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Network Structure and Social Complexity in Primates

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20

Abstract

21 Primates use social grooming to create and maintain coalitions. Because of this, individuals
22 focus their time on a small number of individuals, and this means that in many cases group
23 networks are not fully connected. I use data on primate grooming networks to show that three
24 different social grades can be differentiated in terms of network structuring. These grades
25 seem to arise from a glass ceiling imposed on group size by limits on the time available for
26 social grooming. It seems that certain genera have managed to circumvent this constraint by a
27 phase shift in the behavioural and cognitive mechanisms that underpin social relationships in
28 a way that allows a form of multilevel sociality based on weak and strong ties not unlike
29 those found in human social networks.

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33 **Key words:** social networks, grooming, multilevel sociality, time budgets, cognition

34

35 **Introduction**

36 In primates, social grooming is the principal process by which relationships are built
37 up and serviced (Dunbar & Shultz 2010; Massen et al. 2010; Silk et al. 2010a,b). Although
38 time devoted to grooming increases linearly with group size (Dunbar 1991; Lehmann et al.
39 2007; Dunbar & Lehmann 2013), this does not mean that individuals groom with every other
40 member of the group; rather, it is a consequence of the fact that individuals choose to invest
41 disproportionately in a small number of core relationships (Dunbar 1980; Duboscq et al.
42 2016), probably so as to ensure their functionality as coalitions (Dunbar 2012). In both
43 primates (Dunbar 1980) and humans (Roberts & Dunbar 2011), the quality of a relationship
44 is determined by the amount of time an individual invests in it (in the primate case, by
45 grooming with its partner): grooming partners are more likely to come to each other's aid in
46 altercations (Dunbar 1980) and to alert when a partner gives fear screams (Seyfarth &
47 Cheney 1984). More importantly, these relationships demonstrably influence female stress
48 levels, fecundity and fitness in both primates (Silk et al. 2003, 2010a,b; Wittig et al. 2008)
49 and equids (Cameron et al. 2009). If grooming relationships are the basis of social bonding in
50 primates (Dunbar & Shultz 2010; Dunbar et al. 2009; Silk et al. 2010b), this raises questions
51 about how group cohesion and stability are engineered in social groups that greatly exceed an
52 individual's capacity to groom others (Dunbar 2012). This seems to have been a question
53 that, so far, no one has thought of asking.

54 I use comparative data on grooming networks in a taxonomically wide set of primates
55 to determine how social structure varies with group size. I focus explicitly on grooming
56 relationships, rather than affiliative behaviours like proximity that some recent studies (e.g.
57 Pasquaretta et al. 2014) have used because grooming is the central engine in building
58 relationships for primates: grooming triggers the release of endorphins in the brain in both
59 primates (Fabre-Nys et al. 1982; Keverne et al. 1989; Martel et al. 1993) and humans

60 (Nummenmaa et al. 2016), and endorphins are central to the creation and management of
61 affiliative relationships (Panksepp 1999; Depue & Morrone-Strupinsky 2005; Dunbar 2010;
62 Machin & Dunbar 2011; Pearce et al. 2017). Proximity and huddling merely imply tolerance
63 (a consequence), whereas grooming, and especially its reciprocation, implies something
64 about active engagement and commitment to another individual (a mechanism).

65 I focus on two indices of group social structure: the grooming clique (the number of
66 other adults that an individual grooms with on a regular basis – in other words, its core
67 coalition partners) and the grooming network (the number of individuals linked in a
68 continuous chain of such relationships). The first tells us something about the social skills of
69 an individual monkey (how many relationships it can keep functional at the same time). The
70 second tells us something about the structural stability of a social group: groups that are split
71 into several weakly connected networks may be more likely to fission when the ecological
72 and social costs of group-living become intolerable (Dunbar et al. 2009).

73 I first examine the relationship between these two indices to determine how grooming
74 clique size relates to network size and how network size relates to group size in order to
75 explore the structural properties of groups. In both cases, we are interested in whether two
76 indices form a single monotonic functional relationship or a set of separate but parallel
77 grades. A single relationship in both cases tells us that these indices form a simple fractal
78 pattern in which one layer scaffolds the next; living in large groups is thus a consequence of
79 being able to manage more grooming relationships in the base layer, and nothing more. If the
80 relationship between two indices also involves grades, such that there are two or more
81 monotonic relationships involved, this would imply that some species are able to maintain a
82 higher order grouping (an extended network) without necessarily having to change their
83 lower level grouping (grooming clique size) proportionately; this implies an ability to
84 manage two different kinds of relationships (weak and strong) simultaneously without

85 necessarily having to invest equally in all of them. If so, we will want to know whether these
86 grades coincide with any obvious correlated change in grooming behaviour or cognition. For
87 present purposes, I will use neocortex volume and a direct measure of executive function
88 competence as relevant indices for this.

89

90 **Methods**

91 Data on the frequency of social grooming among adults are taken from Kudo &
92 Dunbar (2001), still the most comprehensive grooming network dataset available,
93 supplemented by three more recent studies. Pair-living species are excluded, since grooming
94 networks are meaningless when there are only two adults. In total, 101 social groups drawn
95 from 34 species are included in the sample, a larger and broader coverage than any previous
96 analysis has used. The grooming data for each group are cast in a triangular matrix and used
97 to calculate the two structural indices (grooming clique size for each individual and the mean
98 size of all grooming networks in the group). In the network analysis literature, these indices
99 are conventionally referred to as the *degree* and *n-clique*, respectively, but I will use the
100 terms grooming clique and network here since they are more meaningful.

101 An important issue in network analysis is that not all relationships are of equal value.
102 This is obvious from an examination of the many sociograms and social networks published
103 in the literature: any given individual only grooms regularly with a proportion of the other
104 members of its group (among many others, see network graphs given by Kummer 1968;
105 Dunbar & Dunbar 1975; Voekl & Kasper 2009; Crofoot et al. 2011; Pasquaretta et al. 2014;
106 Duboscq et al. 2016). Conventionally, the human literature distinguishes between *weak* and
107 *strong* ties (Granovetter 1973; Sutcliffe et al. 2012) for this reason. Casual relationships often
108 have a high turnover through time (for primate examples, see Altmann 1980; Dunbar &
109 Dunbar 1988; Duboscq et al. 2016), as is the case in human social networks (Saramäki et al.

110 2014; Roberts & Dunbar 2015). The inclusion of all social contacts typically inflates the
111 degree and, in the limit, leads unhelpfully to a saturated network (everyone grooms with
112 everyone else) (James et al. 2009). A common strategy is, therefore, to divide ties between
113 stronger more meaningful ones and weaker more casual ones by using some criterion based
114 on the frequency of interaction. For present purposes, I follow previous studies (Dunbar
115 1984; Kudo & Dunbar 2001; Lehmann & Dunbar 2009a) and define a meaningful tie as one
116 that accounts for at least 10% of an individual's total social (i.e. grooming) effort (for
117 justification and details, see *ESM*). This sets an upper limit on grooming clique size at 10
118 partners, but no species, or group, comes close to this. A tie that accounts for more than 10%
119 of an individual's social effort identifies a relationship likely to elicit coalitionary support
120 (Dunbar 1984). I use undirected matrices (i.e. the data do not distinguish the direction of
121 grooming), mainly because close relationships should be those that are reciprocated (i.e. each
122 partner should invest equally in the relationship).

123 For each group, the grooming clique size of every adult in the group was first
124 determined and then averaged, and then these were in turn averaged across all groups of the
125 same species. Similarly, the size of all independent (i.e. non-overlapping) continuous network
126 chains (n-cliques) in a group were first determined, averaged for each group, and then
127 averaged across groups of the same species. Grooming clique size is independent of the
128 actual size of group that animals happen to be in (Fig. S2), mainly because clique size is
129 constrained by the species' cognitive ability to handle relationships, and is thus characteristic
130 of the species (Kudo & Dunbar 2001). Data on mean social group size for individual species
131 are taken from (Campbell et al. 2008), the most recent comprehensive summary available,
132 supplemented where necessary by more recent sources (see Table S1). Neocortex ratio, the
133 best predictor of social group size (Dunbar & Shultz 2007) as well as of executive function
134 cognition (Shultz & Dunbar 2010), is taken from Kudo & Dunbar (2001). Executive function

135 cognition score is the arcsin transform of the mean proportion of correct trials on eight
136 standard executive function tasks, the data for which were compiled from the published
137 literature by Shultz & Dunbar (2010). Data on percent of day devoted to social grooming are
138 taken from Lehmann et al. (2007).

139 In primates, species of the same genus typically exhibit very similar cognitive abilities
140 and behaviour. To avoid inflating significance levels through phylogenetic autocorrelation,
141 both structural indices and group size were averaged across species of the same genus to give
142 mean values for individual genera and all analyses were carried out at genus level. Using
143 generic means usually minimises the impact of phylogenetic effects. However, a genus-level
144 analysis is essential for a second, more important, reason: phylogenetic methods remove
145 grade differences, especially when these grades do not correspond to taxonomic divisions.
146 Grades that cut across phylogeny are the focus of this analysis, and for this reason a genus-
147 level analysis of raw data is necessary. This reduces the original sample from 34 species to 21
148 genera, although all results at genus level are also checked at species level (see *ESM*).

149

150 **Results**

151 *Between-species comparison*

152 Fig. 1 plots mean network size as a function of mean grooming clique size (number of
153 principal grooming partners) for individual genera, and mean group size as a function of
154 mean network size. There is a significant correlation in the case of network/cliue (Fig. 1a:
155 $r=0.841$, $p<0.001$, $N=21$), with a scaling ratio that does not differ significantly from 3
156 ($t_{19}[b=3]=0.03$, $p=0.979$ (cf. Hill et al. 2008), but not in the case of group/network (Fig. 1b:
157 $r=0.303$, $p=0.181$). However, a phylogenetic contrasts analysis (which removes the effect of
158 grades) yields a highly significant relationship in the latter case (Fig. S3; contrasts in
159 degree/cliue, $r=0.827$, $p=0.00008$; contrasts in group/network, $r=0.675$, $p=0.004$), providing

160 strong evidence that there is in fact an underlying relationship in this case too. The loss of
161 significance when not controlling for phylogeny strongly implies that there is a grade effect.
162 present Finally, values for individual species exhibit the same patterns, with similarly
163 significant relationships in both cases (Fig. S4).

164 To explore this further, I examined residuals from the common RMA regression line
165 in Fig. 1b. The residuals have an obviously trimodal distribution, unless one wants to
166 consider a single outlier a grade in its own right (Fig. 2). A *k-means* cluster analysis of these
167 residuals yields an optimal partition into three separate clusters ($F_{2,18}=93.3$, $p<0.0001$), with
168 both lower and higher order clustering yielding much poorer goodness-of-fits. Taken
169 together, the three grades have individual slopes that are significantly positive (Fisher's meta-
170 analysis: $\chi^2=22.65$, $df=6$, $p<0.001$), with intercepts for the two upper grades differing
171 significantly from that for the lower grade ($t_{12}=6.65$, $p<0.0001$; $t_{15}=4.92$, $p=0.0002$) but not
172 from each other ($t_9=1.61$, $p=0.129$), perhaps suggesting that the distinction between the upper
173 and middle grades is less robust than that between them and the lower grade. A multiple
174 regression of group size against network size with grade as a dummy variable yields a
175 significant regression with a radically improved goodness of fit (with grades, $r^2=0.919$ vs
176 $r^2=0.092$ without grades; with grades, $F_{2,18}=102.1$, $p<0.00001$), and significant partial
177 regressions for both network size ($t_p=4.51$, $p=0.0003$) and grade ($t_p=13.56$, $p<0.0001$).

178 The three grades in Fig. 1b include, left to right:

179 Upper grade: *Erythrocebus* [1], *Procolobus* [1], *Papio* [1,1], *Pan* [1,1]

180 Middle grade: *Chlorocebus* [1], *Saimiri* [1], *Sajapus* [1], *Ateles* [1], *Theropithecus* [1],

181 *Semnopithecus* [1], *Macaca* [1,1,1,0]

182 Lower grade: *Colobus* [0], *Propithecus* [0], *Alouatta* [1], *Indri* [0], *Callicebus* [0], *Eulemur*

183 [1], *Trachypithecus* [0,0],

184 *Cercopithecus* [0,0,0], *Cebus* [1], *Presbytis* [0], *Lemur* [1]

185 The network:clique ratios for individual species approximate 3, and do not differ
186 across the three grades (Fig. 3a: $F_{2,30}=0.69$, $p=0.510$). However, the group:network ratios
187 differ significantly across grades (Fig. 3b: $F_{2,29}=15.3$, $p<0.001$), with the three grades
188 differing significantly from each other (Scheffé post hoc tests: $p\leq 0.044$). Mean
189 network:clique ratios are 2.71, 2.95 and 2.53, while mean group:network ratios are 2.31, 4.23
190 and 7.02, respectively, for the three grades.

191

192 *Cognition, time budgets and social structure*

193 The three grades differ significantly in neocortex ratio (Fig. 4: means of 1.78 ± 0.55 vs
194 2.37 ± 0.16 vs 2.78 ± 0.43 ; $F_{2,18}=8.79$, $p=0.002$). Post hoc tests confirm that the lower grade
195 differs significantly from the other two grades (Scheffé tests: $p=0.041$ and $p=0.004$), but the
196 two upper grades do not differ significantly from each other ($p=0.343$). The three grades also
197 differ significantly in executive function cognitive competences (Fig. 5: $F_{2,15}=8.32$, $p=0.004$),
198 with the lower grade being significantly different from the two upper grades (Scheffé tests:
199 $p=0.049$ and $p=0.004$), but the two upper grades again not differing significantly ($p=0.105$).

200 While there is, overall, a significant positive correlation between species mean group
201 size and mean percent of the day devoted to social grooming (Fig. 6: $F_{1,20}=7.47$, $p=0.013$) (cf.
202 Dunbar 1991; Lehmann et al. 2007; Dunbar & Lehmann 2013), the data in fact partition into
203 two distinct grades with parallel slopes. However, this obscures a more complex relationship.
204 A backwards stepwise multiple regression with mean species grooming time as the dependent
205 variable and mean group size, mean network size, mean clique size and grade (as a
206 dichotomous dummy variable: lower versus middle+upper) as independent variables yields a
207 highly significant model ($F_{3,18}=5.59$, $p=0.006$) with a negative relationship with clique size
208 ($p=0.035$), a positive relationship with network size ($p=0.005$), and a significant effect of
209 grade ($p=0.007$), and no effect due to group size (Table 1).

210

211 **Discussion**

212 The results suggest that group-living primates divide into at least two, possibly three,
213 grades of sociality in terms of the relationship between grooming network size and group
214 size. Species from the lower social grade are heavily restricted in the range of group sizes
215 they can have, but the more social species are somehow able to maintain larger groups for a
216 given grooming clique size. For many lower grade taxa, group size and network size are
217 synonymous, but the two higher grades are able to maintain groups that are 4-6 times the size
218 of their grooming networks. In other words, the groups of these species seem to contain a
219 large number of effectively unconnected (or weakly connected) grooming networks that are
220 likely to constitute potential fracture points for group fission. Nonetheless, even though the
221 quality of a dyadic relationship is related to the amount of effort directly invested in it for
222 both monkeys (Dunbar 1980; Seyfarth & Cheney 1984) and humans (Sutcliffe et al. 2012),
223 upper grade species are seemingly able to maintain group cohesion without having to groom
224 with everyone in the group, whereas lower grade species seemingly cannot.

225 Fig. 1a suggests that there is an upper limit at around five individuals that can be
226 maintained as grooming partners. This is identical to the number of intimate social partners
227 found in humans (mean \approx 5: Sutcliffe et al. 2012; Burton-Chellew & Dunbar 2015). In
228 primates, the grooming clique functions as the principal defence coalition: individuals in this
229 category are more likely to come to each other's aid when one of them is challenged (Dunbar
230 1980, 1984; Seyfarth & Cheney 1984). This set of grooming partners also provides the basis
231 for an extended grooming network (or n -clique, the number of individuals that can be reached
232 directly or indirectly through a continuous chain) that is three times larger, and this is true of
233 all the genera in the sample. Hill et al. (2008) found a scaling ratio of \sim 3 for grouping levels
234 in a sample of mammals (including three primate species) that live in multilevel societies,

235 and a similar layering with a scaling ratio of ~ 3 has been widely documented in human social
236 networks (Hill & Dunbar 2003; Zhou et al. 2005; Hamilton et al. 2007; Dunbar et al. 2015;
237 MacCarron et al. 2016). The larger sample provided by this study however, suggests that
238 there may be a distinction between lower grade taxa whose networks more or less correspond
239 to their groups and higher grade taxa (those sampled by Hill et al. 2009) which have much
240 higher group:network scaling ratios such that their groups consist of several weakly
241 connected sub-networks.

242 These results suggest that upper grade taxa can somehow maintain temporal
243 coherence between sub-groups that do not interact directly very often, whereas lower grade
244 taxa cannot. It is noteworthy that the upper grade taxa differ from the middle grade mainly in
245 the fact that all four of the upper grade genera either occupy terrestrial (and therefore
246 predator-risky) habitats (Lehmann & Dunbar 2009b; Bettridge & Dunbar 2012) or typically
247 experience unusually high predation risk, notably from chimpanzees (e.g. *Procolobus*:
248 Stanford 1995). It seems that these species are either being pushed beyond their capacities in
249 order to live where they do or have evolved additional cognitive capacities to cope with
250 larger groups (as may be the case in baboons and chimpanzees).

251 The capacity to maintain social cohesion without grooming with everyone appears to
252 depend on increased neocortex volume, and not phylogeny, and may thus depend on novel
253 aspects of cognition. Indeed, in terms of executive function, there are correlated differences
254 between the grades in cognitive ability. The grooming data (Fig. 6) suggest that while lower
255 grade taxa simply increase grooming time to allow a larger clique (and hence group) size,
256 taxa in the upper grades seem to trade off investment in their close allies (principal grooming
257 partners) to allow time for more casual interactions with other members of their extended
258 network in a way that probably gives these extended networks greater coherence and
259 structural stability. However, upper grade taxa are also managing to do something else, and

260 that is to ensure that several other similar network subgroups remain within their group
261 despite the stresses imposed by having more individuals in the group and despite not
262 grooming with them. In part, this might be because individuals are able to acquire knowledge
263 about third parties with whom they do not interact directly by observing them interacting
264 with other members of the group, and later using this knowledge to infer, for example, where
265 an individual sits in the wider dominance hierarchy (Bergman et al. 2003; Schino et al. 2006),
266 whom they have alliances with (Datta 1999; Cheney & Seyfarth 1999) and, on the basis of
267 observed reputation, how trustworthy they might be (Silk 1999; Russell et al. 2008).
268 Although competences of this kind have often been documented in upper grade taxa,
269 evidence for these capacities is, so far at least, largely absent from any lower grade genus.

270 As Fig. 4 suggests, the structural differences in the way these species' social groups
271 are organised relate to the relative sizes of their brains, in particular the size of the neocortex,
272 and Fig. 5 shows that there are correlated differences in cognitive ability, suggesting these
273 may play an important role in facilitating the higher order competences that underpin the
274 upper grade form(s) of sociality. (Note that these executive function competences have been
275 shown to correlate with neocortex volume across primates, even when correcting for
276 phylogenetic relationships: Shultz & Dunbar 2010.) The frontal lobes play a crucial role in
277 managing social relationships, and hence in individual differences in personal ego-centric
278 network size in both humans (Lewis et al. 2011; Powell et al. 2012; Kanai et al. 2012) and
279 macaques (Sallet et al. 2013), as well as social cognition (such as the capacity to integrate
280 others' perspectives with one's own: Powell et al. 2010, 2014). Brodman area 10 in the
281 frontal pole of the neocortex, which is found *only* in anthropoid primates, seems to be crucial
282 for allowing animals to engage in the kinds of advanced forms of executive function
283 cognition (notably one-trial learning, causal reasoning, strategic comparisons and inhibition:
284 Passingham & Wise 2012) that are likely to be essential for the management of complex

285 social relationships. It may be relevant that no non-primate mammals that lives in primate-
286 like bonded (Silk et al. 2010a; Dunbar & Shultz 2010; Massen et al. 2010) social groups (e.g.
287 equids, canids, tylopods, hyaenids) (Shultz & Dunbar 2010) has a mean group size that
288 exceeds 30 animals; the only exceptions are elephants and delphinids, both of whom have
289 neocortices in the cercopithecine primate range as well as primate-like multilevel social
290 systems (Hill et al. 2008). Clearly, more data on the cognitive and social behaviour of other
291 mammal and primate species are needed in order to explore this further.

292 The grooming data of Fig. 6 suggest (i) that animals adjust their grooming time
293 commitments mainly to the size of their social networks, rather than group size as a whole,
294 (ii) that proportionately more time is committed to grooming in those species where groups
295 are multilevel-structured, and (iii) that they free off time to make this possible by reducing
296 their investment in their core grooming partners (clique members). It seems that the limit on
297 the number of grooming partners that an individual can have (its degree) is ultimately set by
298 the amount of time it can afford to devote to social interaction, and this in turn is likely to be
299 determined by the extent to which its diet imposes demands on foraging and resting time
300 (Dunbar et al. 2009). The lower grade taxa differ from those in the upper grades by being
301 more folivorous ($35.5 \pm 26.9\%$ leaf in diet vs $18.1 \pm 15.4\%$ for upper grade taxa; data in
302 Korstjens et al. 2010). Species that depend on hindgut fermentation to extract nutrients from
303 high-fibre leaf-based diets are obliged to devote significant amounts of time to resting in
304 order to allow fermentation to occur because the heat generated by any form of activity
305 suppresses the gut flora responsible for fermentation (van Soest 1982). This phenomenon is
306 familiar in ruminants, who are obliged to lie down and rest when ruminating (van Soest
307 1982). This severely limits the time available for social interaction in the more folivorous
308 primates (Dunbar 1988; Korstjens & Dunbar 2008), and seems to be mainly responsible for
309 their smaller, less structured groups.

310 A switch from a more leaf-based diet to a more fruit-based one has been shown to be
311 responsible for the contrast in social group size between *Colobus* (a member of the lower
312 grade, mean group size = 9.5; leaf = 59% of diet) and *Procolobus* (a member of the more
313 intensely social upper grade, mean group size = 33.8; leaf = 46%): *Colobus* populations
314 spend an average of 62.4% of their day resting, compared to 44.8% for *Procolobus*
315 populations (Korstjens & Dunbar 2008), and thus have considerably less time available for
316 social grooming, which in turn limits group size. Giving *Colobus* species a *Procolobus*-like
317 diet allows them to live in groups as large as those found in *Procolobus*, and *vice versa*
318 (Korstjens & Dunbar 2008). The issue, then, is that improvements in diet quality allow less
319 time to be spent foraging, thereby freeing off time for social interaction (and hence bonding
320 larger groups) as well as allowing the higher nutrient throughput needed for larger brains to
321 be evolved to handle more complex relationships (Dunbar & Shultz 2017).

322 In sum, the apparent ability to support a larger group with less investment seems most
323 likely to involve a phase shift in socio-cognitive competences, probably dependent on
324 significant increases in brain size that allow novel behaviours (Shultz & Dunbar 2010). One
325 way this might have been achieved is by enabling individuals to maintain several
326 qualitatively different kinds of relationships at the same time in a way reminiscent of
327 Granovetter's (1973) distinction between weak and strong ties in human networks. Whether
328 primates as a whole represent just two or more than two such phase shifts remains to be
329 investigated in more detail.

330

331

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334

- 335 **Ethics statement:** this study did not require ethical approval.
- 336 **Data accessibility:** the data can be found in the ESM.
- 337 **Competing interests:** the author declares no competing interests.
- 338 **Authors' contributions:** The named author is the sole author.

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Legends to Figures

512

513 Fig. 1. (a) Mean grooming network size plotted against mean grooming clique size and (b)
514 mean group size plotted against \log_{10} mean grooming network size for individual
515 primate genera. Symbols in (b) indicate genera assigned to the three distinct social
516 grades. Although the statistical analysis of the slopes for individual grades are based
517 on simple linear regression, the regression lines in (b) are plotted on the assumption
518 that they are in fact power curves anchored on the origin.

519

520 Fig. 2. Distribution of residuals from the common regression line for the genera in Fig. 1(b).

521

522 Fig. 3. Mean (± 2 se) (a) network:clique ratio and (b) group: network ratio for the three grades
523 shown in Fig. 1b. The dashed line marks a scaling ratio of 3.

524

525 Fig. 4. Mean (± 2 se) neocortex ratio for the three social grade shown in Fig. 1b.

526

527 Fig. 5. Mean (± 2 se) executive function ability score for individual species in the three
528 grades. Ability score is the arcsin transform of the proportion of correct trials on 8
529 standard executive function tasks. Data from (8).

530

531 Fig. 6. Mean percentage of daytime devoted to social grooming by individual species,
532 plotted against species mean social group size. Species are distinguished according to
533 whether their genera are classed as upper grade (solid symbols) or lower grade (open
534 symbols) in Fig. 1b. Regression lines are LSR regressions (solid line: upper grade;
535 dashed line: lower grade).

536 Table 1. Best fit backward stepwise multiple regression analysis of percent time spent
537 grooming as the dependent variable.

538

539

540 Variable	Slope	Standardized slope	t	p
541	-----			
542 Constant	0.469			
543 Clique size	-4.218	-0.830	-2.28	0.035
544 Network size	1.135	1.108	3.16	0.005
545 Grade*	5.609	1.835	3.06	0.007

546 Excluded variable: group size

547 * lower grade taxa scored 1; middle and upper grade taxa scored 2

548

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551

Figure 1

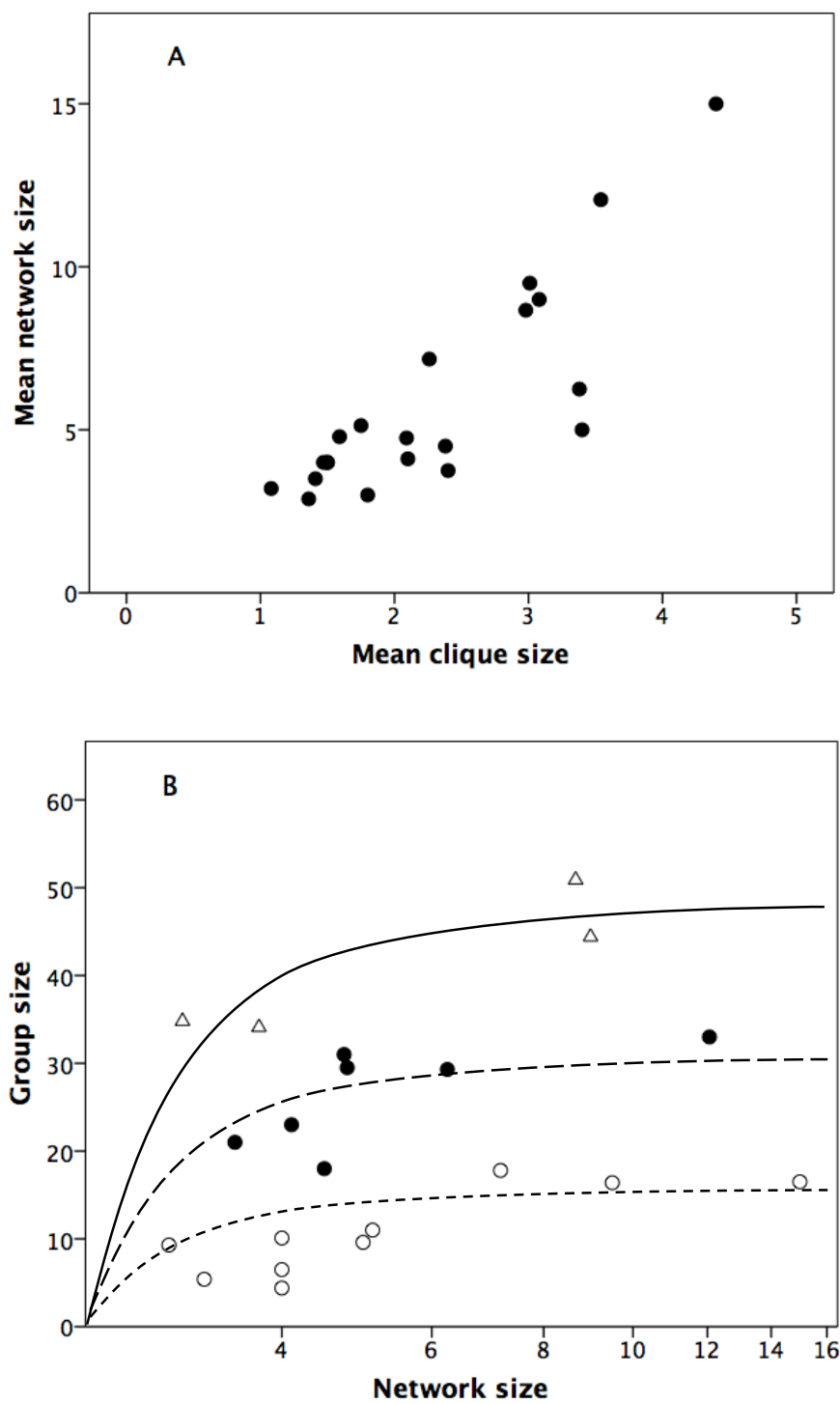


Figure 2

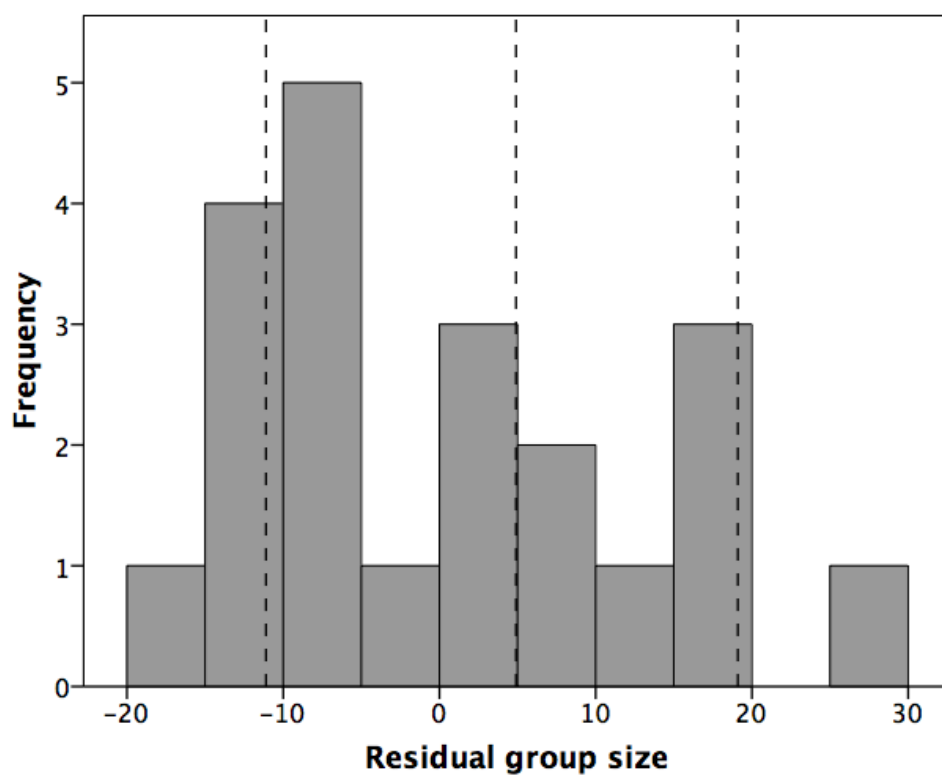


Figure 3

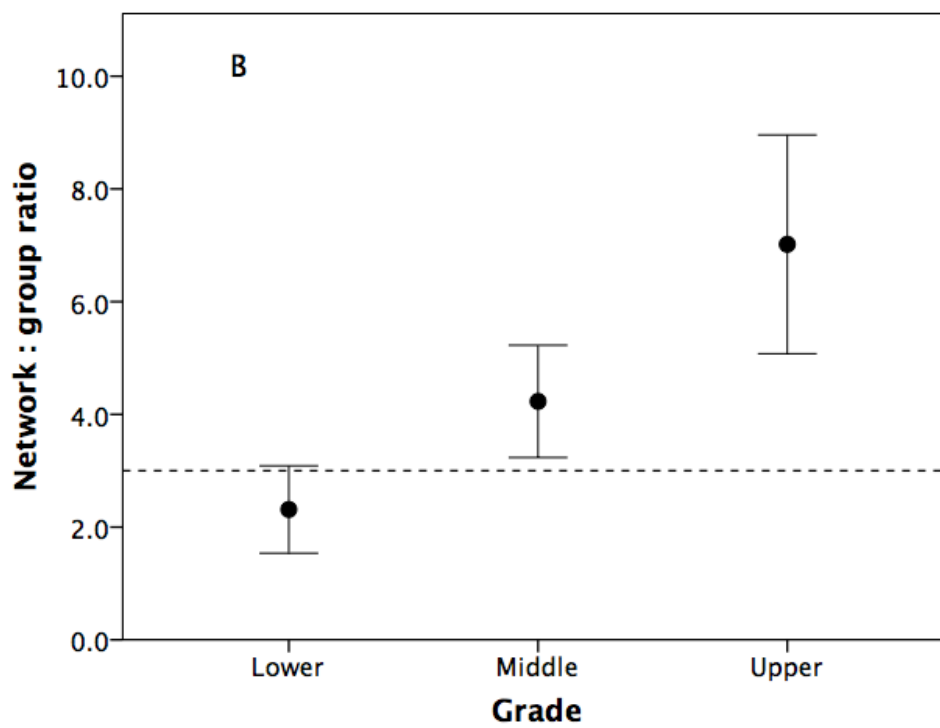
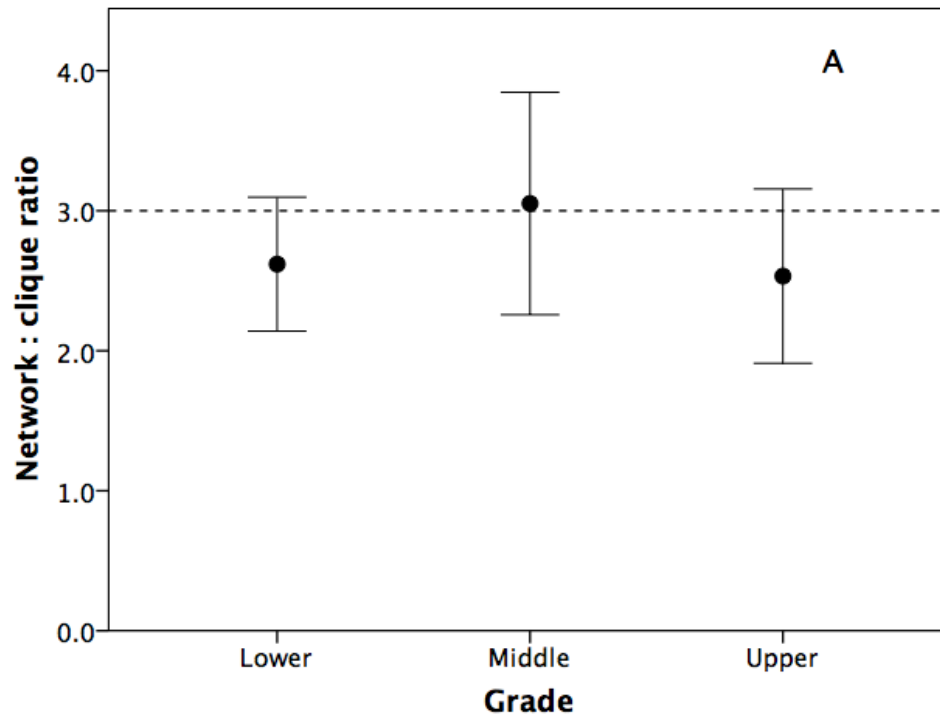


Figure 4

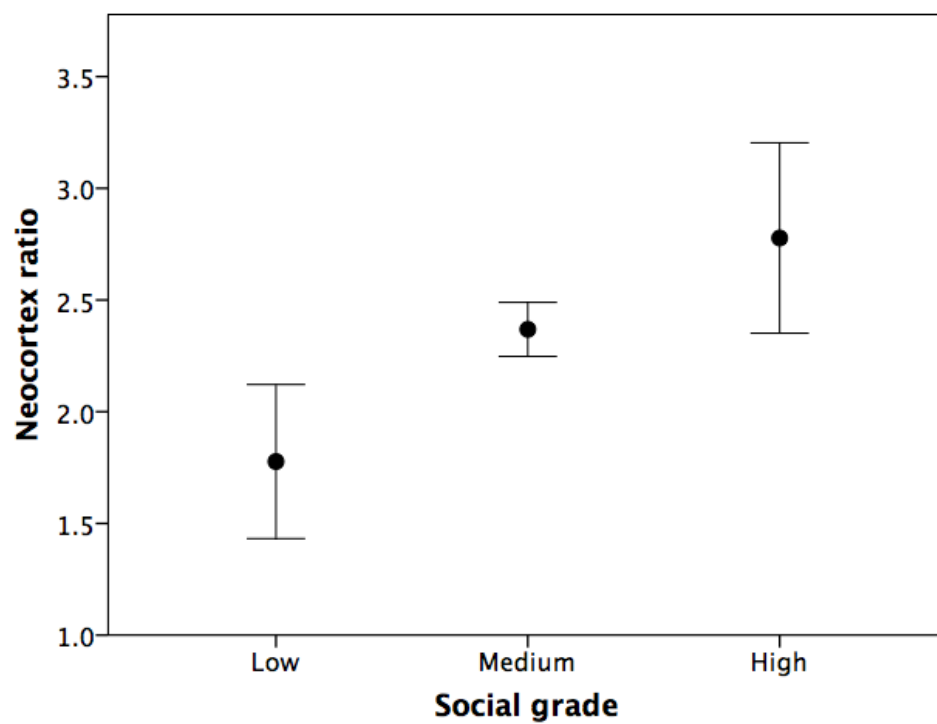


Figure 5

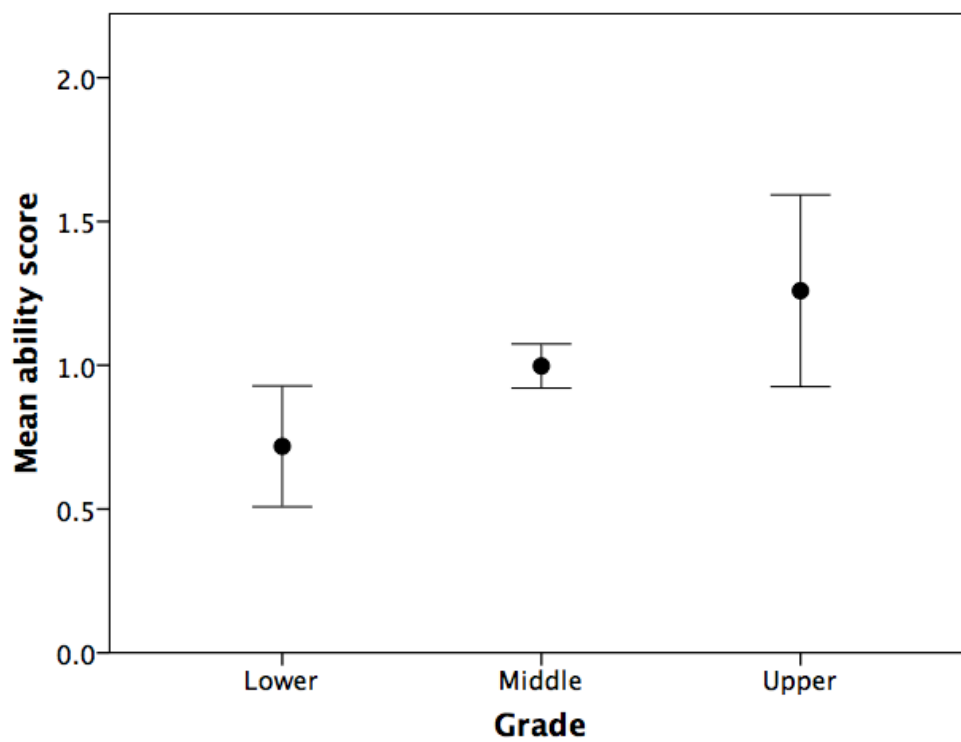


Figure 6

