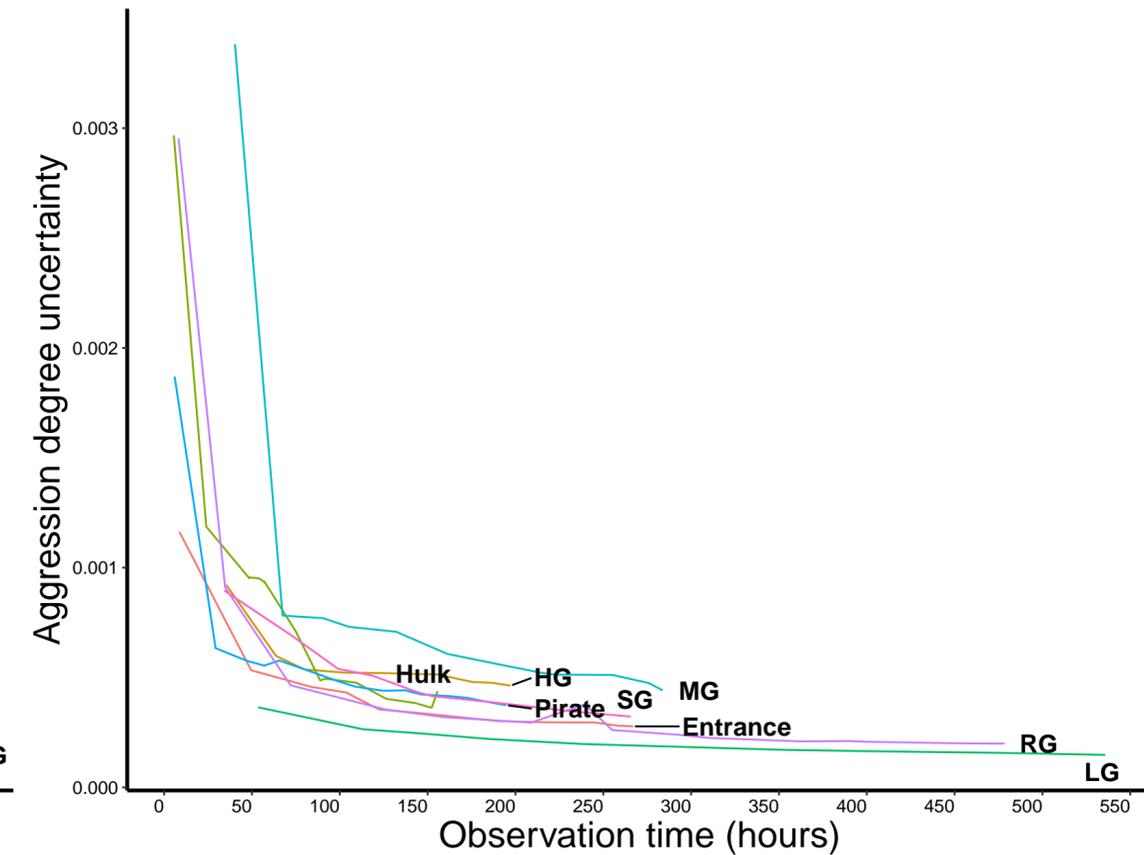
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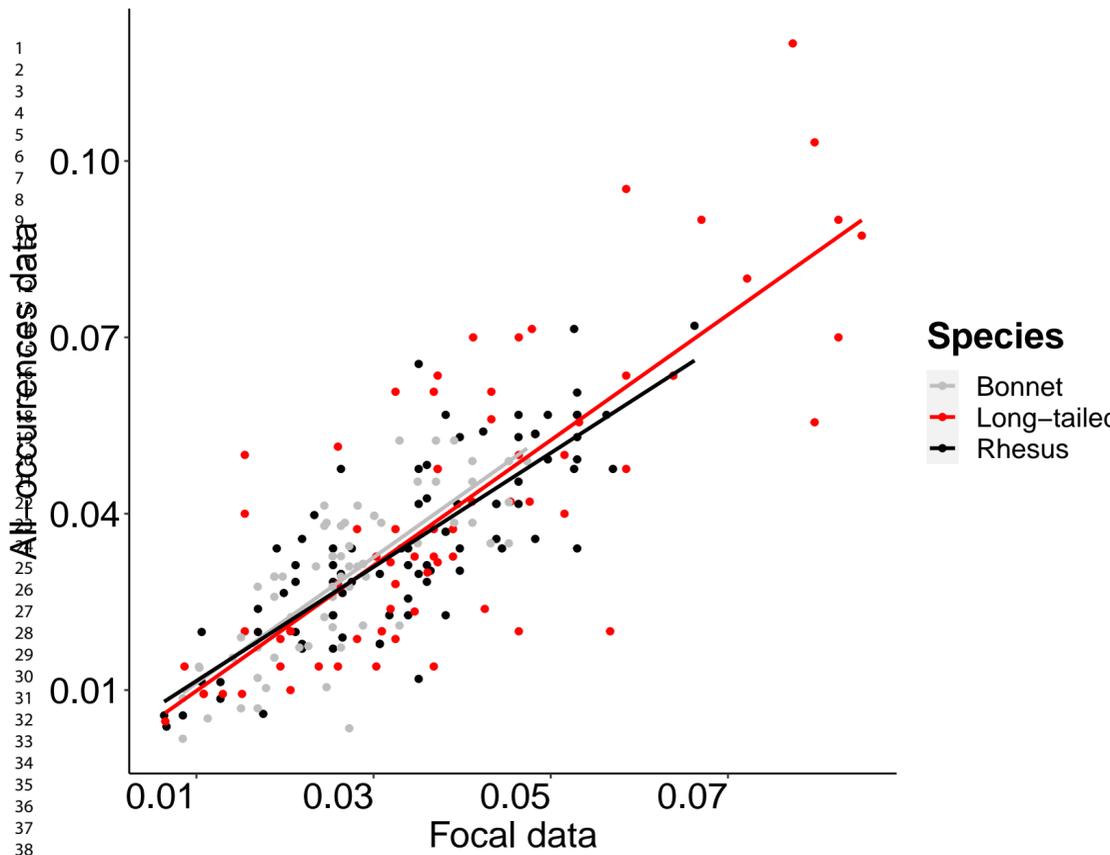
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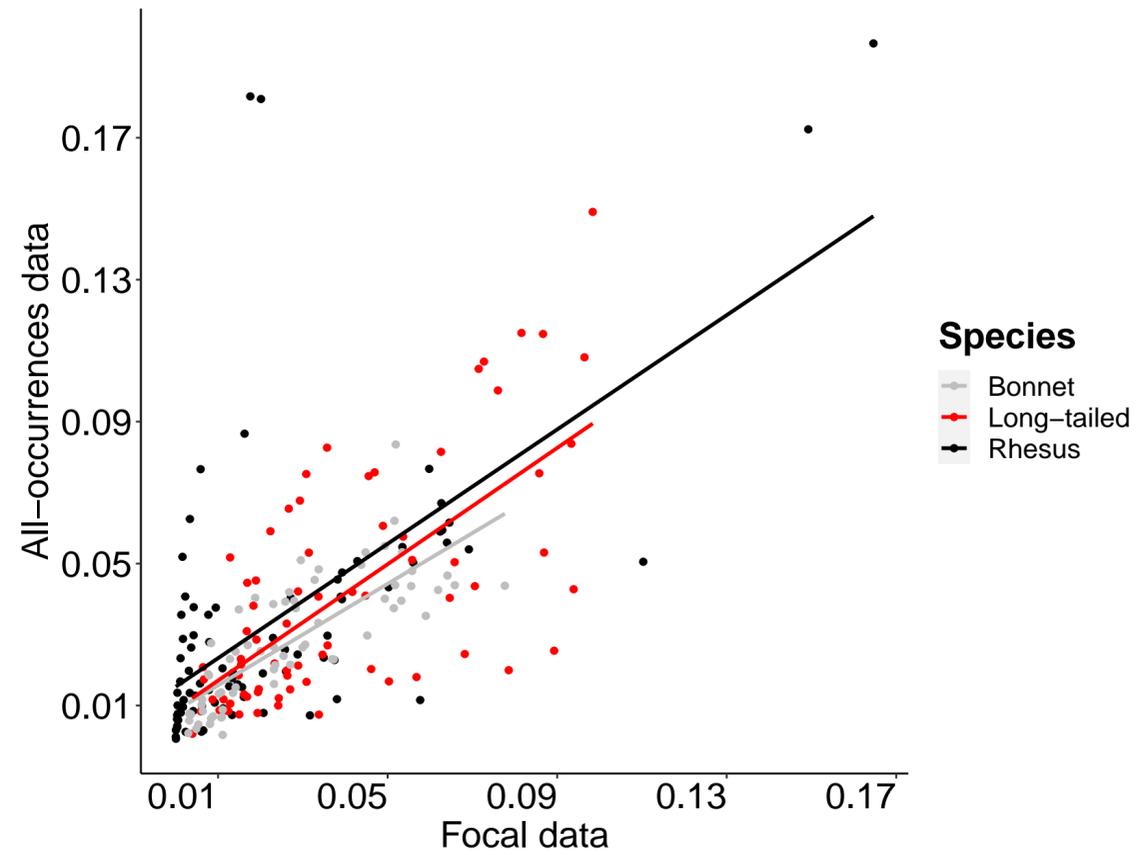
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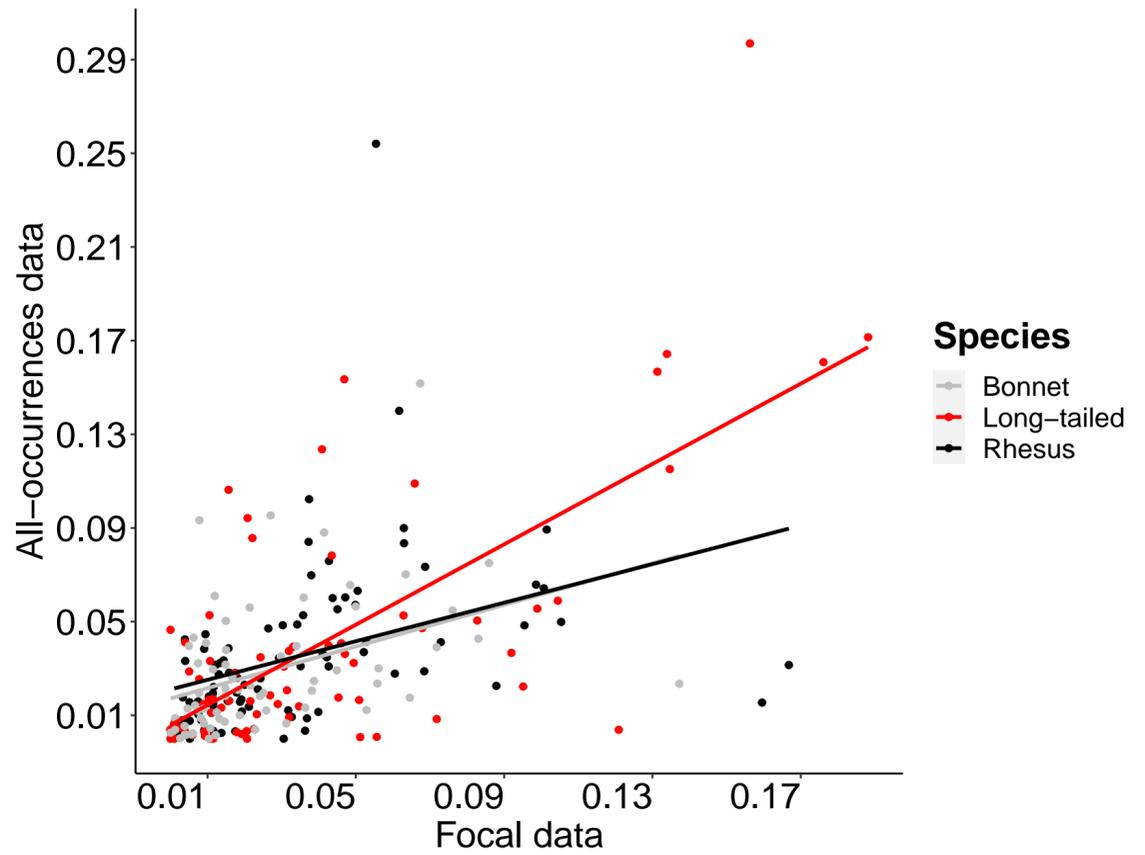
GROOMING NETWORK DEGREE



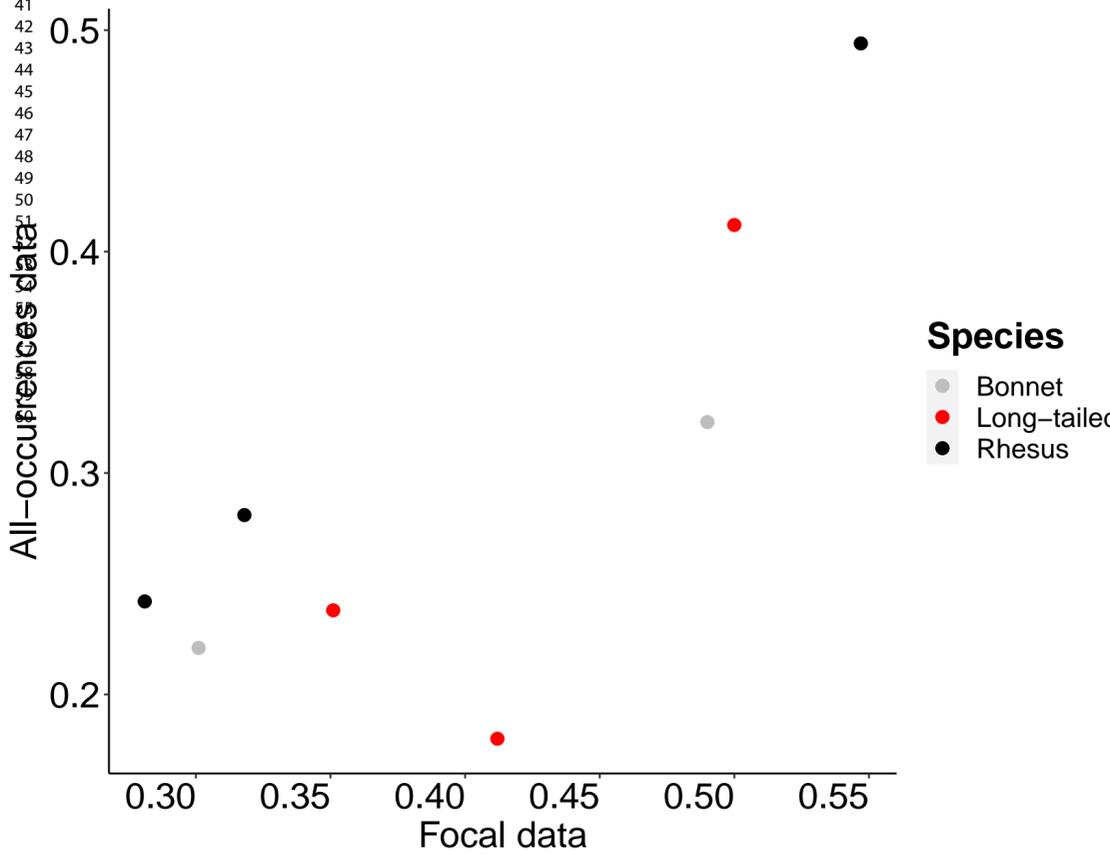
GROOMING NETWORK EIGENVECTOR



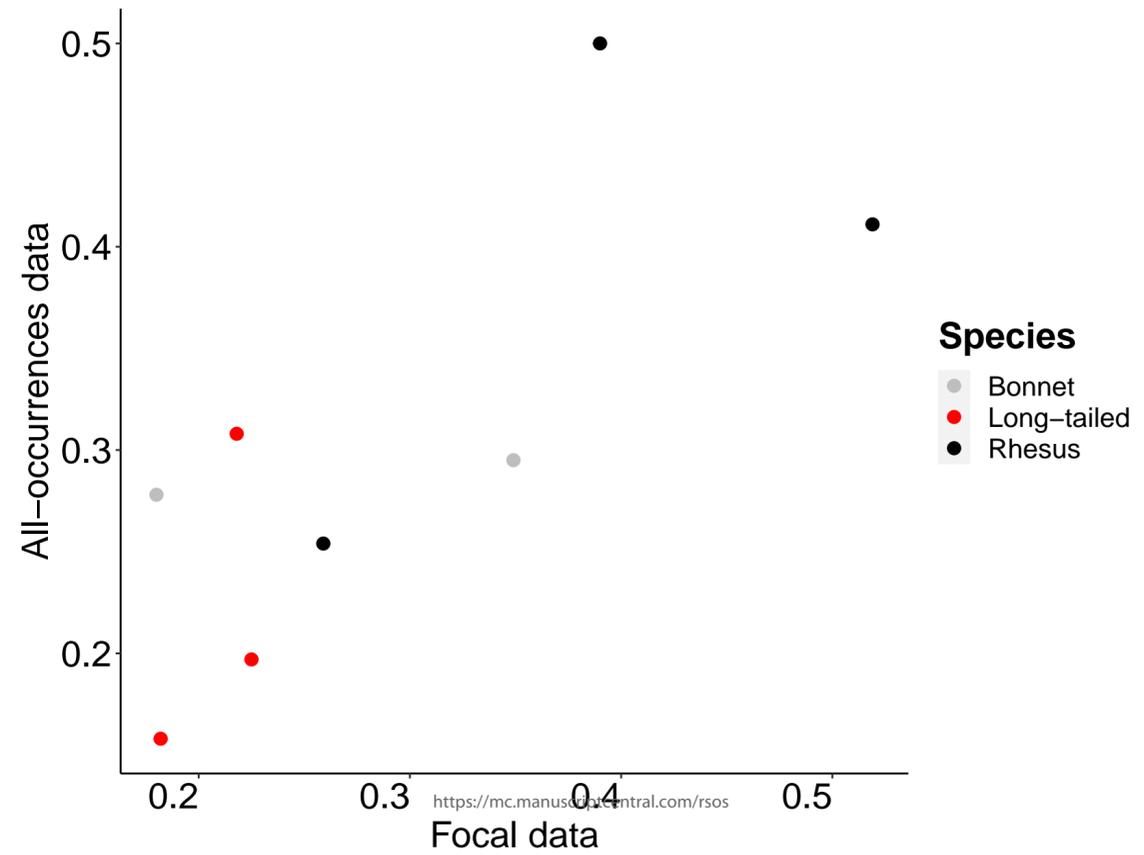
GROOMING NETWORK BETWEENNESS



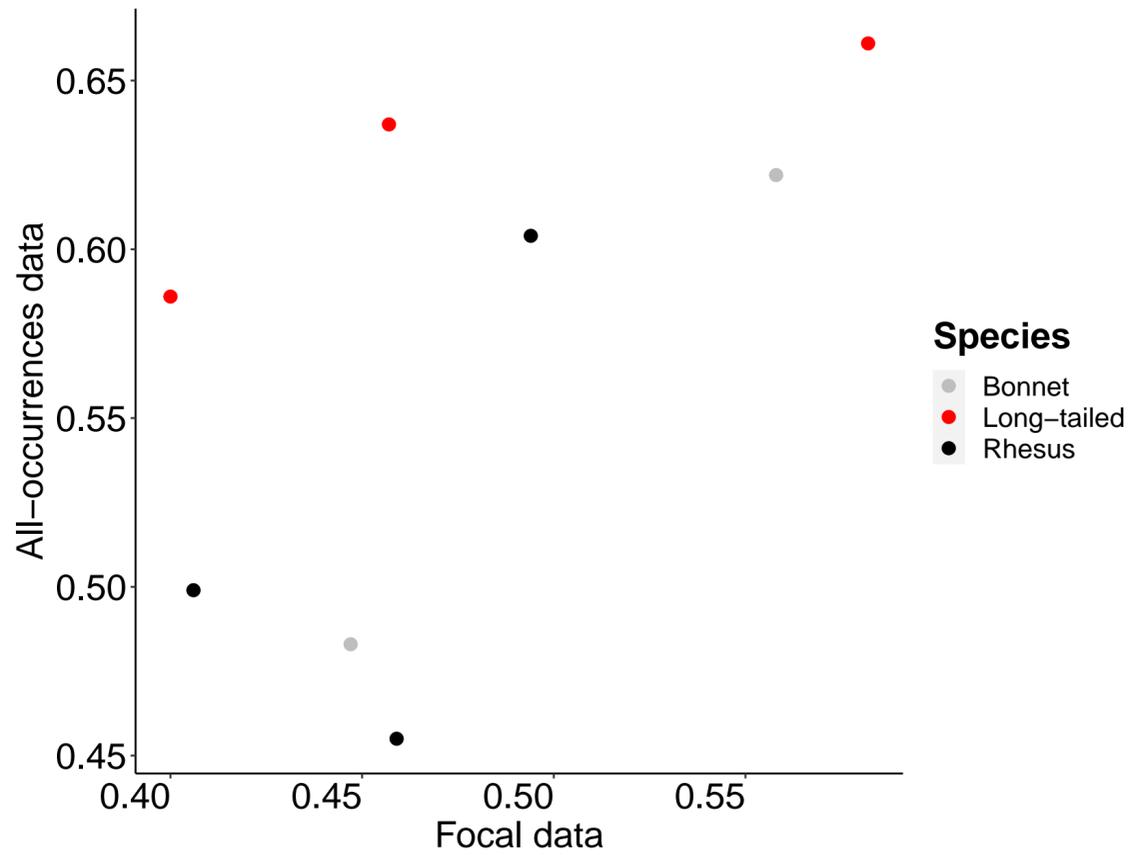
GROOMING NETWORK DENSITY



GROOMING NETWORK MODULARITY

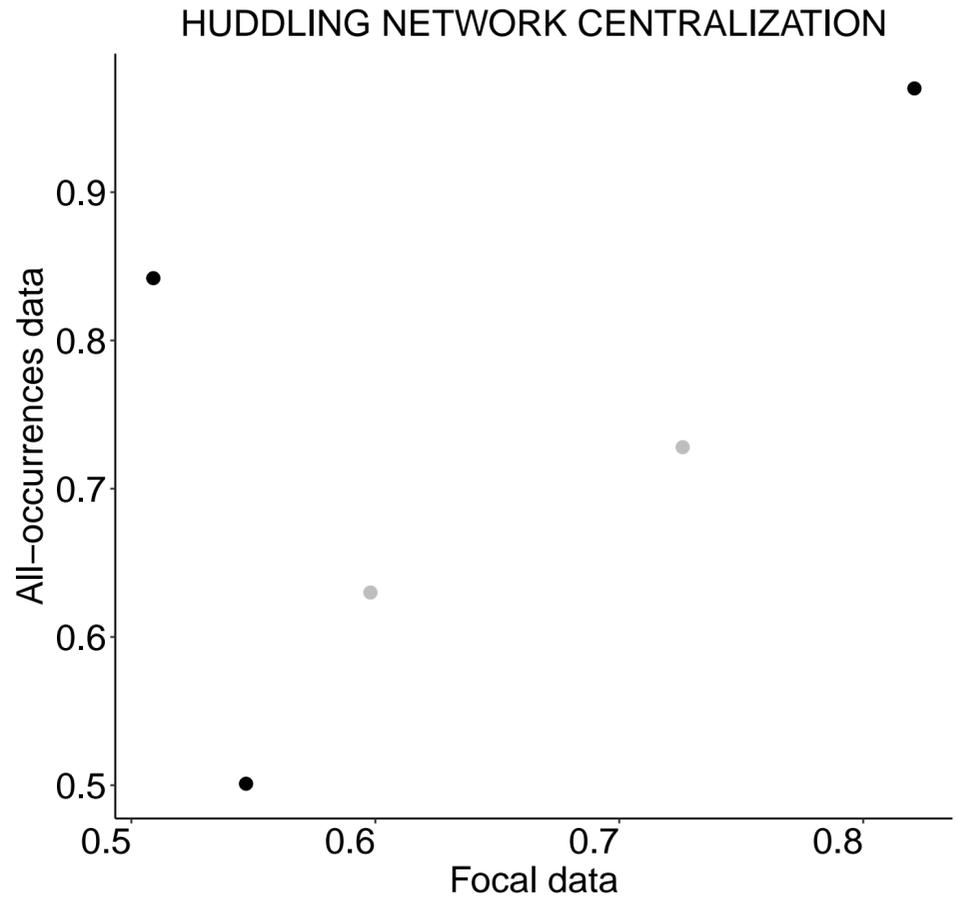
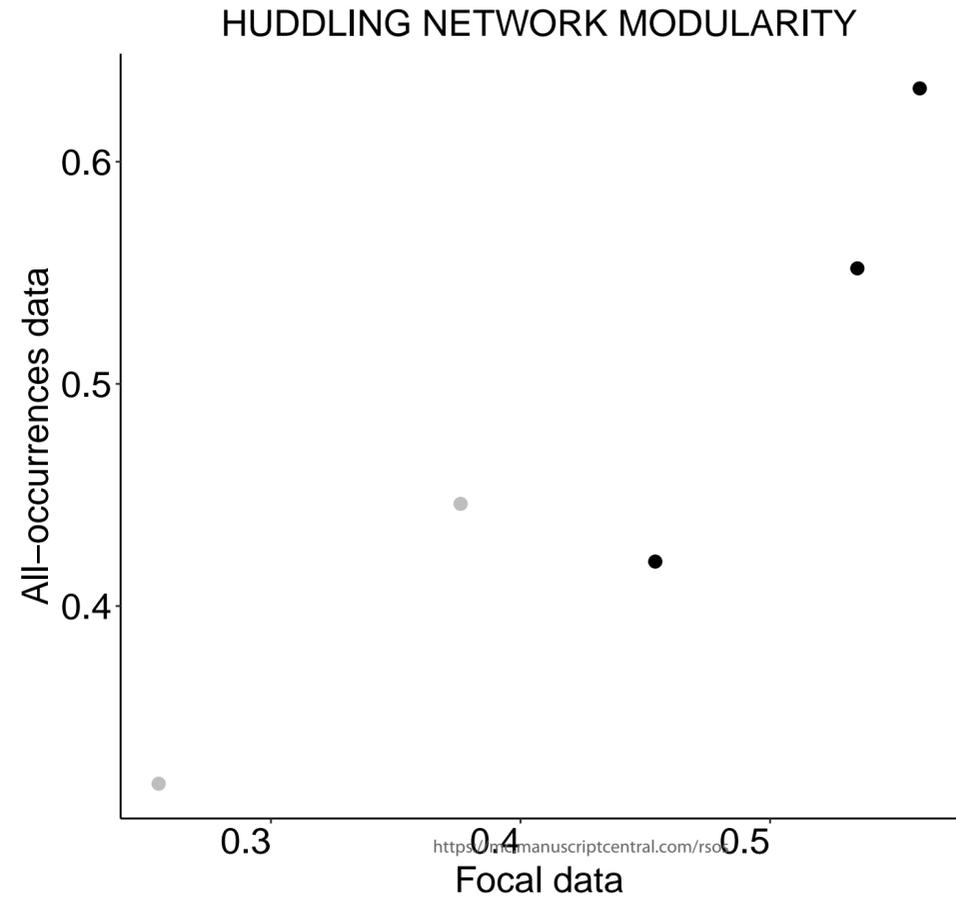
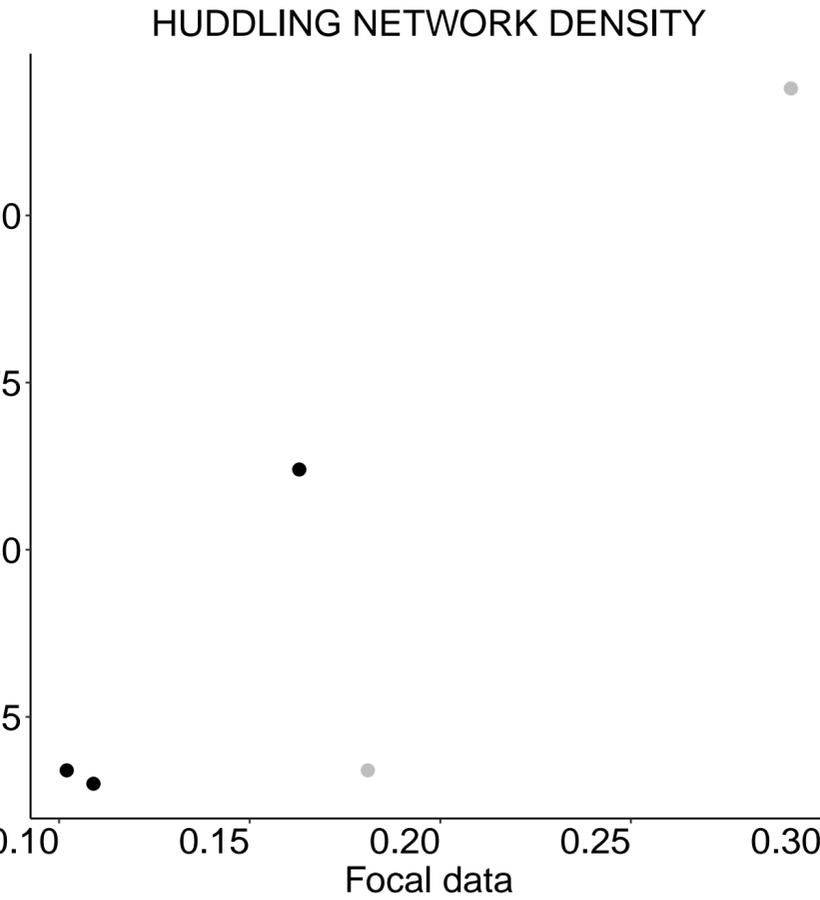
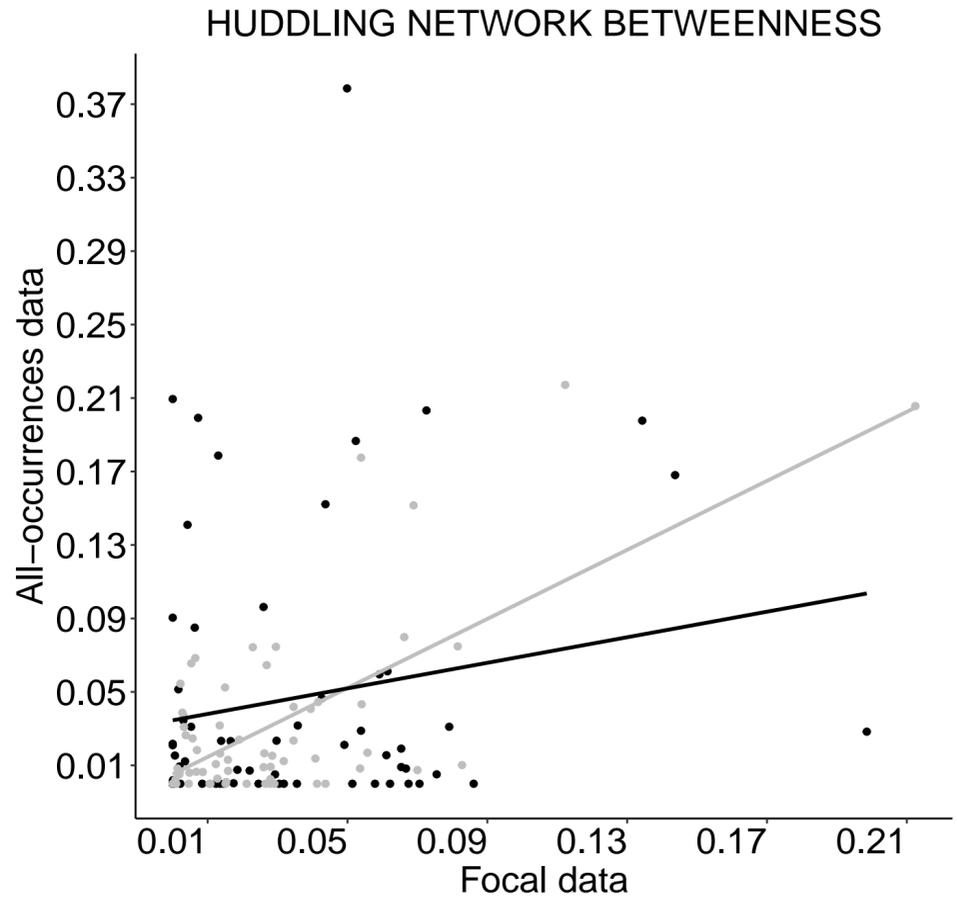
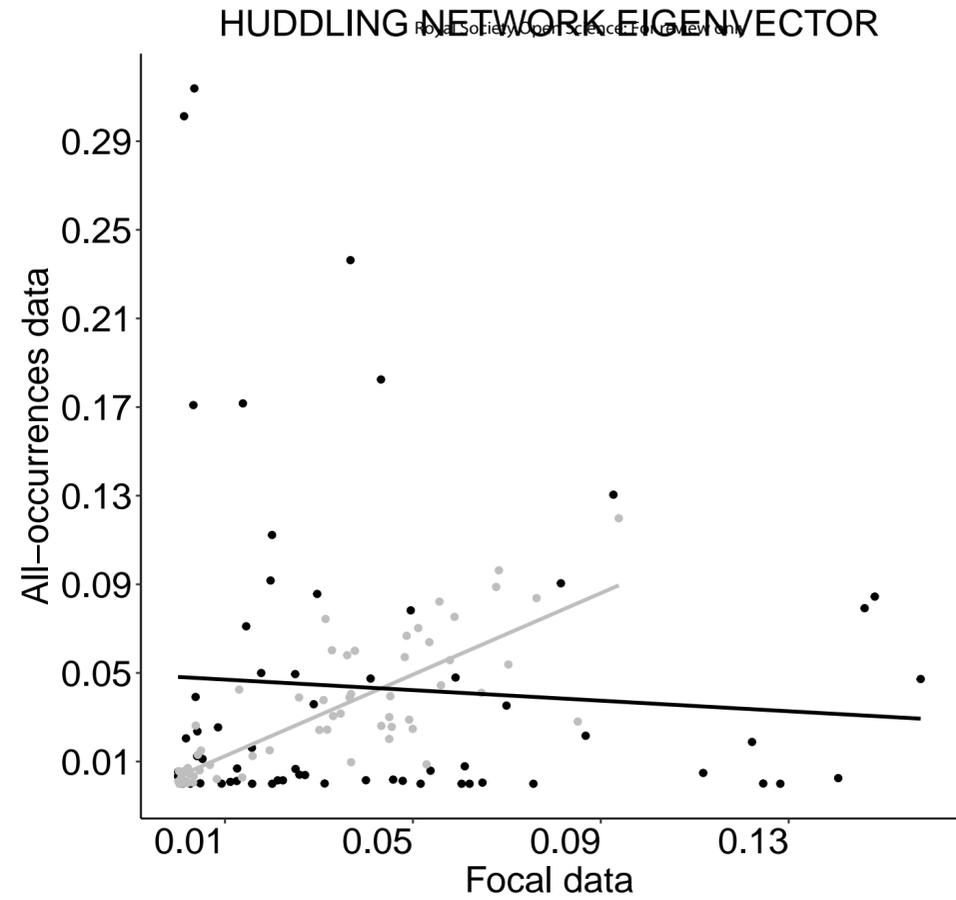
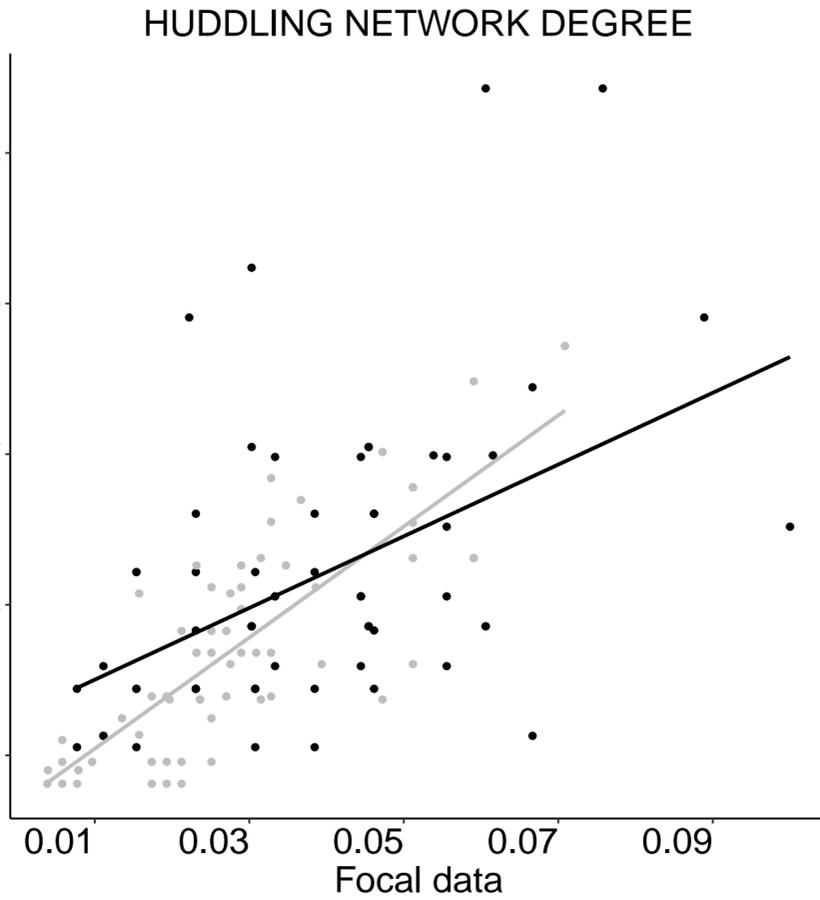


GROOMING NETWORK CENTRALIZATION

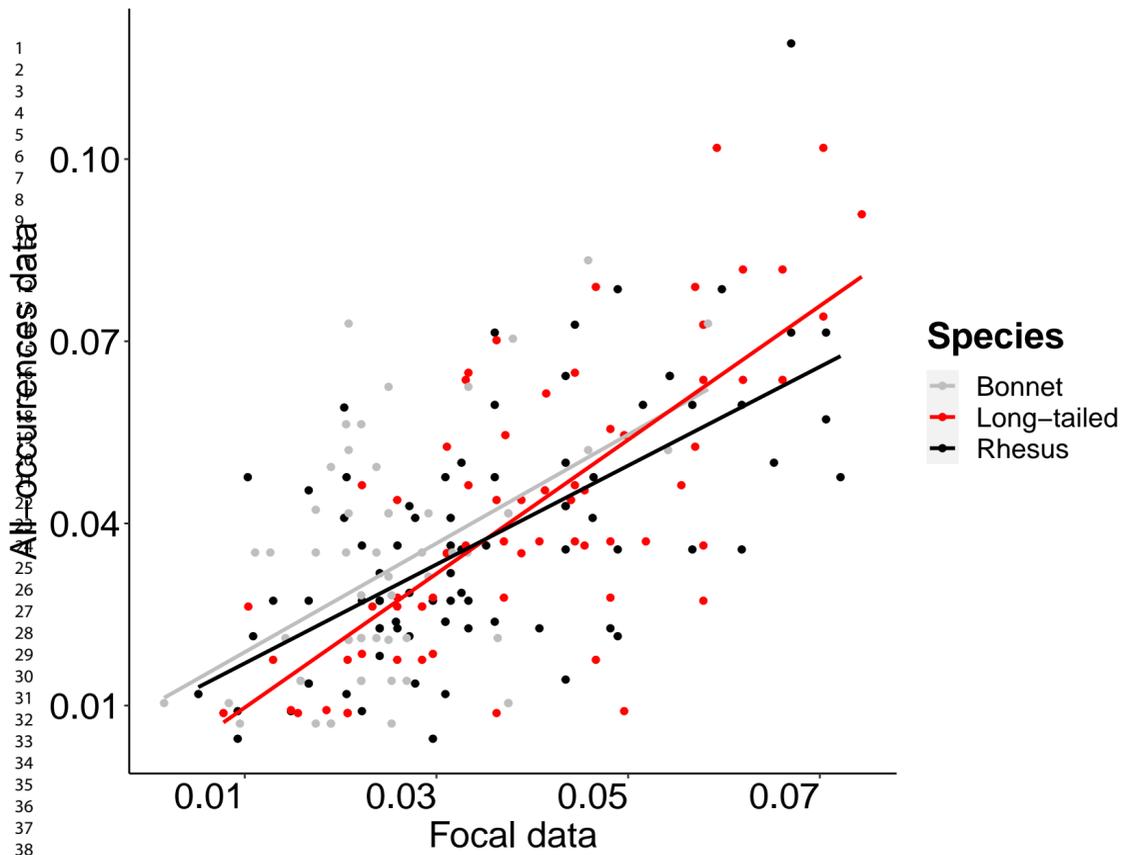


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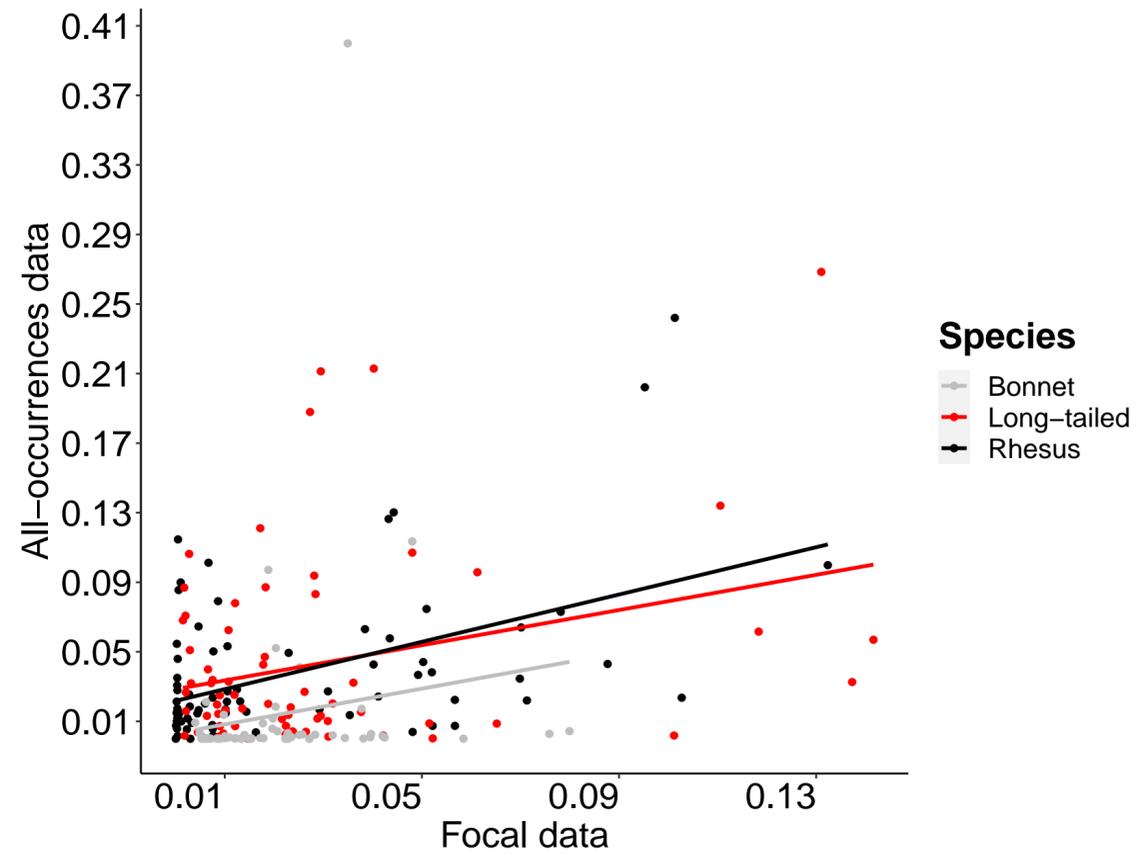
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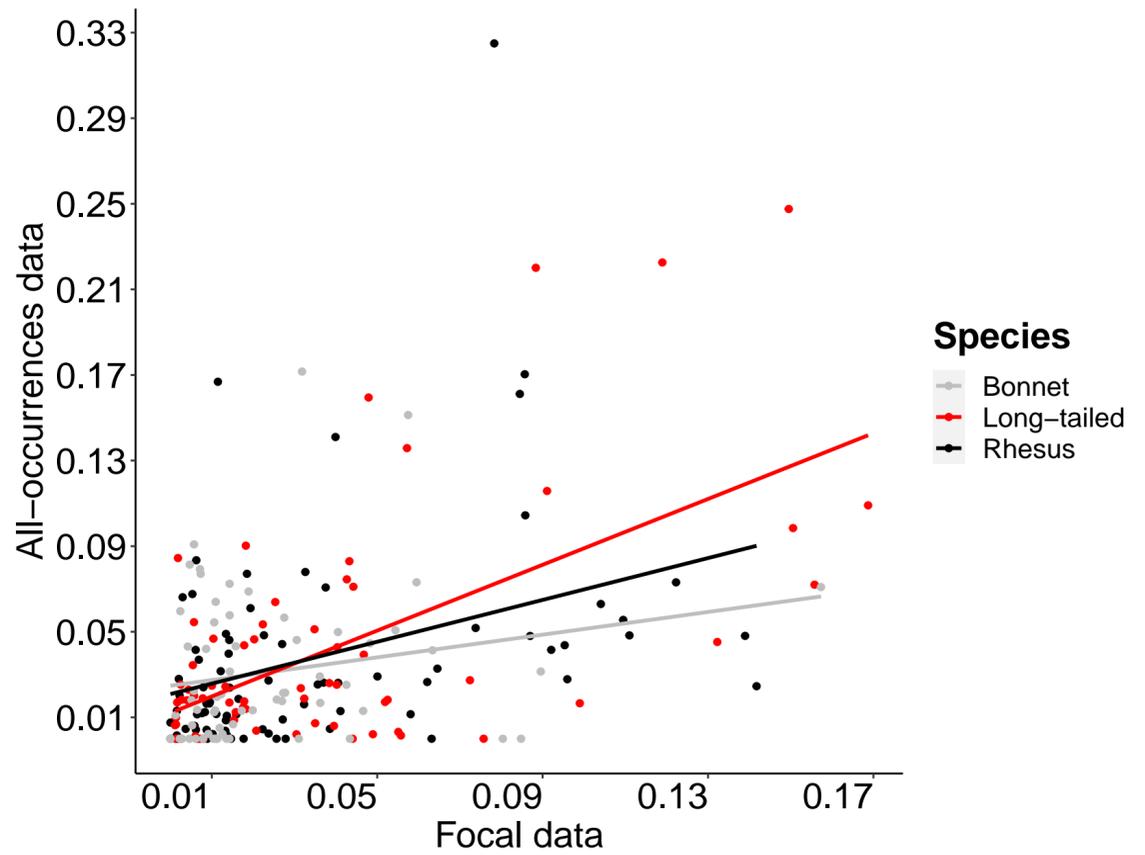
AGGRESSION NETWORK DEGREE



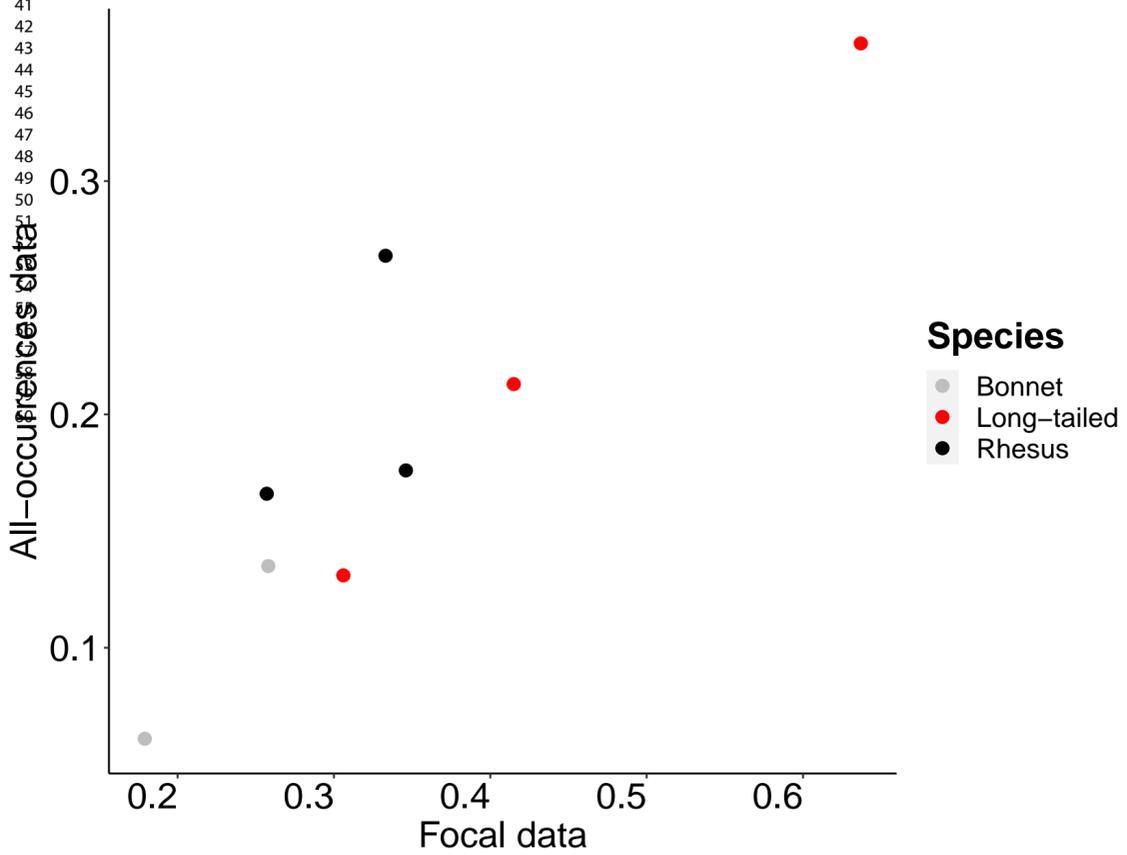
AGGRESSION NETWORK EIGENVECTOR



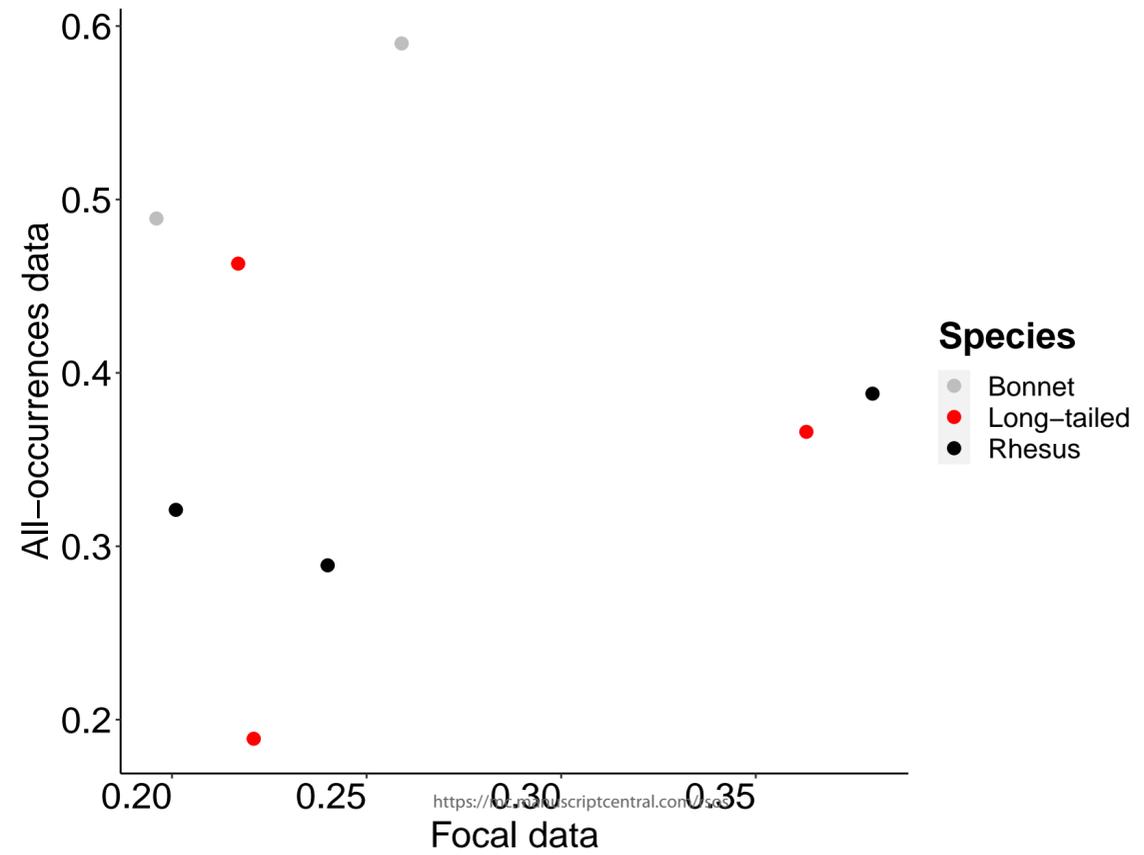
AGGRESSION NETWORK BETWEENNESS



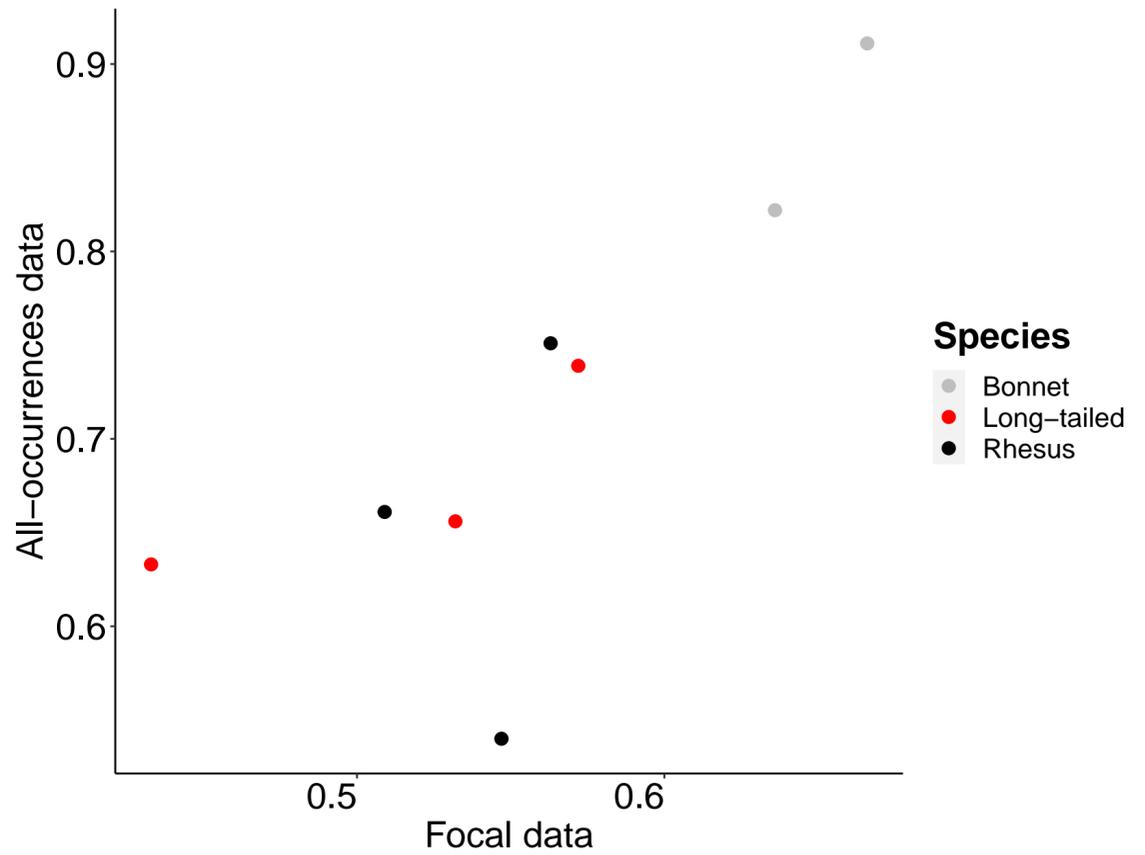
AGGRESSION NETWORK DENSITY



AGGRESSION NETWORK MODULARITY



AGGRESSION NETWORK CENTRALIZATION



<i>Predictors</i>	<i>Estimate</i>	<i>SE</i>	<i>95% CI</i>	<i>z-value</i>	<i>P-value</i>
Intercept	-4.60	0.14	-4.88; -4.32	-32.07	< 0.001
FAS degree	38.67	4.55	29.75; 47.60	8.49	< 0.001
Species (long-tailed vs bonnet)	0.35	0.17	0.02; 0.69	2.07	0.038
Species (rhesus vs bonnet)	0.19	0.18	-0.17; 0.55	1.04	0.297
Species (rhesus vs long-tailed)	0.16	0.15	-0.13; 0.46	1.07	0.282
FAS * Species (long-tailed vs bonnet)	-14.05	4.89	-23.64 -4.47	-2.87	0.004
FAS * Species (rhesus vs bonnet)	-8.38	5.36	-18.89; 2.14	-1.56	0.118
FAS * Species (rhesus vs long-tailed)	-5.68	3.36	-12.27; 0.91	-1.69	0.091
<i>Predictors</i>	<i>Estimate</i>	<i>SE</i>	<i>95% CI</i>	<i>z-value</i>	<i>P-value</i>
Intercept	-3.96	0.10	-4.16; -3.77	-40.10	< 0.001
FAS eigenvector	17.05	1.13	14.82; 19.27	15.03	< 0.001
Species (long-tailed vs bonnet)	0.03	0.12	-0.20; 0.26	0.25	0.800
Species (rhesus vs bonnet)	-0.01	0.12	-0.24; 0.22	-0.11	0.913
Species (rhesus vs long-tailed)	0.04	0.11	-0.17; 0.26	0.40	0.692
<i>Predictors</i>	<i>Estimate</i>	<i>SE</i>	<i>95% CI</i>	<i>z-value</i>	<i>P-value</i>
Intercept	-3.70	0.16	-4.02; -3.38	-22.52	< 0.001
FAS betweenness	11.49	3.15	5.32; 17.65	3.65	< 0.001
Species (long-tailed vs bonnet)	-0.56	0.21	-0.98; -0.15	-2.64	0.008
Species (rhesus vs bonnet)	0.004	0.21	-0.40; 0.41	0.02	0.985
Species (rhesus vs long-tailed)	-0.57	0.20	-0.96; -0.18	-2.86	0.004
FAS * Species (long-tailed vs bonnet)	5.02	3.55	-1.93; 11.98	1.42	0.157
FAS * Species (rhesus vs bonnet)	-2.05	3.78	-9.47; 5.36	-0.54	0.587
FAS * Species (rhesus vs long-tailed)	7.07	2.70	1.84; 12.31	2.65	0.008

Huddling Degree					
<i>Predictors</i>	<i>Estimate</i>	<i>SE</i>	<i>95% CI</i>	<i>z-value</i>	<i>P</i>
Intercept	-4.41	0.17	-4.74; -4.06	-25.27	< 0.001
FAS degree	31.82	4.35	23.3; 40.0	7.31	< 0.001
Species (rhesus vs bonnet)	0.79	0.25	0.30; 1.28	3.16	0.002
Degree * Species (rhesus vs bonnet)	-18.32	5.59	-29.3; -7.40	-3.28	0.001
Huddling Eigenvector					
<i>Predictors</i>	<i>Estimate</i>	<i>SE</i>	<i>95% CI</i>	<i>z-value</i>	<i>P</i>
Intercept	-4.67	0.88	-6.40; -2.95	-5.31	< 0.001
FAS eigenvector	38.98	5.25	28.69; 49.28	7.42	< 0.001
Species (rhesus vs bonnet)	-0.66	1.12	-2.85; 1.53	-0.59	0.553
Eigenvector * Species (rhesus vs bonnet)	-26.42	6.15	-38.48; -14.36	-4.30	< 0.001
Huddling Betweenness					
<i>Predictors</i>	<i>Estimate</i>	<i>SE</i>	<i>95% CI</i>	<i>z-value</i>	<i>P</i>
Intercept	-3.48	0.26	-3.99; -2.96	-13.26	< 0.001
FAS betweenness	9.99	2.53	5.03; 14.95	3.95	< 0.001
Species (rhesus vs bonnet)	-0.38	0.25	-0.87; 0.11	-1.52	0.128

Aggression Degree					
<i>Predictors</i>	<i>Estimate</i>	<i>SE</i>	<i>95% CI</i>	<i>z-value</i>	<i>P</i>
Intercept	-4.06	0.09	-4.23; -3.88	-46.73	-46.730
FAS degree	23.80	2.02	19.84; -27.77	11.77	< 0.001
Species (long-tailed vs bonnet)	-0.06	0.09	-0.24; 0.11	-0.72	0.474
Species (rhesus vs bonnet)	-0.09	0.09	-0.26; 0.081	-1.02	0.309
Species (long-tailed vs rhesus)	0.02	0.07	-0.12; 0.17	0.34	0.735
Aggression Eigenvector					
<i>Predictors</i>	<i>Estimate</i>	<i>SE</i>	<i>95% CI</i>	<i>z-value</i>	<i>P</i>
Intercept	-4.64	0.21	-5.05; 4.22	-21.94	< 0.001
FAS eigenvector	8.85	2.18	4.58; 13.12	4.07	< 0.001
Species (long-tailed vs bonnet)	1.15	0.23	0.87; 1.77	4.96	< 0.001
Species (rhesus vs bonnet)	1.32	0.23	0.70; 1.61	5.75	< 0.001
Species (rhesus vs long-tailed)	-0.16	0.20	-0.56; 0.23	-0.82	0.41
Aggression Betweenness					
<i>Predictors</i>	<i>Estimate</i>	<i>SE</i>	<i>95% CI</i>	<i>z-value</i>	<i>P</i>
Intercept	-4.07	0.21	-4.48; -3.66	-19.56	< 0.001
FAS betweenness	11.17	1.78	7.69; 14.65	6.29	< 0.001
Species (long-tailed vs bonnet)	0.36	0.22	-0.06; 0.79	1.67	0.095
Species (rhesus vs bonnet)	0.47	0.21	0.06; 0.09	2.27	0.023
Species (rhesus vs long-tailed)	-0.10	0.20	-0.49; 0.28	-0.53	0.596

Social behaviour	Social network index	Significant correlation between FAS and ABS data	Main effect/ interaction with species
Grooming	Degree	Yes	Interaction
	Eigenvector	Yes	Main
	Betweenness	Yes	Interaction
Huddling	Degree	Yes	Interaction
	Eigenvector	Yes	Interaction
	Betweenness	Yes	Main
Aggression	Degree	Yes	Main
	Eigenvector	Yes	Main
	Betweenness	Yes	Main

Social behaviour	Social network index	Significant correlation between FAS and ABS data	Notes
Grooming	Density	Yes	–
	Modularity	Yes	–
	Centralization	No	Significant correlation after excluding RG, Hulk & Entrance
Huddling	Density	Yes	–
	Modularity	Yes	–
	Centralization	No	Significant correlation after excluding RG
Aggression	Density	Yes	–
	Modularity	No	–
	Centralization	Yes	–

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3 1 Title **Effect of behavioural sampling methods on local and global social**
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8 3 Running head **Effect of sampling method on social networks**
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12
13 Marty³, Brianne Beisner⁴, Kevin Fuji⁵, Eliza Bliss-Moreau^{6,7} & Brenda
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23 **ABSTRACT**

24 Social network analysis (SNA) is a powerful, quantitative tool to measure animals' direct
25 and indirect social connectedness in the context of social groups. However, the extent to
26 which behavioural sampling methods influence SNA metrics remains unclear. To fill this
27 gap, here we compare network indices of grooming, huddling, and aggression calculated
28 from data collected from three macaque species through two sampling methods: focal
29 animal sampling (FAS) and all-occurrences behaviour sampling (ABS). We found that
30 measures of direct connectedness (degree centrality, and network density) were correlated
31 between FAS and ABS for all social behaviours. Eigenvector and betweenness
32 centralities were correlated for grooming and aggression networks across all species. In
33 contrast, for huddling, we found a correlation only for betweenness centrality while
34 eigenvector centralities were correlated only for the tolerant bonnet macaques but not so
35 for the despotic rhesus macaque. Grooming and huddling network modularity and
36 centralization were correlated between FAS and ABS for all but three of the eight groups.
37 In contrast, for aggression network, we found a correlation for network centralization but
38 not modularity between the sampling methodologies. We discuss how our findings
39 provide researchers with new guidelines regarding choosing the appropriate sampling
40 method to estimate social network metrics.

41
42 **Keywords:** Aggression; All-occurrences behaviour sampling; Focal animal sampling;
43 Grooming; Huddling; Social Network Analysis

59 INTRODUCTION

60 Understanding the proximate and ultimate functions of social behaviour has been a central
61 topic across many disciplines from behavioural ecology [1], to psychology [2] and
62 neurobiology [3]. From an ultimate perspective, work conducted in the last two decades has
63 shown that individuals who engage in more frequent and stronger social relationships live
64 longer [4], are better at coping with social and environmental stressors [5], and produce more
65 offspring that are more likely to survive [6]. Interestingly, accumulating evidence suggests that
66 fitness-related benefits can be accrued not only through direct connections (i.e., how many
67 social partners individuals have) but also through *indirect* connections (i.e., how many social
68 partners each social partner has) [7].

69 In the last two decades, social network analysis (SNA) has proven to be a powerful tool
70 in animal behavioural ecology to measure both direct and indirect connections in social animals
71 [8,9]. SNA represents social interactions in terms of nodes (i.e., subjects involved in the
72 interactions) and edges (i.e., connections between nodes), and provides quantitative, data-
73 driven approaches to evaluate biologically relevant measures of animals' connectedness both
74 at local (i.e., individual/node) and global (i.e., group/network) levels [9]. Given these
75 advantages, it is perhaps not surprising that SNA has been used across different contexts to
76 study animal social relationships, including comparisons of animal social structures [1], the
77 social diffusion of information between group members [10], the spread of infectious disease
78 via social interactions [11,12], and in the conservation of wildlife populations [13].
79 Furthermore, a broad range of studies have used SNA to investigate what individual- and
80 group-level sociodemographic and behavioural attributes, such as individuals' sex [4],
81 dominance rank [14], personality [15], and groups' sizes and compositions can potentially
82 influence animals' social interactions and emergent social structure.

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3 83 While it is crucial that observed networks, defined as “analytical representations of a
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5 84 combined set (or subset) of measures of the true relationships” [8], are as similar as possible to
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8 85 the real networks, namely “the real set of interactions between animals that integrate to form
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10 86 community dynamics” [8], there is increasing evidence that the correspondence between
11
12 87 observed and real networks depends on the behavioural sampling methods employed and/or on
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14 88 the frequency by which animals perform the behaviour of interest [16,17]. This variation may
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16 89 occur because observers might miss recording some real, meaningful interactions between
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19 90 individuals, depending on the sampling technique used and the frequency of the behaviour
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21 91 performed. Since network elements are inter-dependent [8,9], the absence of one or more real
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23 92 connections might generate an observed network that is potentially very different from a real
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25 93 network [8].

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28 94 To date, the majority of studies examining the effect of sampling technique on variation
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30 95 in the structure of social networks has largely relied on simulations [16–18]. This work has
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32 96 suggested that a minimum number of 10-20 observations within a given network might suffice
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34 97 to construct a reliable network [16–18]. For instance, by generating simulated networks, Farine
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36 98 and Strandburgh-Peshkin [19] showed that a minimum of 20 samples is necessary in order to
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38 99 have an accurate estimate of the edge weight (i.e., the rate of interaction or association between
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42 100 two nodes) within a network. Similarly, Davis et al. [16] used proximity data generated by
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44 101 fitting high-resolution GPS collars on free-ranging baboons (*Papio anubis*) to simulate an
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46 102 increase in sampling effort made through two observational methods, focal animal sampling
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48 103 and group scanning. The authors showed that a minimum of 10 samples per individual was
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50 104 necessary in order for the estimated network to be similar to the complete network. In this
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52 105 context, it is pivotal, however, to use real biological data to test whether the reliability of
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54 106 network measures depends on the sampling technique used, as sometimes simulations do not
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56 107 accurately reflect true, biological data [e.g., 20]. Moreover, using real datasets can also better
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3 108 inform researchers on how to best design their methodologies to generate reliable social
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5 109 networks. Notwithstanding, only few studies to date have compared different sampling
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8 110 techniques using actual observations, rather than simulations. McCarthy et al. [21], for
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10 111 instance, compared network measures calculated using data recorded through camera traps and
11
12 112 focal observations among wild chimpanzees (*Pan troglodytes*). The authors found a strong
13
14 113 correlation in network centrality indices between the two data sets, but found differences in
15
16 114 network density and modularity. Conversely, Canteloup et al. [22] found a strong correlation
17
18 115 in both grooming and play networks between data collected via *ad libitum* sampling and those
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20 116 recorded through focal animal sampling among vervet monkeys (*Chlorocebus pygerythrus*).
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23 117 More recently, Gelardi et al. [23] found strong similarities between social networks calculated
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25 118 from direct observations and through wearable proximity sensors. Collectively, these data
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27 119 suggest that different sampling methods yield similar network metrics, at least for local indices
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29 120 while differences may emerge for global indices.
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33 121 While the studies reviewed above have been crucial to understand to what extent
34
35 122 different sampling techniques can lead to differences in social network metrics, they also
36
37 123 lacked a comparative component as they focused either on single animal species or on a single
38
39 124 type of behaviour. Many group-living animal taxa, however, show both intra- and inter-species
40
41 125 differences in group cohesion and social organization, that are largely influenced by ecological
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43 126 factors [24–26]. Moreover, the frequency and directionality of social interactions may vary
44
45 127 broadly across behavioural types and socio-ecological contexts. For example, groups or species
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47 128 may show greater ‘despotism’ in their social structures, characterized by greater frequency and
48
49 129 unidirectionality (from dominants towards subordinates) of agonistic interactions, but lower
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51 130 frequencies of prosocial behaviours that are also more preferentially directed towards sub-sets
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53 131 of preferred prosocial partners such as close kin [27]. Conversely, groups/species that show a
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55 132 more egalitarian/tolerant social system may be expected to show the opposite characteristics
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3 133 [27]. Crucially, it remains unclear to what extent different sampling techniques can produce
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5 134 similar network measurements across different groups/species that display different social
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8 135 systems. In order to fill this gap, our study aims to compare both local and global network
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10 136 measures of three different social networks (aggression, grooming, and huddling) collected
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12 137 through two different sampling techniques, focal animal sampling (FAS) and all-occurrences
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14 138 behaviour sampling (ABS), from three different macaque species, rhesus (*Macaca mulatta*),
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16 139 long-tailed (*Macaca fascicularis*) and bonnet macaques (*Macaca radiata*).

19 140 FAS and ABS are two observational methods that are most commonly used to collect
20
21 141 behavioural data to construct animal social networks [28,29]. FAS allows an observer to focus
22
23 142 their attention on a specific focal subject, thus offering the opportunity to record detailed
24
25 143 information on a wide range of behaviours, both frequent and infrequent, performed by the
26
27 144 animal [28]. However, given that, via FAS, an observer focuses only on a single animal subject,
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29 145 an extended period of time is likely to be needed in order to have a big enough sample size to
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31 146 reliably reconstruct the social network of the whole group. Conversely, by observing the whole
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33 147 group, ABS may reduce the number of behaviours the observer can realistically collect, but it
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35 148 offers the advantage of recording interactions involving multiple individuals [28]. Such cost-
36
37 149 benefit trade-off between these two sampling techniques is likely to be one of the main criteria
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39 150 behind researchers' decision on which data collection method to use. It would, therefore, be
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41 151 pivotal to examine whether data collected via both methods yield similar network
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43 152 measurements.

49 153 Macaques are a well-suited study model to compare social network indices between
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51 154 different sampling techniques. The genus *Macaca* includes 22 species, that show similar social
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53 155 organizations with female philopatry and male dispersal, but marked inter- and intra-specific
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55 156 variation in their social systems [27]. For instance, while some species, such as bonnet
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57 157 macaques, may be typically characterized by relatively more tolerant social relationships, other
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3 158 species such as rhesus macaques may display relatively more despotic social systems [27].
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5 159 Several other species may fall somewhere in between, with some of them, such as long-tailed
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8 160 macaques, classified closer to the “despotic” end of this spectrum [27]. Such a broad variation
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10 161 of social systems makes macaques well-suited models for our aims pertaining to adopting a
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12 162 comparative approach to assess methodological effects of observational techniques on social
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15 163 networks.

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17 164 Here we constructed social networks for multiple, free-living groups of macaques
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19 165 representing three species that are typically characterized by different social systems. Using
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21 166 data collected via FAS and ABS, we calculated six commonly used network measures: three
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23 167 local metrics (degree, eigenvector, and betweenness) and three global metrics (density,
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25 168 modularity and centralization) [9]. We compared network indices constructed from the two
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27 169 types of data to each other, predicting that if network measures were robust to the type of
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29 170 observation technique regardless of the type of social behaviour considered or the study
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31 171 species, then both local and global network measures from FAS data should correlate with
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33 172 those indices generated using ABS data. Conversely, if the accuracy of SNA metrics is
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35 173 contingent on species-typical social systems, we expect: (a) network measures of affiliative
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37 174 behaviours (grooming and huddling) to be more strongly correlated between observation
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39 175 methods among bonnet macaques than among long-tailed and rhesus macaques; and (b)
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41 176 network measures of aggressive interactions to be more strongly correlated across observation
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43 177 methods among the despotic rhesus and long-tailed macaques than among the more tolerant
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45 178 bonnet macaques. Finally, if observers are likely to record different dyadic interactions with
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47 179 FAS and ABS methods, then we would expect a lack of correlation between the social metrics
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49 180 calculated from FAS data and those calculated from ABS data.
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58 182 **MATERIALS AND METHODS**

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3 183 *Study sites and subjects*
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5 184 The study was conducted on a total of eight social groups of macaques. Rhesus
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8 185 macaques were studied in the city of Shimla, in Northern India (31° 05' N-077° 10' E) between
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10 186 August 2016 and February 2018. Here, we observed a total of 92 rhesus macaques (29 males
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12 187 and 63 females) from three macaque groups in two different locations: one group was observed
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14 188 in Mall Road (hereafter “MG”), and two groups (“HG” and “RG”) were observed at Jakhoo
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16 189 temple (for more details on the study site see [30,31]). Although there were some changes in
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18 190 the number of adult males and females across the three groups during the study period, the
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20 191 majority of the individuals remained in the group for most of the study (i.e., 75% of MG
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22 192 macaques, 79% of RG macaques and 69% of HG macaques remained in the group for at least
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24 193 one year of data collection; Fig. S1).
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28 194 Long-tailed macaques were studied in Kuala Lumpur (Malaysia) between September
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30 195 2016 and February 2018 (3°17' N-101°37' E). Here we observed a total of 79 individuals (24
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32 196 males and 55 females) from three macaque groups in two locations: one group (“Pirate”) was
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34 197 observed at Batu Caves, and two groups (“Entrance” and “Hulk”) were observed at Templer
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36 198 Park (for more details of the study site see [32]). Although these groups were subject to some
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38 199 demographic changes, the majority of the individuals remained in the group throughout the
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40 200 study period (Pirate: 80%; Entrance: 71%; Hulk: 84%; Fig. S2).
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44 201 Bonnet macaques were observed in Thenmala, within the state of Kerala, in Southern
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46 202 India between July 2017 and May 2018 (8.9° N- 77.0° E). Here the groups were studied in two
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48 203 locations: one (“LG”) was studied at the Thenmala dam while one group (“SG”) was studied
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50 204 at the Ecotourism Recreational Area (for more details of the study site and group composition
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52 see [33]). Overall, we observed a total of 79 bonnet macaques (39 males and 40 females) and,
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54 205 for both groups, composition was subject to very minimal demographic changes, as the
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3 207 majority of the macaques remained in the group throughout the study period (LG: 71%; SG:
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5 208 83%; Fig. S3).

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10 210 *Data collection*

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12 211 Across the three study sites, and with the help of 4-5 field assistants per site, we
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14 212 recorded information on social grooming, huddling, and aggression using both FAS and ABS.
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16 213 We defined grooming as the manipulation of the skin or hair of a conspecifics with the hands
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18 214 in order to remove debris or ectoparasites, and huddling as the ventral-ventral or ventral-dorsal
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20 215 physical contact between individuals, while we classified as aggression any instance of
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22 216 chasing, aggressive grabbing, biting, slapping, or threatening. Data from the field assistants
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24 217 were allowed to contribute to the final data set only after they reached a Cohen reliability index
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26 218 ≥ 0.85 .

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30 219 Through FAS, we followed each adult macaque for 10 minutes recording any social
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32 220 interaction (i.e., grooming, huddling, and aggression) the focal subject was involved in as well
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34 221 as the identity of the conspecific interaction partners of the focal animal. The order by which
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36 222 focal subjects were selected was randomized every day, with the aim of collecting at least two
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38 223 focal sessions per subject per week. ABS was conducted 12 times per week, half of them in the
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40 224 morning and half in the afternoon. Each ABS session lasted for 10 minutes. At the beginning
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42 225 of an ABS session, the observer would record the individuals who were visible at the time.
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44 226 Subsequently, throughout the session, the observer would scan the group from left to right (and
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46 227 vice versa) to record any new instance of social interaction and the identity of the individuals
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48 228 involved. At the end of this 10-min session, the observer would, again, record the individuals
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50 229 who were present in the group, before searching for a new sub-group and start a new 10-min
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52 230 session. We conducted FASs and ABSs at different times of the day as to avoid recording the
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54 231 same interactions using both methods. Overall, we collected a similar amount of data for both
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3 232 sampling methods (Figs. S4 & S5): for rhesus, we recorded an average of 143.2 and a median
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5 233 of 138 FAS sessions per month (RG: mean = 128.2, median = 139; HG: mean = 118.2, median
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7 = 121.5; MG: mean = 169.2, median = 174), and macaques were sampled via ABS an average
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9 of 166.2 and a median of 165 times per month (HG: mean = 101.2, median = 83; RG: mean =
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11 235 201.8, median = 166; MG: mean = 194.1, median = 193.5). Similarly, for long-tailed macaques,
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13 236 we recorded an average of 91.8 and a median of 97 FAS sessions per month (Pirate: mean =
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15 237 88.7, median = 74; Entrance: mean = 122.2, median = 121; Hulk: mean = 66.4, median = 65.5),
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17 238 whereas individuals were sampled an average of 88.5 and a median of 66 times per month
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19 239 through ABS (Pirate: mean = 77.2, median = 79; Entrance: mean = 120.6, median = 95; Hulk:
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21 240 mean = 71.4, median = 55). Finally, for bonnet macaques, we recorded an average of 219.6
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23 241 and a median of 207.5 FAS sessions per month (SG: mean = 154.7, median = 159; LG: mean
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25 242 = 284.5, median = 320), while macaques were sampled an average of 232.7 and a median of
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27 243 240 times per month via ABS (SG: mean = 183.2, median = 151; LG: mean = 282.3, median
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29 244 =293).

246

247 *Social network analysis*

248 We used the data on social interactions recorded via both FAS and ABS to construct
249 social networks. Since long-tailed macaques were observed huddling only rarely (Table S1),
250 we excluded huddling interactions for this species from the analysis. In order to take into
251 account the fact that individuals might have been present in the group for different lengths of
252 time, due to new individuals joining the group or some individuals disappearing from the
253 group, we calculated interaction frequencies by dividing the number of dyadic social
254 interactions by either the amount of time (for FAS) or the number of sessions (for ABS) in
255 which both members of the dyad were present in the group. We then used the *sna* and *igraph*
256 packages in R to calculate three local and three global metrics. At **individual local** level we

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3 257 measured: 1) *degree centrality* which reflects the number of edges that are connected to a node
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5 258 and thus represents the number of direct connections each subject has [9]; 2) *eigenvector*
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7 259 *centrality*, which is the sum of centralities of a node's neighbours, thereby representing the
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10 260 social support or social capital of an individual through being connected to animals who are in
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12 261 turn well connected themselves [9,34]; and 3) *betweenness centrality*, that is the number of
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14 262 shortest paths that flow through a node, indicating to what extent an individual connects
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16 263 subgroups, or may act as a 'hub' for information flow through the network [9]. These network
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18 264 measures were rescaled in order to take into account the different group sizes, and so ranged
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20 265 between 0 and 1. At global level, we measured: 1) *density* which is the number of edges divided
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22 266 by the total possible number of edges, and so assesses to what extent animals in the network
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24 267 are highly connected to each other [9]; 2) *modularity*, which is measured as the difference
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26 268 between the observed proportion of edges that fall within subgroups and the expected value of
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28 269 the same quantity if edges are assigned randomly and reflects to what degree a network can be
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30 270 subdivided into clusters of animals that more closely interact with each other than they do with
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32 271 animals in other clusters [35]; and 3) *eigenvector centralization*, which is the difference
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34 272 between the eigenvector centrality of the node with the highest eigenvector centrality of the
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36 273 group and the eigenvector centrality of the other group members, and represents to what extent
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38 274 few individuals tend to be more central within a social network [36]. While degree and density
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40 275 were computed as unweighted measures, without taking into account the frequency of each
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42 276 dyadic interaction, eigenvector, betweenness, modularity and centralization were calculated as
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44 277 weighted measures.
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279 *Data analysis*

56 280 We first tested the robustness of each social network. We used two approaches to assess
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58 281 network robustness: we first assessed, for each data collection method and for each social
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3 282 behaviour, the variation in mean value of all three local network measures as well as the
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5 283 variation of all three global measures over time with monthly increases of data collected. We
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7 284 expected the curves to become progressively “flatter” because, if the networks were becoming
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9 285 more and more stable over time, monthly variation in network measures would become smaller
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11 286 and smaller as observers recorded fewer and fewer new edges between nodes. Second, we
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13 287 followed previous approaches [19,22,37], and used bootstrapping to estimate network
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15 288 uncertainty, which reflects the (un)certainty with which network metrics were estimated. For
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17 289 each monthly data and for each social behaviour examined, the identity of the recipient was
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19 290 randomly reshuffled and social network metrics were re-calculated. This procedure was
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21 291 repeated 1000 times, eventually generating a distribution of possible values. From this
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23 292 distribution, we extracted the 95% confidence interval and subtracted the maximum and
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25 293 minimum value of this range in order to calculate the uncertainty index. We then assessed, for
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27 294 both sampling methods, the monthly variation of this uncertainty index, expecting this value to
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29 295 decline as more observations were recorded and networks would become more certain.
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35 296 In order to assess whether local network measures calculated from FAS and ABS data
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37 297 were correlated, we ran Generalized Linear Mixed Model (GLMM) analyses with Beta error
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39 298 structure through the R function *glmmTMB*. In this model, ABS network measures were set as
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41 299 outcome variables in separate models, giving us a total of nine GLMMs. As predictors, we
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43 300 included FAS network measures, and species ID to account for their potential effects on
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45 301 network measures. We selected a Beta error structure for the GLMM models because the
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47 302 outcome variable could only range between 0 and 1 [38]. Finally, group identity was entered
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49 303 as a random factor in order to control for the non-independence of individuals from the same
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51 304 group. To assess whether network measures calculated using the two different methodologies
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53 305 were positively correlated for all species, or only for some species, we compared the Akaike
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55 306 Information Criterion (AIC) value of the null model (i.e., the model that included only the
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3 307 outcome variable and the random factor), with the model that included the predictors only as
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5 308 main effects, and the model that included the interaction between the FAS network measures
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7 309 and the species. We used the *influence_mixed* and *infIndexPlot* functions to check the presence
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10 310 of influential observations. The “performance” package in R was used to both calculate the
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12 311 effect size (R^2) of the GLMM model and verify that all GLMM models met the necessary
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14 312 assumptions of model validity (i.e., distribution of residuals, residuals plotted against fitted
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16 313 values). Given that network measures are not independent as an individual’s network metric
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18 314 depends on other individuals’ network positions, researchers typically use permutation to test
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20 315 the statistical significance of regression models [8,39]. However, recent simulations have
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22 316 suggested that permutation methods do not control for non-independence of the data and that
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24 317 GLMMs can already provide robust results [40]. Because no consensus has yet been reached
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26 318 on the best statistical approach when using regression models for social network data, in the
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28 319 main text we present the results of the GLMM analysis without permutation, while in the
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30 320 supplementary materials we present the results of the permutation analysis, in which we
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32 321 compared the estimates generated from the observed data with a distribution of estimates
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34 322 calculated from random networks [41]. To this end, for each best GLMM model, we conducted
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36 323 a post-network node-swapping randomization which generated 1000 networks from the ABS
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38 324 data by randomly shuffling the identity of the network nodes, and then re-ran the GLMM
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40 325 analysis for each of these 1000 networks. This produced a distribution of estimates from these
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42 326 models and we calculated one-tailed p-values by comparing the number of the random
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44 327 estimates that were higher than the observed estimate.

51 328 Finally, we used Pearson’s correlation test to assess whether global measures calculated
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53 329 from FAS data significantly correlated with the measures calculated from ABS data.

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3 330 R-codes and data are available in our data repository
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5 331 ([https://figshare.com/projects/Effect_of_behavioural_sampling_methods_on_local_and_glob](https://figshare.com/projects/Effect_of_behavioural_sampling_methods_on_local_and_global_social_network_metrics_A_case-study_of_three_macaque_species/166205)
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7 332 [al_social_network_metrics_A_case-study_of_three_macaque_species/166205](https://figshare.com/projects/Effect_of_behavioural_sampling_methods_on_local_and_global_social_network_metrics_A_case-study_of_three_macaque_species/166205)).
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11 334 *Ethical note*

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14 335 All applicable international, national, and/or institutional guidelines for the care and use of
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16 336 animals were followed. All procedures performed in this study were in accordance with the
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18 337 ethical standards of the Institutional Animal Care and Use Committee of the University of
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20 338 California, Davis, and complied with the legal requirements of India and Malaysia.
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26 340 **RESULTS**27
28 341 *Network robustness*

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30 342 Table S1 summarizes the total number and frequencies of social interactions recorded
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32 343 for all three species and for both sampling methods, while ~~visual representations of visual~~
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34 344 ~~representations of Fig. 1 illustrates examples of~~ social networks calculated from both FAS and
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36 345 ABS for all three behaviours examined. ~~A complete representation of all social networks~~ can
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38 346 be found in the supplementary material (Figs. S6-S13). Plotting monthly variation in network
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40 347 metrics (both mean local and global metrics) and their uncertainty values with monthly
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42 348 increases of data recorded across the three species revealed a progressive flattening of the
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44 349 curves for both FAS and ABS data (Fig. ~~1s. 2 & 3~~ and Figs. S14-S~~24~~35). Although network
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46 350 density was expected to either remain the same or increase over time, our analysis showed
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48 351 occasional reductions in network density values. These are likely due to small changes in
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50 352 demographics (i.e., if an individual disappeared from the group, the connections this individual
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52 353 had with other group members will have disappeared too). For both FAS and ABS, mean
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54 354 individual metrics flattened and uncertainty values dropped (suggesting more accuracy in the
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3 355 measurement) relatively early in data collection, although it required substantially more effort
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5 356 to achieve this when data were collected through FAS than when they were collected via ABS.
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8 357 More specifically, when data were collected via FAS, it took at least 50 hours of observations
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10 358 to reach no or minimal fluctuations of local metrics and their uncertainty with progressive
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12 359 increase in observation time (Figs 1-2-3 &and Figs-S14-S1517). Conversely, when data were
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14 360 recorded through ABS, it took less than 10 hours to reach the same result (Figs. S168-S1823).
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17 361 Furthermore, similar to the local network metrics, our analysis of global metrics and their
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19 362 uncertainty values shows a progressive flattening of the curves. However, we found more
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21 363 fluctuation over time of global metrics compared to local indices with larger fluctuations for
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24 364 data collected through ABS than those collected through FAS (Figs. S1924-S2435).
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26 365 Furthermore, interestingly, it appears that it takes longer to reach a stability in global metrics
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28 366 compared to local metrics for both sampling methods. In fact, it took at least 100 hours of
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30 367 observation time with FAS and 15 hours of observation time with ABS to achieve minimal
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33 368 fluctuation in global metrics. Collectively, the fact that our analysis shows that variation in
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35 369 both local and global metrics with progressive increase in observation time reaches a plateau
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38 370 and that uncertainty levels decrease suggest that the social networks measures in this study are
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40 371 accurate and robust.

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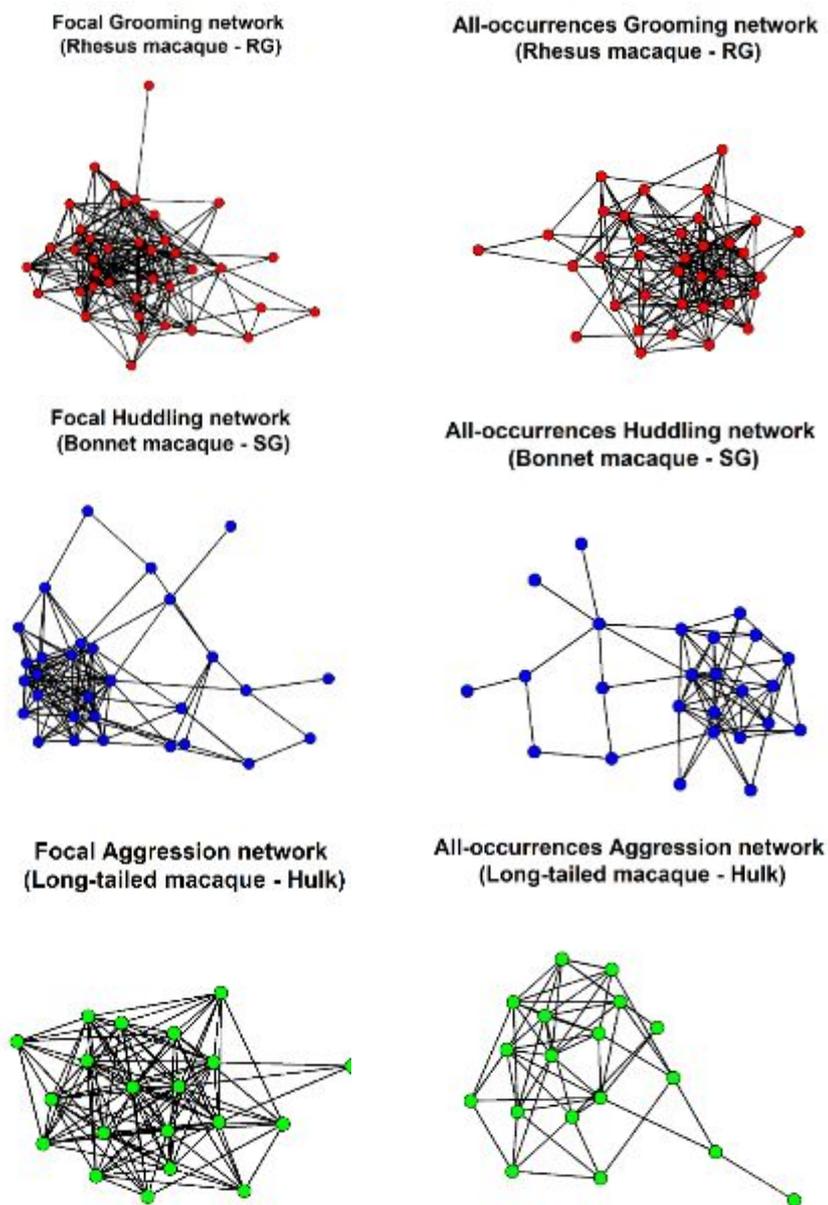


Fig. 1. Examples of grooming (*top*), huddling (*middle*) and aggression (*bottom*) networks for one rhesus (RG-*top*), one bonnet (SG-*middle*) and one long-tailed (Hulk-*bottom*) macaque group. Nodes represent individual subjects while edges represent interactions.

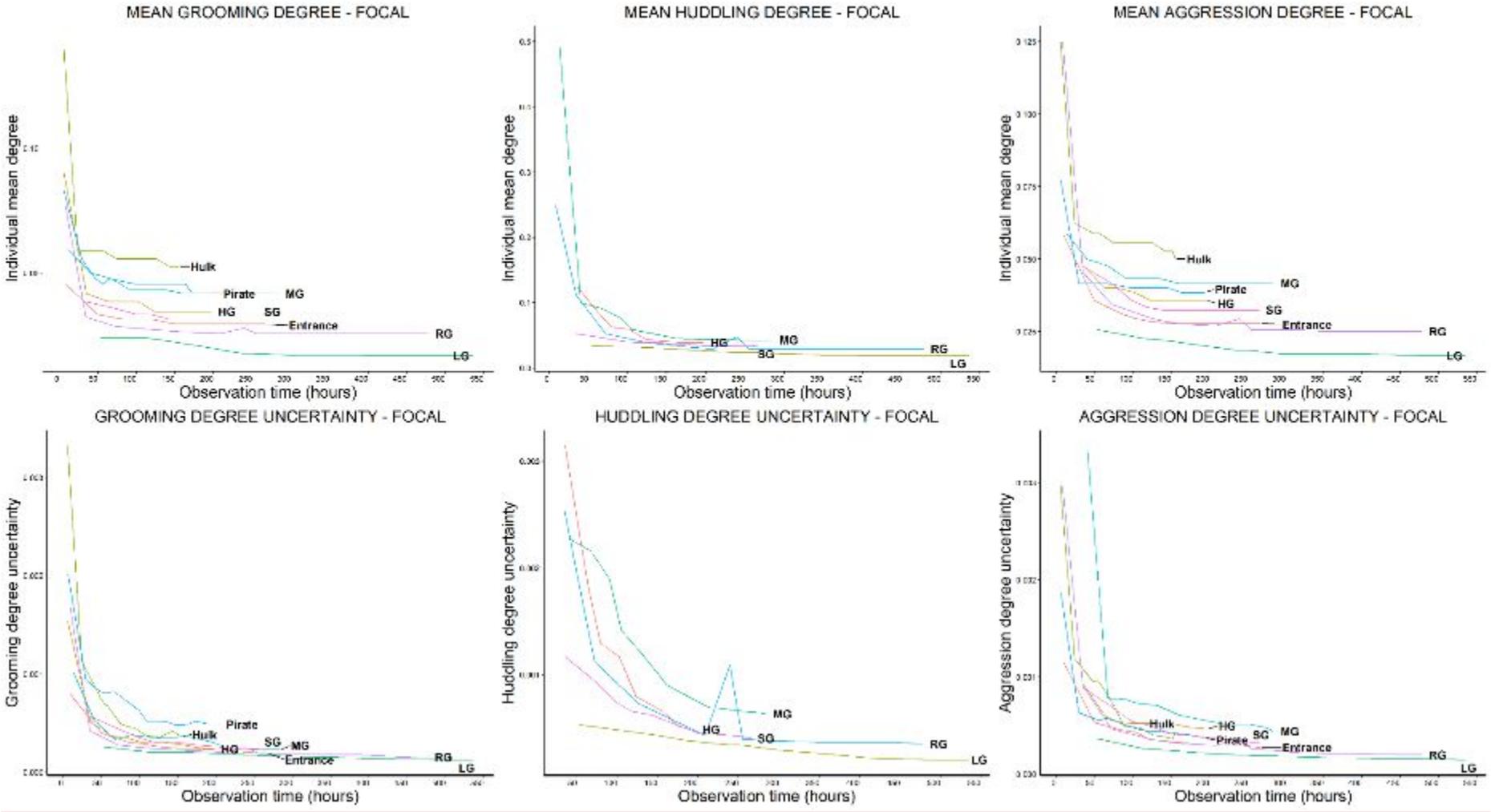


Fig 1. Monthly variation in individual mean grooming, huddling and aggression degree (top row) and degree uncertainty (bottom row) with progressive monthly increases in focal animal sampling observation time. Each line represents a study group. Rhesus macaque groups: RG, HG, MG; long-tailed macaque groups: Pirate, Hulk, Entrance; bonnet macaque groups: SG, LG.

409 GGrooming network analysis

410 The analysis of the grooming network showed a significant effect of the interaction
411 between FAS data and species on ABS network metrics for both degree and betweenness
412 (Tables 1 & S2). While all three species showed a positive relationship between FAS and ABS
413 networks, this relationship was stronger for long-tailed macaques than for the other two species
414 (Fig. 24). Conversely, we found a significant main effect of FAS eigenvector on ABS
415 eigenvector (Tables 1 & S2). In other words, the macaques who were more central in the
416 grooming network (through both direct and indirect connections) as measured by the FAS data,
417 were also more central in the grooming network as estimated by ABS data, across all three
418 species.

419 For global measures, we found a significant correlation between FAS and ABS data for
420 both grooming density ($r(6) = 0.79$; $p = 0.02$) and modularity ($r(6) = 0.76$; $p = 0.03$, Fig. 25),
421 but not centralization ($r(6) = 0.59$; $p = 0.11$, Fig. 25). A close look at the centralization values
422 shows that these values were particularly different between sampling methods in one rhesus
423 (RG) and two long-tailed macaque groups (Hulk and Entrance). In fact, when these data points
424 were removed, we found a significant correlation between ABS and FAS centralization values
425 ($r(3) = 0.91$; $p = 0.03$).

426 Collectively, this analysis showed that grooming network density and modularity were
427 both highly consistent (correlated) across sampling methods for all three macaque species,
428 whereas we did not find evidence that grooming network centralization was correlated between
429 ABS and FAS. This lack of correlation is likely driven by one rhesus and two long-tailed
430 macaque groups.

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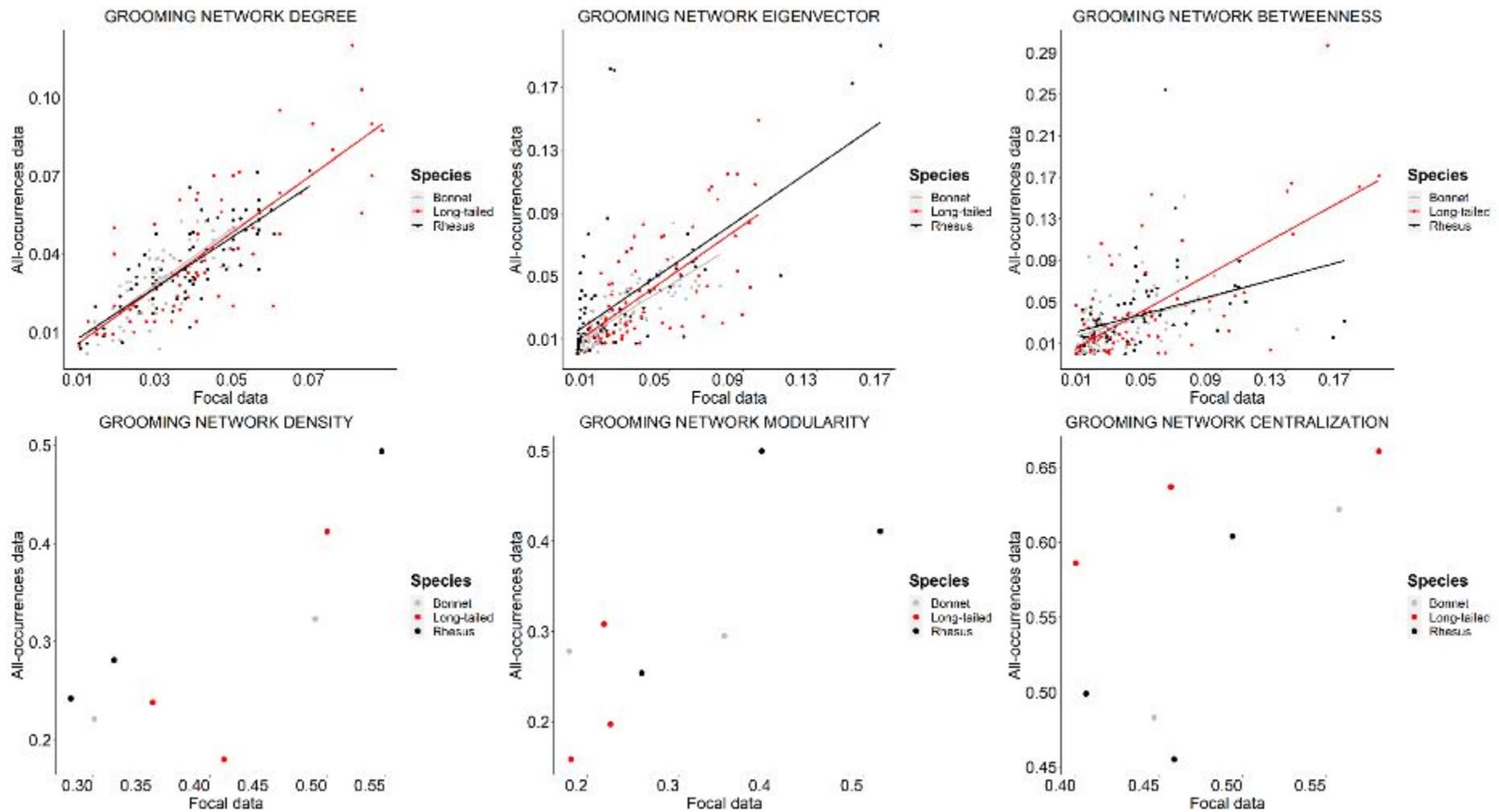
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Table 1. Results of the GLMM analysis testing whether individuals' grooming centrality measures calculated from the focal animal sampling (FAS) data and species identity (rhesus, long-tailed, bonnet) significantly predicted grooming centrality measures calculated from the all-occurrences behaviour sampling (ABS) data. Significant predictors are indicated in bold.

<i>Predictors</i>	<i>Estimate</i>	<i>SE</i>	<i>95% CI</i>	<i>z-value</i>	<i>P-value</i>
Intercept	-4.60	0.14	-4.88; -4.32	-32.07	< 0.001
FAS degree	38.67	4.55	29.75; 47.60	8.49	< 0.001
Species (long-tailed vs bonnet)	0.35	0.17	0.02; 0.69	2.07	0.038
Species (rhesus vs bonnet)	0.19	0.18	-0.17; 0.55	1.04	0.297
Species (rhesus vs long-tailed)	0.16	0.15	-0.13; 0.46	1.07	0.282
FAS * Species (long-tailed vs bonnet)	-14.05	4.89	-23.64 -4.47	-2.87	0.004
FAS * Species (rhesus vs bonnet)	-8.38	5.36	-18.89; 2.14	-1.56	0.118
FAS * Species (rhesus vs long-tailed)	-5.68	3.36	-12.27; 0.91	-1.69	0.091
<i>Predictors</i>	<i>Estimate</i>	<i>SE</i>	<i>95% CI</i>	<i>z-value</i>	<i>P-value</i>
Intercept	-3.96	0.10	-4.16; -3.77	-40.10	< 0.001
FAS eigenvector	17.05	1.13	14.82; 19.27	15.03	< 0.001
Species (long-tailed vs bonnet)	0.03	0.12	-0.20; 0.26	0.25	0.800
Species (rhesus vs bonnet)	-0.01	0.12	-0.24; 0.22	-0.11	0.913
Species (rhesus vs long-tailed)	0.04	0.11	-0.17; 0.26	0.40	0.692
<i>Predictors</i>	<i>Estimate</i>	<i>SE</i>	<i>95% CI</i>	<i>z-value</i>	<i>P-value</i>
Intercept	-3.70	0.16	-4.02; -3.38	-22.52	< 0.001
FAS betweenness	11.49	3.15	5.32; 17.65	3.65	< 0.001
Species (long-tailed vs bonnet)	-0.56	0.21	-0.98; -0.15	-2.64	0.008
Species (rhesus vs bonnet)	0.004	0.21	-0.40; 0.41	0.02	0.985
Species (rhesus vs long-tailed)	-0.57	0.20	-0.96; -0.18	-2.86	0.004
FAS * Species (long-tailed vs bonnet)	5.02	3.55	-1.93; 11.98	1.42	0.157
FAS * Species (rhesus vs bonnet)	-2.05	3.78	-9.47; 5.36	-0.54	0.587
FAS * Species (rhesus vs long-tailed)	7.07	2.70	1.84; 12.31	2.65	0.008

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441 **Fig. 24.** Scatterplot plotting the three grooming local (top row) and global (bottom row) network metrics (i.e., degree, eigenvector and
442 betweenness) calculated from all-occurrences behaviour sampling (ABS) data against those calculated from focal animal sampling (FAS) data.

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8 445 ~~For global measures, we found a significant correlation between FAS and ABS data for~~
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10 446 ~~both grooming density ($r(6) = 0.79$; $p = 0.02$) and modularity ($r(6) = 0.76$; $p = 0.03$, Fig. 5),~~
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12 447 ~~but not centralization ($r(6) = 0.59$; $p = 0.11$, Fig. 5). A close look at the centralization values~~
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14 448 ~~shows that these values were particularly different between sampling methods in one rhesus~~
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16 449 ~~(RG) and two long-tailed macaque groups (Hulk and Entrance). In fact, when these data points~~
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18 450 ~~were removed, we found a significant correlation between ABS and FAS centralization values~~
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20 451 ~~($r(3) = 0.91$; $p = 0.03$).~~

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24 452 ~~Collectively, this analysis showed that grooming network density and modularity were~~
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26 453 ~~both highly consistent (correlated) across sampling methods for all three macaque species,~~
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28 454 ~~whereas we did not find evidence that grooming network centralization was correlated between~~
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30 455 ~~ABS and FAS. This lack of correlation is likely driven by one rhesus and two long-tailed~~
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32 456 ~~macaque groups.~~

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36 37 38 458 *Huddling network analysis*

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40 459 The analysis of huddling network at local level showed that, for both degree and eigenvector
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42 460 centrality, the interaction between FAS data and species was better fit compared to the null
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44 461 model and the model which included only the main effects terms (Tables 2 & S5; Fig. 6).
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46 462 Exploring this interaction term further revealed that, for both rhesus and bonnet macaques,
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48 463 FAS degree positively predicted the corresponding ABS centrality measures, but that the
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50 464 relationship was stronger for bonnet macaques compared to rhesus macaques (Fig. 36), which
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52 465 supports our prediction. Conversely, for huddling network eigenvector, there was a positive
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54 466 relationship between FAS and ABS data for bonnet, while a negative relationship for rhesus
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56 467 macaques (Fig. 36). Finally, for betweenness centrality, the model that included only the main
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3 468 effect was a significantly better fit compared to the model that included the interaction term
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5 469 (Table S5). As predicted, this model showed a positive relationship between FAS and ABS
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8 470 betweenness (Table 2).

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10 471 Global analysis revealed a significant correlation between ABS and FAS data for both
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12 472 network density ($r(3) = 0.89$; $p = 0.04$) and modularity ($r(3) = 0.93$; $p = 0.02$, Fig. 37). In
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14 473 contrast, we did not find a significant correlation between the two sampling methods for
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16 474 network centralization ($r(3) = 0.57$; $p = 0.32$). Again, data from the RG group appeared to be
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18 475 an outlier. When this group was excluded, there was a significant correlation between ABS and
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20 476 FAS huddling network centralization values ($r(2) = 0.97$; $p = 0.03$, Fig. 37).

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24 477 Collectively, these results suggest that FAS and ABS yield similar, consistent network
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26 478 metrics for all local network metrics. At the global level, these methods yield consistent metrics
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28 479 for network density and modularity, while for network centralization ABS and FAS sampling
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30 480 methods produced similar values for all but one group.

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Table 2. Results of the GLMM analysis testing whether individuals' huddling centrality measures calculated from the focal animal sampling (FAS) data and species identity (rhesus and bonnet) predicted centrality calculated from the all-occurrences behaviour sampling (ABS) data. Significant predictors are indicated in bold.

Huddling Degree					
<i>Predictors</i>	<i>Estimate</i>	<i>SE</i>	<i>95% CI</i>	<i>z-value</i>	<i>P</i>
Intercept	-4.41	0.17	-4.74; -4.06	-25.27	< 0.001
FAS degree	31.82	4.35	23.3; 40.0	7.31	< 0.001
Species (rhesus vs bonnet)	0.79	0.25	0.30; 1.28	3.16	0.002
Degree * Species (rhesus vs bonnet)	-18.32	5.59	-29.3; -7.40	-3.28	0.001
Huddling Eigenvector					
<i>Predictors</i>	<i>Estimate</i>	<i>SE</i>	<i>95% CI</i>	<i>z-value</i>	<i>P</i>
Intercept	-4.67	0.88	-6.40; -2.95	-5.31	< 0.001
FAS eigenvector	38.98	5.25	28.69; 49.28	7.42	< 0.001
Species (rhesus vs bonnet)	-0.66	1.12	-2.85; 1.53	-0.59	0.553
Eigenvector * Species (rhesus vs bonnet)	-26.42	6.15	-38.48; -14.36	-4.30	< 0.001
Huddling Betweenness					
<i>Predictors</i>	<i>Estimate</i>	<i>SE</i>	<i>95% CI</i>	<i>z-value</i>	<i>P</i>
Intercept	-3.48	0.26	-3.99; -2.96	-13.26	< 0.001
FAS betweenness	9.99	2.53	5.03; 14.95	3.95	< 0.001
Species (rhesus vs bonnet)	-0.38	0.25	-0.87; 0.11	-1.52	0.128

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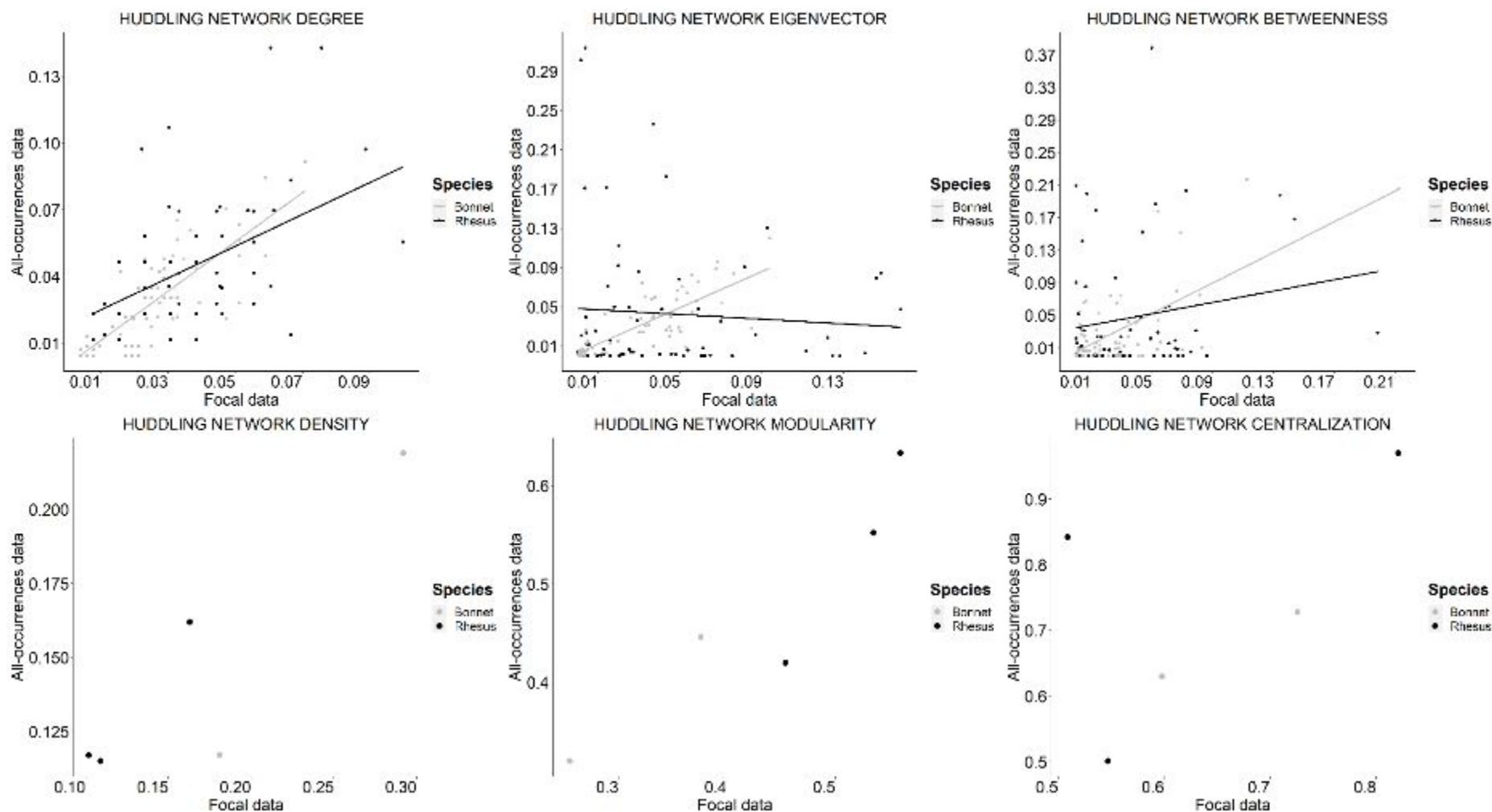


Fig. 36. Scatterplot plotting the three huddling local (top row) and global (bottom row) network metrics (i.e., degree, eigenvector and betweenness) calculated from all-occurrences behaviour sampling (ABS) data against those calculated from focal animal sampling (FAS) data.

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3 502 ~~Global analysis revealed a significant correlation between ABS and FAS data for both network~~
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5 503 ~~density ($r(3) = 0.89$; $p = 0.04$) and modularity ($r(3) = 0.93$; $p = 0.02$, Fig. 7). In contrast, we did~~
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7 504 ~~not find a significant correlation between the two sampling methods for network centralization~~
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9 505 ~~($r(3) = 0.57$; $p = 0.32$). Again, data from the RG group appeared to be an outlier. When this~~
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11 506 ~~group was excluded, there was a significant correlation between ABS and FAS huddling~~
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13 507 ~~network centralization values ($r(2) = 0.97$; $p = 0.03$, Fig. 7)~~

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17 508 Collectively, these results suggest that FAS and ABS yield similar, consistent network
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19 509 metrics for all local network metrics. At the global level, these methods yield consistent metrics
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21 510 for network density and modularity, while for network centralization ABS and FAS sampling
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23 511 methods produced similar values for all but one group.

512 513 *Aggression network analysis*

514 The analysis of aggression network showed that, across all three local measures, the
515 models that included the predictors as main effects only had a better fit compared to the models
516 that included the interaction between FAS network and species (Tables 3 & S6). For all three
517 measures, there was a positive relationship between FAS and ABS data across all three species
518 (degree: $\beta \pm SE = 23.80 \pm 2.02$, $z = 11.77$, $p < 0.001$; eigenvector: $\beta \pm SE = 8.85 \pm 2.18$, $z =$
519 4.07 , $p < 0.001$; betweenness: $\beta \pm SE = 11.17 \pm 1.78$, $z = 6.29$, $p < 0.001$; Table 3; Fig. 48),
520 suggesting that individuals that displayed higher aggression network degree, eigenvector and
521 betweenness centrality values when data were collected through FAS, exhibited similar
522 centrality values when data were collected through ABS.

523 At global level, we found a significant correlation between FAS and ABS data for both
524 aggression network density ($r(6) = 0.90$; $p = 0.002$) and centralization ($r(6) = 0.78$; $p = 0.02$;
525 Fig. 49). In contrast, we found no evidence that aggression network modularity was
526 significantly correlated between the two sampling methods ($r(6) = 0.02$; $p = 0.95$).

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3 527 Collectively, our results showed that, for aggressive interactions, FAS data produce
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5 528 similar network measures as those produced by ABS data for all local network indices (i.e.,
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7 529 degree, eigenvector and betweenness) and for two of the three global metrics examined (i.e.,
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9 530 density and centralization), while aggression modularity was not correlated between the two
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11 531 sampling methods.
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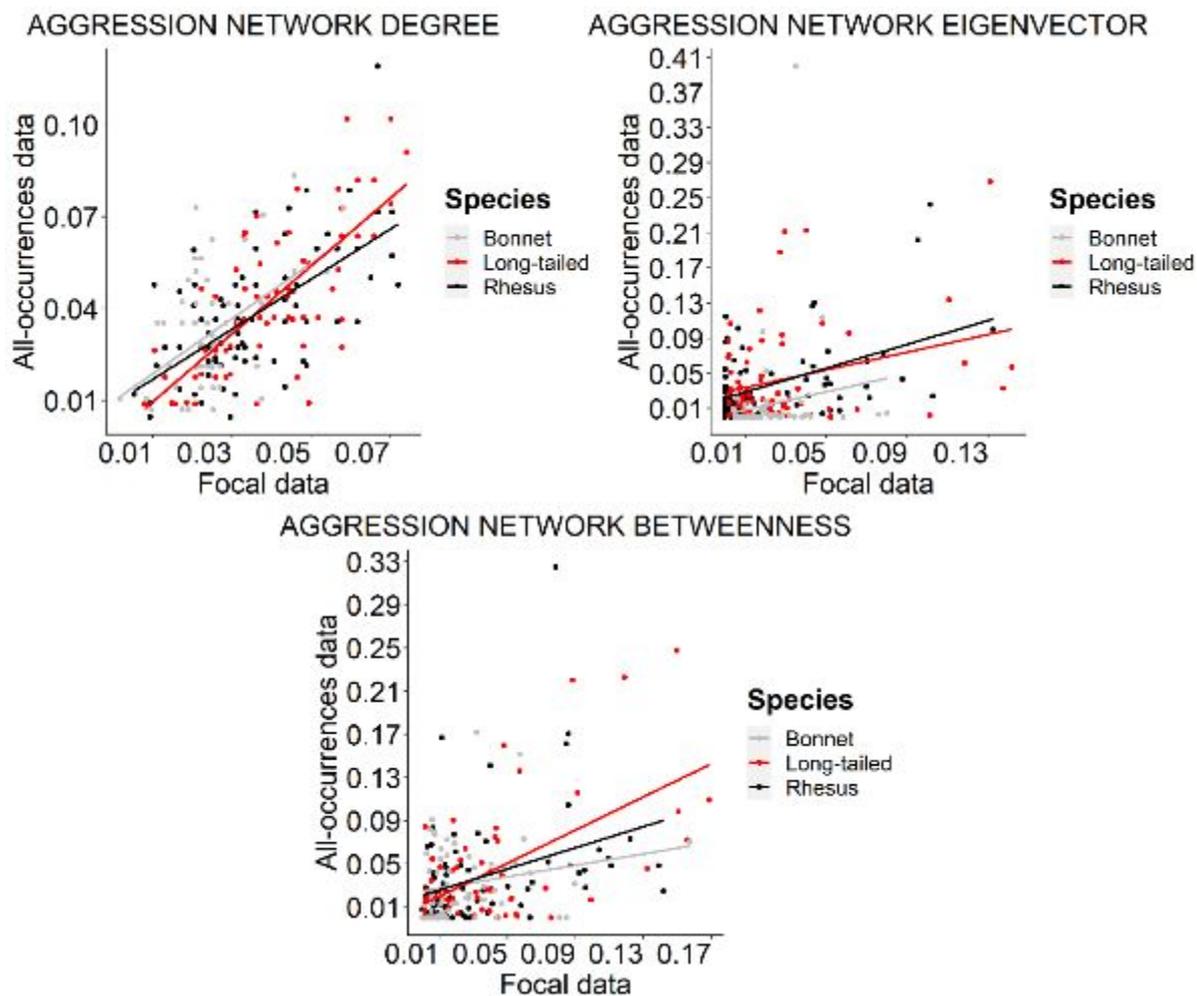
Table 3. Results of the GLMM analysis testing whether individuals' aggression centrality measures calculated from the focal animal sampling (FAS) data and species identity (rhesus, long-tailed, bonnet) significantly predicted aggression centrality calculated from the all-occurrences behaviour sampling (ABS) data. Predictors that are significant are indicated in bold

Aggression Degree					
<i>Predictors</i>	<i>Estimate</i>	<i>SE</i>	<i>95% CI</i>	<i>z-value</i>	<i>P</i>
Intercept	-4.06	0.09	-4.23; -3.88	-46.73	-46.730
FAS degree	23.80	2.02	19.84; -27.77	11.77	< 0.001
Species (long-tailed vs bonnet)	-0.06	0.09	-0.24; 0.11	-0.72	0.474
Species (rhesus vs bonnet)	-0.09	0.09	-0.26; 0.081	-1.02	0.309
Species (long-tailed vs rhesus)	0.02	0.07	-0.12; 0.17	0.34	0.735
Aggression Eigenvector					
<i>Predictors</i>	<i>Estimate</i>	<i>SE</i>	<i>95% CI</i>	<i>z-value</i>	<i>P</i>
Intercept	-4.64	0.21	-5.05; 4.22	-21.94	< 0.001
FAS eigenvector	8.85	2.18	4.58; 13.12	4.07	< 0.001
Species (long-tailed vs bonnet)	1.15	0.23	0.87; 1.77	4.96	< 0.001
Species (rhesus vs bonnet)	1.32	0.23	0.70; 1.61	5.75	< 0.001
Species (rhesus vs long-tailed)	-0.16	0.20	-0.56; 0.23	-0.82	0.41
Aggression Betweenness					
<i>Predictors</i>	<i>Estimate</i>	<i>SE</i>	<i>95% CI</i>	<i>z-value</i>	<i>P</i>
Intercept	-4.07	0.21	-4.48; -3.66	-19.56	< 0.001
FAS betweenness	11.17	1.78	7.69; 14.65	6.29	< 0.001
Species (long-tailed vs bonnet)	0.36	0.22	-0.06; 0.79	1.67	0.095
Species (rhesus vs bonnet)	0.47	0.21	0.06; 0.09	2.27	0.023
Species (rhesus vs long-tailed)	-0.10	0.20	-0.49; 0.28	-0.53	0.596

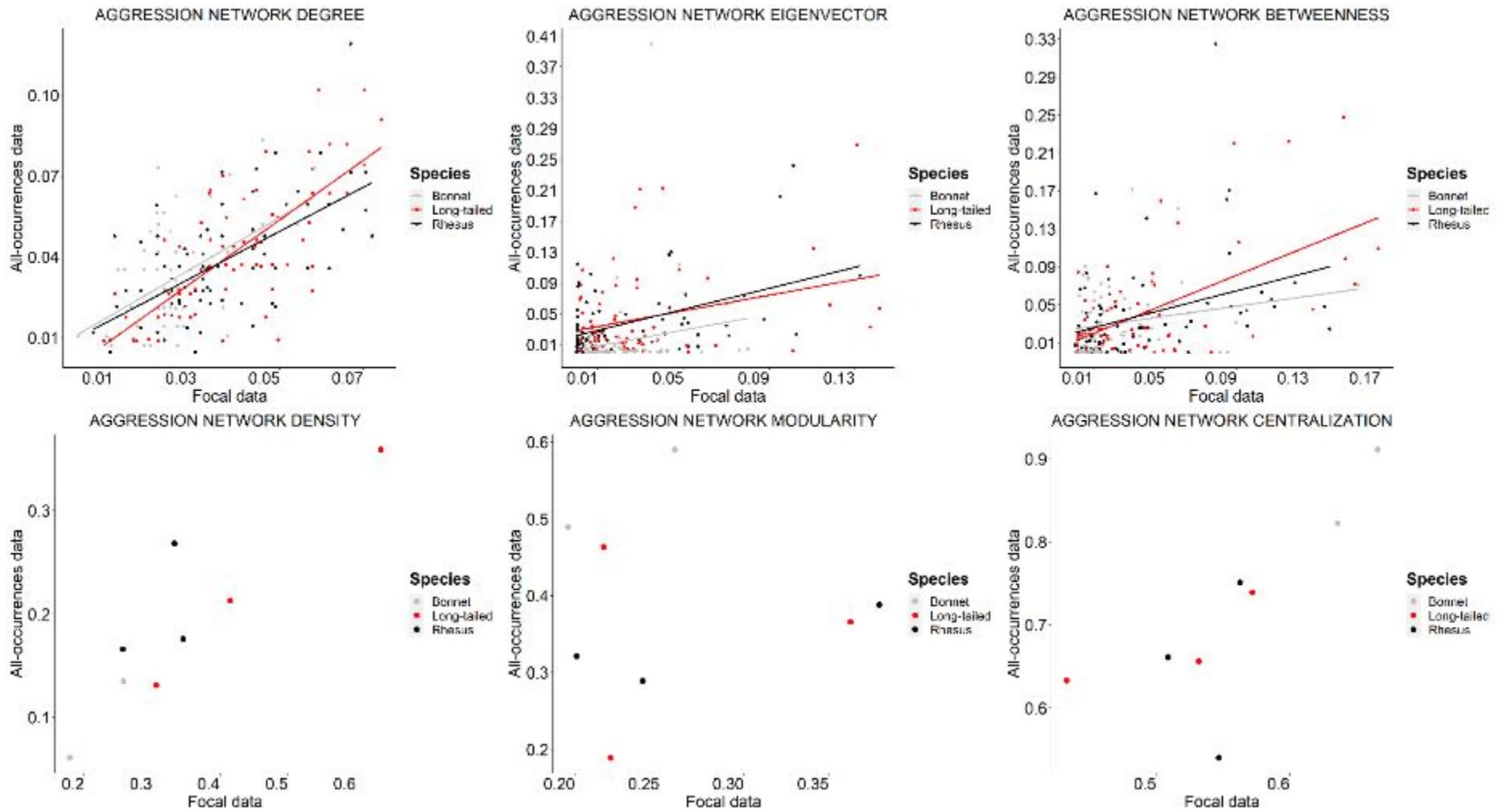
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562 **Fig. 48.** Scatterplot plotting the three aggression local and global metrics (i.e., degree, eigenvector and betweenness) calculated from all-
 563 occurrences behaviour sampling (ABS) data against those calculated from focal animal sampling (FAS) data.

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Tables 4 and 5 provide a summary of the results.

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Table 4. Summary of the results of the analysis testing the correlation of local network measures between data collected through focal animal sampling (FAS) and all-occurrences behaviour sampling (ABS).

Social behaviour	Social network index	Significant correlation between FAS and ABS data	Main effect/ interaction with species
Grooming	Degree	Yes	Interaction
	Eigenvector	Yes	Main
	Betweenness	Yes	Interaction
Huddling	Degree	Yes	Interaction
	Eigenvector	Yes	Interaction
	Betweenness	Yes	Main
Aggression	Degree	Yes	Main
	Eigenvector	Yes	Main
	Betweenness	Yes	Main

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592 **Table 5.** Summary of the results of the analysis testing the correlation of global network
593 measures between data collected through focal animal sampling (FAS) and all-occurrences
594 behaviour sampling (ABS). Rhesus macaque groups: RG, HG, MG; long-tailed macaque
595 groups: Pirate, Hulk, Entrance; bonnet macaque groups: SG, LG.
596

Social behaviour	Social network index	Significant correlation between FAS and ABS data	Notes
Grooming	Density	Yes	–
	Modularity	Yes	–
	Centralization	No	Significant correlation after excluding RG, Hulk & Entrance
Huddling	Density	Yes	–
	Modularity	Yes	–
	Centralization	No	Significant correlation after excluding RG
Aggression	Density	Yes	–
	Modularity	No	–
	Centralization	Yes	–

598 **DISCUSSION**

599 The overarching goal of our study was to investigate whether two commonly used data
600 collection methods, FAS and ABS, produce similar social network measures. To this end, we
601 compared three local (degree, eigenvector and betweenness) and three global (density,
602 modularity and centralization) network indices for three social behaviours (aggression,
603 grooming, and huddling) in three macaque species (rhesus, long-tailed and bonnet) that display
604 different levels of species-typical social structures.

605 Previous simulation-based work suggested that researchers would need to collect at
606 least 15-20 interactions per dyad in order to construct a reliable social network [16–18]. For
607 large groups containing many individuals and potential interactions, this would mean having
608 to collect thousands of observations [16]. In contrast, our analysis examining variation in local
609 and global metrics over time revealed that it took no more than a total of 50 hours for data
610 collected through FAS, and 10 hours for data collected through ABS, to reach a stable network
611 with minimal or no fluctuation of local network metric values with progressive increases in
612 observation time. This was true across all group sizes, from the small rhesus macaque MG
613 group, with 24 adults, to the large bonnet macaque group LG, with 60 individuals. This
614 discrepancy is likely due to the fact that, while previous research was largely based on
615 simulations [17,18], our study relied on actual behavioural observations. One possible reason
616 why it takes less effort than expected to construct and estimate reliable social network measures
617 could be that, in the attempt to establish or maintain long-term social relationships with their
618 groups such as social bonds [6] or dominance ranks [42], animals direct social behaviours, such
619 as grooming, huddling and aggression, towards specific group members. This means that with
620 only few hours of observations, individuals' network position would become apparent.
621 Crucially, this means that species characterized by sparser and less kin-directed social
622 interactions might require a greater sampling effort to generate a reliable social network [18].

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3 623 Interestingly, it takes more observation hours (at least 100) to reach a stability in global
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5 624 compared to local metrics, probably because global network metrics are more sensitive to
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8 625 missing edges compared to local network metrics [16] and so a larger number of observations
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10 626 are needed to record all or most dyadic interactions, including the more infrequent ones.

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12 627 Our comparison of the network metrics calculated from the two sampling methods
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14 628 revealed that, for grooming and aggression networks, all three local network centrality
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17 629 measures were significantly, positively correlated across the two behavioural sampling
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19 630 methods, and for all three macaque species. This suggested that methodological differences in
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21 631 behavioural data collection did not seem to impact node degree, eigenvector and betweenness
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24 632 centrality measures, regardless of species-typical social structure or social styles. In contrast,
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26 633 for huddling networks, only degree and betweenness centralities were correlated between the
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28 634 two sampling methods for both bonnet and rhesus macaques, while eigenvector centrality
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30 635 measures were correlated between the two sampling methods only for the tolerant bonnet
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33 636 macaques but not for the despotic rhesus macaques.

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35 637 The analysis and comparisons of global metrics revealed that correlations between
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37 638 metrics calculated using the two sampling methods depended both on the species, the type of
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40 639 behaviour and network metric examined. In particular, for grooming behaviour, we found a
41
42 640 positive correlation for grooming network density and modularity while grooming network
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44 641 centralization was correlated between FAS and ABS data only if three groups (one rhesus and
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46 642 two long-tailed macaque groups) were excluded from the analysis. Similarly, we found that
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48 643 FAS huddling network metrics correlated with the respective ABS global network metrics for
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50 644 density and modularity but not for centralization. Yet, when one rhesus macaque group was
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53 645 excluded from the analysis, we did find a correlation in huddling centralization between the
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56 646 two sampling methods. Finally, for aggression networks, we found a positive correlation
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3 647 between the two sampling methods only for network density and centralization but not for
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5 648 network modularity.

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7 649 Collectively, our study shows that, for all social behaviours examined and for all the
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10 650 macaque species investigated, network attributes that measure *direct* interactions, namely
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12 651 degree (at local level) and density (at global level) were strongly correlated between the two
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14 652 sampling techniques. This indicates that researchers who are interested in assessing how many
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16 653 direct interactions each animal has and/or how many edges are present in the group, can employ
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18 654 either sampling technique regardless of the social behaviour examined or the degree of specie-
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20 655 specific sociality. However, despite the fact that ABS and FAS data produce comparable social
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22 656 network measures of direct interactions, the usefulness of SNA lies in its ability to provide
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24 657 measurements of animals' *indirect* connections [7,43]. In this regard, our study showed that
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26 658 the correspondence between FAS and ABS network metrics largely depends on the social
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28 659 behaviour examined, and group- or species-typical characteristics such as social organization
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30 660 and emergent social structure or social style. More specifically, we found that for those social
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32 661 behaviours performed at high frequency, namely social grooming and aggression for all three
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34 662 species, and huddling for bonnet macaques, there was a strong positive relationship in
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36 663 eigenvector and betweenness centrality values calculated from both sampling methods. This
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38 664 suggests that both sampling methods yield similar local network metrics that reflect indirect
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40 665 connections regardless of group- or species-typical social style. In this context, ABS seems to
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42 666 be the most cost-effective sampling method as it requires less effort to collect more dyadic
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44 667 interactions.

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46 668 While our findings indicate that either sampling method can be used to construct
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48 669 reliable social networks from frequently occurring social behaviours, they also suggest that
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50 670 network measures calculated from *infrequent behaviours* are especially vulnerable to the type
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52 671 of sampling method used. In fact, for huddling interactions, we found that eigenvector
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3 672 centrality was correlated between the two sampling methods only for the tolerant bonnet
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5 673 macaque, but not so for the despotic rhesus macaques which were observed huddling at a much
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8 674 lower frequencies. When or where feasible, we therefore suggest the use of ABS rather than
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10 675 FAS in order to construct reliable social networks from infrequent behaviours as ABS allows
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12 676 researchers to record more dyadic interactions compared to FAS. In fact, via ABS, we collected
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14 677 a frequency of huddling behaviour from rhesus macaques that was nearly 5 times higher
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17 678 compared to the frequency of interactions recorded through FAS (see Table S1).

19 679 For prosocial behaviours (i.e., grooming and huddling), we found that FAS network
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21 680 centralization correlated with ABS network centralization only if one rhesus macaque (RG)
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23 681 and two long-tailed macaque (Hulk and Entrance) groups were excluded from the analysis.
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25 682 Network centralization reflects the proportion of social interactions that involve one or few
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27 683 individuals, and, in macaques, variation in this index has been found to be associated with
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29 684 dominance rank and species' degree of tolerance/despotism [36]. In other words, in despotic
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31 685 species such as rhesus macaques, which exhibit marked rank relationships, social grooming
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33 686 tends to be largely directed towards high-ranking individuals, and so these species tend to have
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35 687 a highly centralized network, while in more tolerant macaque species, grooming interactions
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37 688 tend to be more equally distributed across dyads exhibiting, therefore, a less centralized
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39 689 network [36]. Here we suggest that the variation in key demographic components and the
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41 690 degree of social (in)stability of the study groups might explain why, for some macaque groups,
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43 691 network centralizations calculated from both FAS and ABS data were not correlated. In RG,
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45 692 for instance, some high-ranking individuals, including the dominant female, disappeared from
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47 693 the group during our study period. Similarly, the long-tailed macaque groups experienced
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49 694 several turnovers in the male dominance hierarchy. These demographic changes might have
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51 695 shifted the rank relationships within the study groups influencing the effect of rank on the
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53 696 direction of grooming interactions, affecting, thereby, grooming network centralizations.
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3 697 Finally, we did not find evidence that network modularity was correlated between the
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5 698 two sampling methods. Network modularity reflects the degree to which animals form clusters
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8 699 of social interactions by interacting preferably with partners belonging to their own clusters
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10 700 compared to partners from other clusters. For this reason, this network metric is commonly
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12 701 assessed in prosocial behaviours such as grooming and huddling [44], whereby behaviours tend
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14 702 to be directed to preferred partners based on long-term affiliations dictated by, for instance, the
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16 703 degree of social bonds [6], or kinship [45]. Aggressive interactions, in contrast, tend to be less
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18 704 modular/clustered as they tend to be distributed more dynamically and may be affected by
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20 705 multiple factors, such as food distribution, or seasonality.
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24 706 In conclusion, our analysis suggests the use of ABS as a suitable alternative to FAS,
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26 707 particularly if researchers are interested in local network measures, such as degree, eigenvector
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28 708 or betweenness as this seems the most cost-effective method: it allows researchers to collect
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30 709 data on multiple dyads in a shorter amount of time, compared to FAS, while providing similar
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32 710 network metrics as FAS. ABS is likely to be a particularly suitable sampling method for
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34 711 infrequent behaviours such as huddling interactions in despotic species. Finally, we found
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36 712 limited evidence that the degree of despotism/tolerance of a species affects the reliability of the
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38 713 sampling method used to construct social networks. Overall, our results may provide
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40 714 researchers with new guidance on whether to use FAS or ABS to collect their social network
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42 715 data.
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4 Dear Dr Thompson,

5 Many thanks for the prompt revision of our manuscript *RSOS-231001 Effect of behavioural*
6 *sampling methods on local and global social network metrics: a case-study of three macaque*
7 *species*. We are happy to hear that the manuscript has been accepted for publication, pending
8 minor revisions, which we have now addressed as detailed below.
9

10
11 Yours sincerely,

12
13 Stefano S.K. Kaburu, on behalf of the authorship team

14
15 Krishna Balasubramanian, Pascal R. Marty, Brianne Beisner, Kevin Fuji , Eliza Bliss-
16 Moreau, & Brenda McCowan
17

18 *****

19
20 **Associate Editor: The number of figures (nine, plus five tables) is still excessive**
21 **relative to the length of the manuscript. As suggested by former reviewer #2, I**
22 **recommend pulling out a few highlights from the remaining figures to feature in**
23 **the main text. Alternatively, you may consider combining similar figures (e.g. Figs**
24 **2-3; Fig 4-9) into a condensed figure panel for readers to more easily compare**
25 **results. For Fig. 7—do N=5 data points warrant a figure in the main text?**
26
27

28
29 *Authors: We have now reduced the number of figures from 9 to 4 as detailed below:*

30
31 *1) we have removed the former figure 1 since it did not refer to any statistical analysis and*
32 *visual representations of social networks are included in the supplementary material*
33

34
35 *2) we have now merged both Figs 2-3, Figs 4-5, Figs. 6-7, and Figs 8-9 into single figures;*
36 *for consistency, we have also merged the figures included in the supplementary material*
37
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40 **AE: I. 256 still uses the term “individual level” rather than “local”**

41 A: We have now replaced individual with local.
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