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3	Group size, grooming and social cohesion in primates
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26 Abstract

27 Most primates live in social groups in which affiliative bonds exist between 28 individuals. Because these bonds need to be maintained through social interactions 29 (grooming in most primates), sociality will be limited by time constraints. It has 30 previously been shown that the time primates invest in grooming increases with group 31 size. However, when groups become too large, individuals will not have enough time 32 available to service all possible social relationships and group cohesion is expected to 33 decrease. In this study, we use data from previously published studies to determine 34 how large groups compromise on their grooming time and how ecological, 35 phylogenetic and lifehistory variables affect time invested in grooming (across species 36 as well as within taxa). We use path analysis to analyse direct and indirect (via group 37 size) effects on grooming. We show that not only is grooming time determined by 38 group size, but it is also affected by dispersal patterns and sex ratio. Furthermore, we 39 found that grooming time is asymptotic when group size exceeds 40 individuals, 40 indicating that time constraints resulting from ecological pressure force individuals to 41 compromise on their grooming time. This was true across species, but a similar effect 42 was also found within taxa. Cognitive constraints and predation pressure strongly 43 affect group sizes and thereby have an indirect effect on primate grooming time. 44 Primates that were found to live in groups larger than predicted by their neocortex 45 size usually suffered from greater predation risk. However, most populations in our 46 analysis were placed well within what we define as their eco-cognitive niche.

47 A number of factors are known to influence social group size in mammals (Caraco & 48 Wolf, 1975; Pulliam & Caraco, 1984; Hass & Valenzuela, 2002). Among these, food 49 distribution and predation pressure are the two best studied factors (Chapman et al., 50 1995; Janson & Goldsmith, 1995; Hass & Valenzuela, 2002; Downes & Hoefer, 51 2004). In addition to these, the social brain hypothesis suggests that, in species that 52 live in socially bonded groups (such as many primates and carnivores), group size can 53 be constrained by cognitive abilities (Dunbar, 1992a). This hypothesis is based on the 54 finding that group size is strongly correlated with brain size (and specifically 55 neocortex size in relation to the rest of the brain). The size of the neocortex is 56 assumed to limit the number of social relationships an individual can keep track of. If 57 group size becomes too large, it becomes impossible for an individual to maintain 58 close social bonds with all group members. As a consequence, group cohesion will 59 decrease and the group will eventually split (see (Henzi et al., 1997a; Henzi et al., 60 1997b).

61 In support of this, Kudo and Dunbar (Kudo & Dunbar, 2001) have shown that 62 social network size in primates is correlated with neocortex ratio, indicating that the 63 number of grooming partners that primates can maintain as a coherent set is also 64 related to the size of their neocortex. However, maintaining relationships not only 65 requires cognitive abilities but also time. The bonding mechanism used in most 66 primate species is grooming – a time consuming activity that can occupy up to 20% of 67 the total day for some of the most social species (Dunbar, 1991). When group size 68 (and the number of available social partners) increases, each individual will have to 69 spend more time grooming. Dunbar (1991) was able to demonstrate that the time 70 primates engage in social activities (i.e. the time spent servicing social relationships) 71 is positively related to group size (at least among anthropoid primates), supporting the

72 idea that when groups are large, individuals have to spend more time servicing their 73 social network than they do when in smaller groups. If groups become too large, 74 individuals cannot afford to spend the necessary time grooming (because of the 75 demands of other essential activities such as foraging) and group cohesion will 76 decrease, leading eventually to group fission.

77 Thus, group size in primates will be constrained by two independent variables 78 - neocortex size, which sets an upper limit to manageable group sizes, and the amount 79 of time that is available for grooming. While the former is a species-specific 80 parameter, the latter depends ultimately on environmental variables that determine 81 how much time an individual will need for all other essential activities, such as 82 moving, feeding and resting (e.g. Dunbar, 1992b). In this study, we investigate the 83 interactive effects of all three variables (group size, brain size and grooming time) 84 simultaneously in Old World primates. It is important to note that, in this study, we 85 draw a distinction between social time and grooming time. Although Dunbar (1991) 86 argued that the difference between these two is minimal, this may not in fact be true: social time includes, in addition to grooming, a wide range of other activities (play, 87 88 courtship and mating, agonistic interactions, territorial behaviour) that are not directly 89 related to social bonding among adults and which might occupy a significant 90 proportion of time in some species. In the present study, we have therefore limited our 91 data to studies reporting grooming time rather than social time. We also tested 92 whether the previously reported relationship between grooming and group size is best 93 explained by a linear or by a logarithmic function. This distinction is important 94 because a logarithmic relationship in which grooming time reaches an asymptotic 95 value would indicate that primates are compromising on grooming time when they 96 live in very large groups. Because bonding mechanisms may differ between primates

97 with different lifehistory patterns, we included several lifehistory variables (e.g. 98 dispersal patterns) as well as habitus (terrestrial vs arboreal), social system, predation 99 pressure and phylogenetic distance (seeBarton, 1993; Martins, 1993) into our analysis. 100 We used path analysis to determine possible causal relations between variables 101 determining group size and grooming across primate species and to explore the role of 102 indirect effects as determinants of grooming time. We also tested whether the 103 relationship between group size and grooming that we observe across species can be 104 found across different populations within a taxon. Finally, we use the relationships 105 between grooming, group size and neocortex size to define a state space that allows us 106 to explore the extent to which species and individual populations experience social 107 and environmental stress. This allows us to explore the influence of environmental 108 variables on both grooming time and social cohesion.

109

110 Methods

111 Data

112 Data on time spent grooming, group size, body weight, neocortex ratio, sex ratio, 113 terrestriality, predation risk, female dispersal and social system (one male groups 114 versus multi-male groups) were accumulated from published studies for as many Old 115 World primate species/populations as we could find (see Table 1). For our literature 116 search, we used the previously published study by Dunbar (1991) as a starting point 117 and subsequently screened the more recent literature (using the internet search engine 118 Web of Science) for additional studies reporting grooming times in a comparable way. 119 A study was included in our data set if it reported (i) the percentage of the time spent 120 grooming (or in social activities if the authors specifically stated that this was 121 essentially grooming time) and (ii) the group size of the study group. In a few cases,

Table 1 around here

group size information was derived from other authors studying the same groupduring the same time period.

124 Initially, we also collected data on social time (which, in addition to grooming, 125 also includes other social behaviours such as e.g. sexual behaviour, aggression or 126 play). Social time provides a more diffuse measure as, in contrast to grooming which 127 can easily be defined, there is no common definition for social time that is used by all 128 researchers. In line with our hypothesis (that social bonding is a function of time 129 devoted to grooming), the results for social time were often different to (or less clear 130 than) those for grooming time, suggesting that the two variables are not the same and 131 that social time adds considerable noise to the data. Since it is specifically grooming 132 that is expected to play an essential role in group cohesion, we have confined our 133 analyses here to studies reporting grooming time.

134 Whenever grooming times were available from more than one 135 study/population per species, we used average values across those studies for all 136 between-species comparisons, while data from individual studies (although averaged 137 across different study groups of the same population) were used for within-taxa 138 comparisons. The one exception to this was in the case of baboons (genus *Papio*): 139 because baboon taxonomy remains somewhat arguable, the five (sub-)species differ 140 significantly in behaviour and ecology, and there are more data available for this 141 genus than any other, we have opted to treat the conventional (sub-)species as 142 separate taxa for the between-species analyses. Since comparative analysis methods 143 are opaque to taxonomic level providing phylogenetic relationships can be specified 144 between them, it does not matter much whether these are really good species or 145 merely subspecies.

146	Because we are interested in the possible limiting effects of brain size, a
147	species was only included into our analysis if we were able to derive a value for
148	species-specific neocortex ratio. Whenever possible, we calculated neocortex ratios
149	(volume of the neocortex /volume of the rest of the brain) based on actual brain tissue
150	volumes as given by Stephan et al. (Stephan et al., 1981) or by Rilling & Insel
151	(Rilling & Insel, 1999). For those species for which no published data on neocortex
152	volumes were available, we estimated neocortex ratio from brain weight or brain
153	volume using the equations given by Kudo & Dunbar (2001).
154	
155	Across-Species Comparison
156	We first identified the general form of the relationship between grooming and group
157	size (linear vs curvilinear) using stepwise regression analysis. Data on group size,
158	grooming and body weight were log-transformed to improve normality and to enable
159	us to fit linear models to curvilinear distributions. Because grooming time was zero
160	for some species, we added 1 to all grooming times before the log-transformation.
161	To assess the extent to which all other variables affect grooming time, we used
162	generalized linear models. The best model was selected using the Akaike Information
163	Criterion (AIC). The selection procedure started with a maximally parameterized
164	model (using phylogenetic generalized least squares, see below) from which
165	subsequently the parameter with the lowest effect size (partial squared η) was
166	removed before the next run. The model with the fewest number of variables and the
167	lowest AIC was taken to be the best model. The minimal model tested was the
168	relationship between grooming and group size excluding all other variables.
169	The effects of phylogeny were assessed using the method of phylogenetic
170	generalized least squares (PGLS) (Grafen, 1989; Martins, 1999; Garland & Ives,

171 2000). PGLS incorporates the expected covariance among species due to phylogeny 172 into a statistical model using generalized least squares: the correlation between error 173 terms is altered so that it reflects the degree of phylogenetic relatedness amongst the 174 species to which they relate (see Shultz et al., 2005). The PGLS was implemented in 175 R (Ihaka & Gentleman, 1996) using the Analysis of Phylogenetics and Evolution 176 (APE) package (Paradis et al., 2004) and code written by R. P. Duncan. Phylogenies 177 were derived from Purvis (1995). Because we did not know exact branch lengths in 178 the phylogeny for all the species in our data, we used relative branch lengths, where 179 branch lengths were set to be proportional to the number of taxa below each node in 180 the phylogeny. PGLS allows us to add phylogenetic relationships to the full model, 181 using λ as an indicator for the explanatory effect of phylogeny on the dependent 182 variable (0=no effect, 1=max effect).

Finally, to establish the extent to which species compromise on their grooming time, we determined the group size at which the data were equally well explained by a linear and by a logarithmic model. Once this group size was found, we repeated the model selection procedure, using original (not log-transformed) data to find the best linear model describing the data. The model obtained in this way allows us to estimate how much time primates *ought* to spend grooming in a group of a given size.

189 Data were analysed in SPSS 13.0 and R.

190

191 Within-Taxon Analyses

192 To determine whether the relationship between grooming and group size can also be 193 found across populations within taxa, we fitted linear and logarithmic models to the 194 available data on grooming time and group sizes for three different taxa. We then

tested whether these relationships reached significance and identified the best modelusing the amount of variance explained as the criterion for best fit.

197

198 Path Analysis

199 In order to identify how various lifehistory variables affect grooming time and group 200 size, we compared alternative models for the possible relationships between the 201 variables using path analysis (e.g. Byrne, 2001; Schumacker & Lomax, 2004). Path 202 analysis allows us not only to include indirect effects (i.e. effects through another 203 variable) but also to test likely causal directions. Path analyses and diagrams were 204 derived with the AMOS5 software, using maximum likelihood estimations. A full 205 model is specified in which the relations between variables were defined as optional 206 (with the exception of error terms and the group size/grooming relationship). AMOS 207 then calculates the model parameters for all possible nested model combinations, 208 allowing the best model to be identified based on several selection criteria, such as 209 AIC and BIC (Bayes Information Criterion: Schwarz 1978). In the analysis, error 210 terms are included for four variables (neocortex ratio, group size, sex ratio and female 211 dispersal). Because path analysis models linear relations, we used log-transformed 212 values for body weight, group size and grooming time. Multivariate normality was 213 tested using kurtosis (Mardia's coefficient: Mardia, 1970).

214

215 Observed and Predicted Values

216 Using the equation for the linear relationship between grooming and group size, we

217 calculated the amount of time primates *ought* to spend grooming in their respective

218 group sizes. Similarly, we calculated expected species-specific (cognitive) group sizes

219 based on the relationship between neocortex ratio and group size, using the set of

equations given by Dunbar (1993). Dunbar (1993) identified different grades for this

- relationship for prosimians, monkeys and apes, and we used the respective equations
- for these grades:
- 223 Prosimians: $Log_{10}(group size) = 0.419 + 4.688 * log_{10}(NCr)$
- 224 Monkeys: $Log_{10}(group size) = -0.221+4.135*log_{10}(NCr)$
- 225 Apes: $Log_{10}(group size) = -1.683 + 6.527 * log_{10}(NCr)$

where NCr is neocortex ratio. Observed values were then expressed as percentage of

227 predicted values for group sizes and for grooming time. This analysis identifies

228 whether or not the populations in this study were found to live in groups larger or

- smaller than expected and by how much they were forced to compromise on
- 230 grooming time; and these values were, in turn, used to determine the social and
- ecological pressure for each population.
- 232

233 RESULTS

234 Group Size and Grooming Across Species

235 To test whether grooming time increases linearly with group size or is traded against

236 more important activities when group size becomes large, we compared the predictive

power of a linear model with that of a logarithmic model by including both original

and log-transformed values into a stepwise regression analysis. The logarithmic model

is expected to provide a better fit if grooming time no longer increases in larger

240 groups because the demands of other activities such as foraging impose a natural

ceiling on the time available.

242 Overall, the relationship between group size and grooming was better

- explained by a logarithmic equation ($r^2=0.46$) than by a linear relationship ($r^2=0.44$)
- 244 (Table 2, Fig. 1); although the difference in overall r^2 values is marginal, the

Table 2 around here 245 logarithmic model was the one selected by the stepwise regression procedure. This 246 was especially true when the data set was split into terrestrial and arboreal species or 247 into single-male versus multi-male species: the logarithmic model was favoured over the linear model for both terrestrial and arboreal species, and for multi-male species. 248 249 However, in one-male groups, the linear model provided a better fit and was chosen 250 over the logarithmic model (Table 2), possibly reflecting the fact that one-male groups 251 are usually smaller and grooming time may thus not reach its ecologically limited 252 value.

253 In order to establish the group size at which the linear relation starts to flatten 254 out in the multimale-grouping dataset, we progressively excluded large groups and 255 assessed the amount of variance explained by a linear as compared to a logarithmic 256 model in the residual dataset. This analysis also allows us to check whether the 257 superior fit of the logarithmic model is solely driven by outliers that have unusually 258 large group sizes. The difference between the two models only disappeared when 259 group size was restricted to 40 individuals or less, at which point the linear and logarithmic models explained the same amount of variance $(r^2=0.30)$. This suggests 260 261 that it is only when group size exceeds 40 individuals that group members start to 262 compromise on their grooming time (see Fig. 1) and are forced to trade grooming for 263 ecologically more urgent activities, such as feeding or travelling.

We then used a generalized linear modelling approach to determine whether any other variables influenced time spent grooming in addition to group size. This analysis revealed that the best model explaining grooming time in primates includes not only group size but also sex ratio, neocortex ratio and female dispersal (i.e. whether or not females disperse) (see Table 3). However, excluding neocortex ratio from the model results in only a minimal change in the AIC (from 2.6 to 3.0), and we

Table 3 around here

270 therefore excluded neocortex ratio from the final model. The factor "dispersal" 271 indicates that, independently of group size, grooming time is generally higher in 272 species with female philopatry. Grooming time, however, decreases in groups with a 273 strongly female-biased sex ratio. Collinearity diagnostics on the final model show that 274 the condition index is low and that none of the variables are redundant. No effect of 275 phylogeny on grooming time was found (λ =0 in the full model) and phylogeny was 276 subsequently excluded from all further analyses. We checked this further by removing 277 the prosimian species (see Dunbar 1991) and recalculating the regression: the slope 278 parameters did not change.

279

280 Constraints on Group Size

281 Since grooming is assumed to be essential to maintain group cohesion in primates, the 282 amount of time that can be invested in grooming will inevitably limit group size in 283 primates (Dunbar, 1996). We used path analysis to compare possible alternative 284 models to assess the most likely causal links between the different variables that 285 influence group size and grooming in primates. Because indirect relationships can be 286 modelled using path analysis (but not by multivariate regression analysis or 287 generalized linear models), we can estimate more accurately the effects of lifehistory 288 and demographic variables on primate grooming time. Figure 2 depicts the best-fit 289 model given by the AIC (solid lines). The most parsimonious causal model as based 290 on the AIC is that neocortex ratio and predation pressure independently influence 291 group size, which in turn affects grooming time. The model also includes an effect of 292 body weight on neocortex ratio and assumes a correlated error term for body weight 293 and predation risk. In addition, grooming time is affected by female dispersal and sex 294 ratio. (If we use the more conservative BIC criterion, the model remains the same,

except that we lose the two weakest effects: namely, sex ratio→grooming and
dispersal→grooming.) The full model is multivariate normally distributed (Mardias
coefficient=1.5) and the data do not deviate significantly from the model distribution
(AIC model: χ² = 12.4, df=13, p>0.5; BIC model: χ² = 19.0, df=15, p>0.2).
Within-Taxon Analysis
For three taxa, papionins (baboons plus gelada), colobins, and apes (including

302 gibbons), we have sufficient data to analyse how the amount of time spent grooming

303 relates to group size across populations. Table 4 summarizes the results. Because it

304 has previously been suggested that grooming time might be related to body size (due

305 to the hygienic function of grooming: see Dunbar 1991), we also controlled for body

306 weight using partial correlation analysis.

307

308 <u>Apes</u>

309 The best model, which explains 72% of the variance in grooming time, is a

310 logarithmic relationship between time spent grooming and group size (Table 4, Figure

311 3a). Controlling for body weight only marginally improved the model.

Table 4 around here

312

313 <u>Papionins</u>

314 As with the apes, the model which explains the most variance (and is selected by the

315 stepwise procedure) is the logarithmic model, which accounts for 44% of the variance

316 in grooming time (Table 4, Fig. 3b). However, this effect seems to be due mainly to

- the two outliers with unusually large group sizes; if only groups with less than 200
- 318 individuals are considered, the linear model does equally well. Controlling for species
- 319 body weight did not improve the model. Note that, in line with previous studies (see

320 (Dunbar, 1992b; Hill, 1999), we did not find a relationship between group size and
321 social time (which includes, in addition to grooming, behaviours such as sexual
322 behaviour, aggression and play).

323

324 <u>Colobins</u>

325 Across all colobins, there is no significant correlation between group size and

326 grooming (Table 4). However, if we analyse the data for *Colobus* and *Piliocolobus*

327 separately, we find a significant logarithmic relationship in *Piliocolobus*, while in

328 *Colobus* the relationship is not significant. The fact that there is a significant

329 logarithmic relation between grooming and group size in multi-male groups but not in

330 one-male groups (see Table 5, Fig. 3c) is probably explained by the socio-

331 demographic differences between *Piliocolobus* and *Colobus*: small one-male groups

are more characteristic of the latter genus, whereas multimale groups are

333 characteristic of the former. Controlling for species body weight did not improve the

334 models. Note that, in line with the findings for baboons, the relationship between

335 group size and grooming in *Piliocolobus* disappeared when we used social time rather

than grooming time.

337

338 The Eco-Cognitive Niche

Figure 1 shows that some species/populations spend less time grooming than would be expected based on a linear relationship between grooming time and group size. If we assume that in such cases grooming time is traded against more urgent activities (such as for example feeding), we can then use the deviation from expected values to estimate the 'ecological stress' that these populations are experiencing (i.e. those cases where individuals are forced to give up grooming time due to time budgeting

345 problems). The cost of trading grooming time for other activities is presumed to be a 346 decrease in group cohesion (Dunbar, 1996). Following a similar rationale, neocortex 347 ratio has been hypothesised as setting an upper limit on primate group sizes by 348 determining the number of relationships an individual can keep track of (Dunbar, 349 1992a; Dunbar, 1996). This limit is not an absolute limit that cannot be exceeded, but 350 if groups do exceed this limit, group cohesion can be expected to decrease (Dunbar, 351 1998). We used this relationship between group size and neocortex ratio (using the 352 equations given by Dunbar 1993) to calculate expected cognitive group sizes, and 353 then used the difference between observed and expected values as an estimate of the 354 amount of 'cognitive stress'.

355 Figure 4 depicts the deviations for group size and grooming time from their 356 respective expected values (expressed as % deviation from expected) for 40 primate 357 (sub-)species. The state-space created by the axes of equality then defines what we 358 might consider the "eco-cognitive niche". The two left quadrants identify 359 species/populations that live in smaller than expected groups for the neocortex size, 360 and the two righthand quadrants those that live in larger than expected groups, while 361 those in the upper half groom more than expected for group size and those in the 362 lower half groom less than expected.

In theory, all species/populations should be found either within the upper left quadrant (the situation in which there are no time budget problems and groups are smaller than the species' cognitive limit) or around the intersection of the two lines (where expected and observed values for the two dimensions are equal). Deviations from this can be interpreted as population-specific (rather than species-specific) responses to ecological or cognitive constraints. Populations in the lower half of the graph (which appear to groom less than expected) might be under strong ecological

370 pressure that does not allow them to invest the required amount of time in grooming.
371 Populations in the two right quadrants on the other hand may be living in ecological
372 conditions which oblige them to live in larger groups than they can really cope with
373 cognitively; these groups can be expected to be relatively unstable, especially when
374 individuals are also found to groom less than expected.

375 When species are distinguished by typical levels of predation risk (as defined 376 by Nunn and van Schaik 2000), those that were classified as experiencing high 377 predation pressure are found significantly more often on the right-hand side of the 378 graph (i.e. in larger than expected groups), while those species with low predation risk 379 are more likely to be found on the left-hand side of the graph (Kruskal Wallis Test: 380 χ^2 =10.2, df=2, n=40, p<0.01). However, high and low predation species do not occur more often in the upper half of the graph than they do in the lower half ($\chi^2=1.70$, 381 382 df=2, n=40, p>0.4).

383

384 DISCUSSION

385 Our data strongly support the hypothesis that, in primates, grooming behaviour 386 is a function of group size: this is true not only across but also within taxa. Some 387 aspects of the social system (specifically, female philopatry and sex ratio) also had a 388 strong effect on overall grooming times, but ecological variables (e.g. predation risk, 389 terrestriality, mating system) did not. The relationship with group size is not strictly 390 linear, but follows a logarithmic equation indicating that individuals living in very 391 large groups do not have enough time available to invest as much time in grooming as 392 they ought to. There was no indication of an effect of phylogeny on grooming time. 393 Cognitive constraints as well as ecological variables do not affect grooming directly 394 but help to explain indirect effects. Groups which are larger than predicted by

neocortex size and/or where individuals have to compromise their grooming time
should either be unstable or will have to maintain cohesion by other means. This may
lead to fragmentation and fission-fusion type social systems where smaller networks
(e.g. matrilines) are loosely linked together. As indicated by the path analysis,
cognitive constraints limit primate group sizes, which in turn determine grooming
times; however, the latter relationship might be reversed under tough ecological
conditions, when the time available for grooming might limit group size.

402 Grooming behaviour in primates is highly flexible and varies not only between 403 species but also across populations (see Fig. 3). Thus, it is not surprising that we did 404 not find an effect of phylogeny on grooming. Our analyses support the claim that 405 grooming is used to service relationships and that the time needed to do so in bonded 406 groups increases with group size. If there was unlimited time available, we would 407 expect to see a linear relationship between group size and grooming, as was observed 408 for groups with less than 40 members. However, across species (Fig. 1) as well as 409 within taxa (Fig. 3), grooming time appears to be limited to some maximum value, so 410 that further increases in group size do not result in the expected increase in grooming 411 time. This was true for apes, papionins and red colobus monkeys, all of which live in 412 large multimale social groups. In contrast, black-and-white colobus monkeys (which 413 live in small one male groups) did not show the expected relationship between group 414 size and grooming; instead, in this taxon, we find relatively large amounts of time 415 devoted to grooming despite small group sizes. The fact that, in contrast to previous reports (Dunbar, 1992b; Hill, 1999), we found a positive relationship between group 416 417 size and grooming in papionins requires comment. The difference most probably lies 418 in the definition of social time used in these studies. We limited our dataset to studies 419 that explicitly provided data on grooming times, whereas Dunbar (1992b) and Hill

420 (1999) additionally included studies that gave data on overall social time. When we 421 used a slightly larger data set with the more inclusive definition for social time, we 422 obtained the same non-significant results. Interestingly, we found exactly the same 423 dissociation between grooming time and social time in our *Piliocolobus* data set. We 424 interpret this as highlighting a crucial difference between social bonding based on 425 grooming and social activity in general: social activity includes not only aggression 426 and mating, but more importantly play which is a common social activity in baboons. 427 Since play is typically confined to immature animals, including it may add significant 428 noise to data on grooming time when the focus of the latter is mainly on adults. This 429 seems to have been the case here. In baboons, time spent playing correlates positively 430 with rainfall (Barrett et al 1992), while birth rates (and hence the number of 431 immatures engaging in play) correlates negatively with group size (Hill et al 2000). In 432 our sample group size is negatively correlated with average moisture index (another 433 variable indicating habitat quality); as a result, the proportion of social time that is 434 play (and hence not grooming) should be (and, for the very limited sample available, 435 actually is) negatively related to moisture and hence to group size.

436 The exact point at which the linear relationship between grooming and group 437 size asymptotes is presumed to be habitat dependent. In other words, populations in 438 rich habitats are expected to be able to devote more time to grooming than 439 populations in harsher habitats where group members will have to spend more time 440 foraging (thus reducing the time available for activities like grooming). When the 441 deviation between expected (linear) and observed grooming time becomes too large, 442 group cohesion will suffer and groups will eventually split, as has been previously 443 demonstrated in baboons (Henzi et al., 1997a; Henzi et al., 1997b). During this 444 process, sub-grouping within the larger group is likely to take place and we might

445 expect grooming time to decrease as compared to more stable but larger groups. 446 Indeed, the data on apes (Fig. 3a) are best explained by a quadratic relationship 447 (inverse U-shaped), possibly because some of the larger groups (i.e. communities) 448 may be in the process of fissioning and in reality already constitute two smaller 449 groups. Species that habitually live in large groups will have to find other ways to 450 maintain social cohesion. One solution may be to form more tightly bonded smaller 451 subgroups which are then connected by a few mediating individuals (Kudo & Dunbar, 452 2001), thus creating a form of fission-fusion social system. The one male groups 453 embedded within multimale/multifemale bands characteristic of gelada and 454 hamadryas baboons (Kummer, 1968; Dunbar & Dunbar, 1975; Stammbach, 1987) 455 may be examples of this.

456 Species with female philopatry were found to spend more time grooming than 457 species with female dispersal, suggesting that intense social bonding among females 458 may be at a premium in female-philopatric species (see also Wrangham, 1980; 459 Cheney, 1992) in order to maintain group integrity and coherence through time. The 460 fact that species with a strongly female-biased sex ratio showed a reduction in 461 grooming time indicates that it is female philopatry that is the issue here, not the 462 absolute or relative number of females in the group. However, the negative effect of 463 sex ratio on grooming time may indicate that, in female-bonded species, not every 464 individual has to groom every other individual (grooming occurs primarily within 465 matrilines: for a review, see Gouzoules & Gouzoules, 1987) so that the overall time 466 spend grooming can be reduced.

As discussed previously (Dunbar 1996), primate group sizes are strongly
influenced by predation pressure (which sets a minimum group size), as well as by
ecological pressures (which limit the number of individuals that can live together in a

470 given habitat) and cognitive limitations (which set an upper limit to the number of 471 individuals that can coexist as a coherent group). These relationships are also reflected 472 in Fig. 2, which shows how neocortex size, body weight, predation pressure, dispersal pattern, sex ratio, group size and grooming relate to each other. Importantly, predation 473 pressure as well as body weight and neocortex ratio play an important role in 474 475 predicting group size, but not in predicting grooming time. Grooming time was 476 primarily predicted by group size and the path model did not improve when we 477 included the limiting effect of grooming on group size as a negative feedback loop. 478 This suggests that species-typical group sizes are primarily determined by cognition 479 and predation pressure and not so much by time constraints. Time constraints will 480 presumably only come into play when populations live in marginal habitats, where 481 time becomes more of a critical factor. However, primate behaviour is extremely 482 flexible and this flexibility can be used to overcome such constraints (Byrne & 483 Whiten, 1988; Byrne, 1999). Note that the path analysis model differs from the model 484 described in Table 3, mainly because path analysis allows us to model indirect effects 485 such as those for neocortex ratio and predation on grooming via group size.

486 Cognitive limitations, predation pressure and ecological time constraints thus 487 create a multi-dimensional species-specific state space of realisable group sizes 488 (Dunbar 1996). However, as discussed above, these limits are not fixed boundaries 489 that make large groups impossible. Species can always live in larger groups if 490 ecological conditions demand it, but in these cases we would expect to see 491 significantly reduced cohesion (as, for example, in gelada baboons where bands and 492 herds represent rather loose associations compared to typical Papio troops: (Dunbar, 493 1983). Figure 4 places primate populations into what we have defined as their eco-494 cognitive niche, using neocortex ratio to determine cognitive limits and deviations

495 from expected grooming time to index ecological pressures. Since primates show 496 large inter-population variation in group size and in grooming behaviour, our 497 classification into larger/smaller than expected groups and strong/weak ecological 498 pressure does not reflect species-specific traits but rather reflects population-specific 499 characteristics. However, within this dataset, the contributing populations of 500 Propithecus verreauxi, Piliocolobus badius and P. tephrosceles, Macaca fasicularis 501 and *Theropithecus gelada* live in groups that are much larger than expected for their 502 neocortex ratios. Such large groups may either have an altered (multi-level) social 503 system in which cohesion between units is relatively low (Stammbach, 1987); 504 alternatively, it may be that the particular populations included in our sample 505 happened to be in the process of group fission. Group instability prior to the 506 occurrence of fission events has been reported for many species (e.g. Piliocolobus: 507 Siex & Struhsaker, 1999; Korstjens, 2001). Given that the populations in this sector of 508 the graph also typically experience high predation risk, it may well be that predation 509 pressure forces them to live in groups larger than their cognitive limits would ideally 510 allow. Populations of species classified as not especially vulnerable to predation were 511 found to live most often in smaller than expected groups. Figure 4 also allows us to 512 predict levels of both group cohesion and ecological stress. A population living in 513 larger than expected groups where individuals spend less time grooming than they 514 *ought* to do can be expected to have reduced group cohesion; similarly, if grooming 515 time is much lower than expected despite the fact that group sizes are not above the 516 cognitive limits, we would predict that time constraints (i.e. ecological stress) must be 517 limiting grooming behaviour. Those species, in which neither cognition nor time 518 appear to limit group sizes (populations in the upper left corner of Fig. 4) may simply

not benefit from living in large groups, and observed group sizes were thus relativelysmall.

521

522 In conclusion, our data demonstrate that grooming behaviour is not only 523 linked to primate group size but also to sex ratio and patterns of female dispersal. The 524 latter may reflect the fact that philopatric females invest a larger amount of time into 525 grooming behaviour than dispersing females. The fact, that the relationship between 526 grooming and group size follows a logarithmic equation indicates that individuals in 527 large groups have to compromise on their grooming time. This should lead to less 528 cohesive, less stable grouping patterns, eventually resulting in group fission. Thus, 529 grooming time as well as cognitive constraints can limit group sizes/cohesion in 530 primates. One has to keep in mind, however, that these constraints do not create 531 absolute limits for primate group sizes. Indeed, we found that many populations live 532 in larger than predicted groups; but in these cases, the groups are predicted to be less 533 cohesive or to depend on other mechanisms for maintaining cohesion (e.g. the kinds 534 of vocal exchanges seen in gelada and in forest guenons such as Cercopithecus 535 diana). More data on group cohesion and stability are needed to test this hypothesis. 536 Interestingly, those species that were found to live in larger than expected groups, 537 were also found to experience high predation pressure, which may have provided a 538 strong selection pressure for large group sizes.

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545 REFERENCES

- 546 Baldellou, M. & Adan, A. 1997. Time, gender, and seasonality in vervet activity: A
 547 chronobiological approach. *Primates*, **38**, 31-43.
- 548 Baldellou, M. & Adan, A. 1998. Diurnal and seasonal variations in vervet monkeys'
 549 activity. *Psychological Reports*, 83, 675-685.
- 550 Barrett, L., Dunbar, R.I.M & Dunbar, P. 1992. Environmental influences on play
- behaviour in immature gelada baboons. *Animal Behaviour*, **44**, 111-115.
- 552 Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E. & Hill, R. A. 1999. Market forces
- predict grooming reciprocity in female baboons. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **266**, 665-670.
- 555 Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E. & Hill, R. A. 2000. Female
- baboons do not raise the stakes but they give as good as they get. *Animal Behaviour*, **59**, 763-770.
- Barton, R. A. 1993. Independent contrasts analysis of neocortical size and

socioecology in primates. *Behavioral and Brain Sciences*, **16**, 694-695.

- 560 Bocian, C. M. 1997. Niche seperation of black-and-white colobus monkeys (Colobus
- *angolensis* and *C. guereza*) in the Ituri Forest. In: *Biology*, pp. 202. New York:
 City University of New York.
- 563 Boesch, C. & Boesch-Achermann, H. 2000. *The chimpanzees of the Taï Forest:*
- 564 *Behavioural Ecology and Evolution*. Oxford: Oxford University Press.
- 565 Bronikowski, A. M. & Altmann, J. 1996. Foraging in a variable environment: weather
- patterns and the behavioral ecology of baboons. *Behavioural Ecology and Soiciobiology*, **39**, 11-25
- *Soleloolology*, **c***y*, 11 **2***c*
- Butynski, T. M. 1990. Comparative ecology of blue monkeys (*Cercopithecus mitis*) in
 high- and low-density subpopulations. *Ecological Monographs*, 60, 1-26.

- Buzzard, P. J. 2004. Interspecific competition among *Cercopithecus campbelli*, *C. petaurista*, and *C. diana* at Taï Forest, Cote d'Ivoire. pp. 212. New York:
 Columbia University.
- 573 Byrne, B. M. 2001. Structural equation modeling with AMOS: basic concepts,
- 574 *applications, and programming.* London: Lawrence Erlbaum Associates.
- 575 Byrne, R. W. 1999. Cognition in great ape ecology. Skill learning ability opens up
- foraging opportunities. *Symposia of the Zoological Society of London*, **72**,
 333-350.
- 578 Byrne, R. W. & Whiten, A. 1988. *Machiavellian Intelligence: Social Expertise and*579 *the Evolution of Intellect in Monkeys, Apes and Humans*. Oxford: Oxford
 580 University Press.
- 581 Caraco, T. & Wolf, L. L. 1975. Ecological determinants of group sizes of foraging
 582 lions. *American Naturalist*, **109**, 343-352.
- 583 Chapman, C. A. & Chapman, L. J. 2000. Constraints on group size in red colobus and
- red-tailed guenons: examining the generality of the ecological constraints
 model. *International Journal of Primatology*, 21, 565-585.
- 586 Chapman, C. A., Wrangham, R. W. & Chapman, L. J. 1995. Ecological constraints on
- 587 group-size an analysis of spider monkey and chimpanzee subgroups.

588 Behavioral Ecology and Sociobiology, **36**, 59-70.

- 589 Cheney, D. L. 1992. Intragroup cohesion and intergroup hostility: the relation
- between grooming distribution and intergroup competition among female
 primates. *Behavioral Ecology*, **3**, 334-345.
- 592 Chivers, D. J. 1974. *The siamang in Malaya, a field study of a primate in tropical rain*593 *forest.* Basel: Karger.

- 594 Clutton-Brock, T. H. 1974. Activity patterns of red colobus (*Colobus badius*595 *tephrosceles*). *Folia Primatologica*, **21**, 161-187.
- 596 Clutton-Brock, T. H. 1975. Feeding behaviour of red colobus and black and white
 597 colobus in East Africa. *Folia Primatologica*, 23, 165-207.
- 598 Cords, M. 1986. Interspecific and intraspecific variation in diet of 2 forest guenons,
- 599 *Cercopithecus ascanius* and *C. mitis. Journal of Animal Ecology*, **55**, 811-827.
- 600 Cords, M. 1995. Predator vigilance costs of allogrooming in wild Blue Monkeys.

601 *Behaviour*, **132**, 559-569.

- 602 Cords, M. 2002. Friendship among adult female blue monkeys (*Cercopithecus mitis*).
 603 *Behaviour*, **139**, 291-314.
- 604 Cowlishaw, G. C. 1993. Trade-offs between feeding competition and predation risk in
 605 baboons. University College London.
- 606 Dasilva, G. L. 1989. The ecology of the western black and white colobus (Colobus
- 607 *polykomos polykomos* Zimmerman 1780) on a riverine island in southeastern
 608 Sierra Leone. Oxford, England: University of Oxford.
- 609 Davies, A. G., Oates, J. F. & Dasilva, G. L. 1999. Patterns of frugivory in three west
- 610 African colobine monkeys. *International Journal of Primatology*, **20**, 327-357.
- 611 Davies, G. 1984. An ecological study of the Red Leaf monkey (*Presbytis rubicunda*)
- 612 in dipterocarp forests of North Borneo. University of Cambridge.
- 613 Decker, B. S. 1994. Effects of habitat disturbance on the behavioral ecology and
- 614 demographics of the Tana river red colobus (*Colobus badius ruformitratus*).
- 615 *International Journal of Primatology*, **15**, 703-737.
- 616 Downes, S. & Hoefer, A. M. 2004. Antipredatory behaviour in lizards: interactions
- 617 between group size and predation risk. *Animal Behaviour*, **67**, 485-492.

- Dunbar, R. I. M. 1974. Observations on the ecology and social organization of the
 green monkey (*Cercopithecus sabaeus*), in Senegal. *Primates*, 15, 341-350.
- 620 Dunbar, R. I. M. 1983. Relationships and social structure in gelada and hamadryas
- 621 baboons. In: *Primate social relationships: An integrated approach* (Ed. by
- 622 Hinde, R. A.). Oxford: Blackwell.
- 623 Dunbar, R. I. M. 1984. Reproductive Decisions: An Economic Analysis of Gelada
- 624 *Baboon Social Strategies*. Princeton: Princeton University Press.
- Dunbar, R. I. M. 1991. Functional significance of social grooming in primates. *Folia Primatologica*, 57, 121-131.
- Dunbar, R. I. M. 1992a. Neocortex size as a constraint on group size in primates. *Journal of Human Evolution*, 20, 469-493.
- Dunbar, R. I. M. 1992b. Time: A hidden constraint on the behavioural ecology of
 baboons. *Behavioral Ecology and Sociobiology*, **31**, 35-49.
- Dunbar, R. I. M. 1993. Coevolution of neocrotecal size, group size and language in
 humans. *Behavioral and Brain Sciences*, 16, 681-735.
- Dunbar, R. I. M. 1996. Determinants of group size in primates: a general model.
 Proceedings British Academy, 88, 33-57.
- Dunbar, R. I. M. 1998. The social brain hypothesis. *Evolutionary Anthropology*, 6,
 178-190.
- Dunbar, R. I. M. & Dunbar, E. P. 1974. Ecology and population dynamics of *Colobus guereza* in Ethiopia. *Folia Primatologica*, 21, 188-208.
- 639 Dunbar, R. I. M. & Dunbar, E. P. 1975. Social dynamics of gelada baboons. Basel:
 640 Karger.
- Eley, R. M., Strum, S. C., Muchemi, G & Reid, G. D. F. 1989. Nutrition, body
 condition, activity patterns, and parasitism of free-ranging troops of Olive

- 643 Baboons (Papio anubis) in Kenya. American Journal of Primatology 18, 209-219
- 644
- 645 Ellefson, J. 1974. A natural history of white-handed gibbons in the Malayan 646 penninsula. In: Gibbon and Siamang (Ed. by Rumbaugh, D. M.). Basel: Karger. 647
- 648 Fashing, P. J. 2001. Activity and ranging patterns of guerezas in the Kakamega
- Forest: intergroup variation and implications for intragroup feeding 649

650 competition. International Journal of Primatology, 22, 549-577.

- 651 Fawcett, K. A. 2000. Female relationships and food availability in a forest community 652 of chimpanzees. University of Edinburgh.
- 653 Fimbel, C., Vedder, A., Dierenfeld, E. & Mulindahabi, F. 2001. An ecological basis
- 654 for large group size in *Colobus angolensis* in the Nyungwe Forest, Rwanda. African Journal of Ecology, **39**, 83-92. 655
- 656 Fossey, D. & Harcourt, A. H. 1977. Feeding ecology of free-ranging mountain gorilla
- 657 (Gorilla gorilla beringei). In: Primate Ecology: Studies of feeding and
- ranging behaviour in lemurs, monkeys and apes (Ed. by Clutton-Brock, T. 658
- 659 H.), pp. 415-447. New York: Academic Press.
- 660 Garland, T. & Ives, A. R. 2000. Using the past to predict the present: confidence
- 661 intervals for regression equations in phylogenetic comparative methods. 662 American Naturalist, 155, 346-364.
- 663 Gittins, P. & Raemakers, J. 1980. Siamang, lar und agile gibbons. In: Malayan forest
- 664 primates: Ten years' study in tropical rain forest (Ed. by Chivers, D. J.), pp.
- 63-105. New York: Plenum Press. 665

- 666 Gouzoules, S. & Gouzoules, H. 1987. Kinship. In: Primate Societies (Ed. by Smuts,
- B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T.),
 pp. 299-305. Chicago: University of Chicago Press.
- Grafen, A. 1989. The phylogenetic regression. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **326**, 119-157.
- Harding, R. S. O. 1976. Ranging of a troop of baboons (*Papio anubis*) in Kenya.
- 672 *Folia Primatologica*, **25**, 143-185.
- Hass, C. C. & Valenzuela, D. 2002. Anti-predator benefits of group living in white-
- nosed coatis (Nasua narica). *Behavioral Ecology and Sociobiology*, **51**, 570578.
- Henzi, S. P., Lycett, J. E. & Piper, S. E. 1997a. Fission and troop size in a mountain
 baboon population. *Animal Behaviour*, 53, 525-535.
- 678 Henzi, S. P., Lycett, J. E. & Weingrill, T. 1997b. Cohort size and the allocation of
- social effort by female mountain baboons. *Animal Behaviour*, **54**, 1235-1243.
- 680 Hill, R. A. 1999. Ecological and demographic determinants of time budgets in
- baboons: implications for cross-populational models of baboon socioecology.
 Liverpool: University of Liverpool.
- Homewood, K. M. 1976. Ecology and behaviour of the Tana Mangaby, *Cercocebus galeritus galeritus*. University of London.
- Howarth, C. J., Wilson, J. M., Adamson, A. P., Wilson, M. E. & Boase, M. J. 1986.
- Population ecology of the ringtailed lemur, *Lemur catta*, and the white sifaka, *Propithecus verreauxi*, at Berenty, Madagaskar. *Folia Primatologica*, 47, 3948.
- 689 Ihaka, R. & Gentleman, R. 1996. R: a language for data analysis and graphics. J.
 690 *Comput. Graph. Stat.*, 5, 299-314.

- Iwamoto, T. & Dunbar, R. I. M. 1983. Thermoregulation, habitat quality and the
 behavioural ecology of gelada baboons. *Journal of Animal Ecology*, 52, 357366.
- Janson, C. H. & Goldsmith, M. L. 1995. Predicting group size in primates: foraging
 costs and predation risks. *Behav Ecol Sociobiol*, **36**, 326-336.
- 696 Kaplin, B. A. & Moermond, T. C. 2000. Foraging ecology of the mountain monkey
- 697 (Cercopithecus l'hoesti): Implications for its evolutionary history and use of
 698 disturbed forest. *American Journal of Primatology*, **50**, 227-246.
- 699 Korstjens, A. H. 2001. The mob, the secret sorority, and the phantoms. An analysis of
- the socio-ecological strategies of the three colobines of Taï. pp. 174. Utrecht:Utrecht University.
- Kudo, H. & Dunbar, R. I. M. 2001. Neocortex size and social network size in
 primates. *Animal Behaviour*, 62, 711-722.
- Kummer, H. 1968. Social organization of hamadryas baboons. Chicago: University
 Press of Chicago.
- 706 Lawes, M. J. 1991. Diet of Samango Monkeys (Cercopithecus-Mitis-Erythrarchus) in
- the Cape Vidal Dune Forest, South-Africa. *Journal of Zoology*, **224**, 149-173.
- Lee, P. C. 1981. Ecological and social influences on the development of Vervet
 Monkeys. University of Cambridge.
- 710 Li, Z. Y. & Rogers, E. 2004. Habitat quality and activity budgets of white-headed
- 711 langurs in Fusui, China. *International Journal of Primatology*, **25**, 41-54.
- 712 Mackinnon, J. 1974. Behavior and ecology of wild orangutans (*Pongo pygmaeus*).
- 713 *Animal Behaviour*, **22**, 3-74.

- 714 Maisels, F., Gauthierhion, A. & Gautier, J. P. 1994. Diets of 2 sympatric colobines in
- 715 Zaire: more evidence on seed-eating in forests on poor soils. *International*716 *Journal of Primatology*, **15**, 681-701.
- 717 Mardia, K. V. 1970. Measures of multivariate skewness and kurtosis with
- 718 applications. *Biometrika*, **57**, 519-530.
- Marsh, C. W. 1979. Comparative aspects of social organization in the Tana river red
 colobus, *Colobus badius ruformitratus*. Z. Tierpsychol., 51, 337-362.
- Marsh, C. W. 1981. Time budget of Tana River red colobus. *Folia Primatologica*, 35, 30-50.
- 723 Martins, E. P. 1993. Comparative studies, phylogenies and predictions of
- coevolutionary relationships. *Behavioral and Brain Sciences*, **16**, 714-716.
- Martins, E. P. 1999. Estimation of ancestral states of continuous characters: a
 computer simulation study. *Syst. Biol.*, 48, 642-650.
- Matsumoto-Oda, A. & Oda, R. 1998. Changes in the activity budget of cycling female
 chimpanzees. *American Journal of Primatology*, 46, 157-166.
- 729 McKey, D. & Waterman, P. G. 1982. Ranging behaviour of a group of black colobus
- 730 (Colobus satanas) in the Douala-Edea Reserve, Cameroon. Folia
- 731 *Primatologica*, **39**, 264-304.
- 732 McKey, D. B., Gartlan, J. S., Waterman, P. G. & Choo, G. M. 1981. Food selection
- 733 by black colobus monkeys (*Colobus satanas*) in relation to plant chemistry.
- 734 *Biological Journal of the Linnean Society*, **16**, 115-146.
- Nagel, U. 1973. Comparison of anubis baboons, hamadryas baboons and their hybrids
- at a species border in Ethiopia. *Folia Primatologica*, **19**, 104-165.

- 737 Nakayama, Y., Matsuota, S. & Watanuki, Y. 1999. Activity patterns of a troop of
- Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island, Japan. *Ecological Research*, 14, 291-301.
- Nishida, T. 1990. *The chimpanzees of the Mahale mountains*. Tokyo: University of
 Tokyo Press.
- Nunn, C. L. & van Schaik, C. P. 2000. Social evolution in primates: the relative roles
- 743 of ecology and intersexual conflict. In: *Infanticide by males and its*
- 744 *implications* (Ed. by Van Schaik, C. P. & Janson, C. H.), pp. 388-419:
- 745 Cambridge University Press.
- Oates, J. F. 1977a. The guereza and its food. In: *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes* (Ed. by Clutton-Brock, T.
- H.), pp. 275-321. London: Acadamic Press.
- Oates, J. F. 1977b. The social life of a black-and-white colobus monkey, *Colobus guereza. Z. Tierpsychol.*, 45, 1-60.
- 751 Oates, J. F., Davies, A. G. & Delson, E. 1994. The diversity of living colobines. In:
- 752 Colobine monkeys (Ed. by Davies, A. G. & Oates, J. F.), pp. 45-73:
- 753 Cambridge University Press.
- 754 Onderdonk, D. A. & Chapman, C. A. 2000. Coping with forest fragmentation: the
- primates of Kibale National Park, Uganda. *International Journal of Primatology*, 21, 587-611.
- Paradis, E., Claude, J. & Strimmer, K. 2004. APE: analyses of phylogenetics and
 evolution in R language. *Bioinformatics*, 20.
- Pollock, J. 1977. The ecology and sociology of feeding in *Indri indri*. In: *Primate ecology* (Ed. by Cluttonbrock, T. H.), pp. 37-68. London: Academic Press.

- 761 Pulliam, H. R. & Caraco, T. 1984. Living in groups: Is there an optimal group size?
- 762 In: Behavioural Ecology: An Evolutionary Approach (Ed. by Krebs, J. R. &

763 Davies, N. B.), pp. 122-147. Oxford: Blackwell Scientific Publications.

- 764 Purvis, A. 1995. A composite estimate of primate phylogeny. Philosophical
- 765 Transactions of the Royal Society of London Series B-Biological Sciences, 766 348, 405-421.
- Rilling, J. K. & Insel, T. R. 1999. The primate neocortex in comparative perspective 767 768 using magnetic resonance imaging. Journal of Human Evolution, 37, 191-223.
- 769 Schumacker, R. E. & Lomax, R. G. 2004. A beginner's guide to structural equation 770 modeling. London: Lawrence Erlbaum Associates.
- 771 Schwarz, G. 1978. Estimating the dimension of a model. The Annals of Statistics, 6, 772 461-464.
- Seth, P. K. & Seth, S. 1986. Ecology and behaviour of rhesus monkeys in India. In: 773
- 774 Primate ecology and conservation (Ed. by Else, J. G. & Lee, P. C.), pp. 89-775 103. Cambridge: Cambridge University Press.
- 776 Sharman, M. 1981. Feeding, ranging and social organisation of the guinea baboon 777
- rate. St. Andrews University.
- 778 Shultz, S., Bradbury, R. B., Evans, K. L., Gregory, R. D. & Blackburn, T. M. 2005.
- 779 Brain size and resource specialization predict long-term population trends in 780 British birds. Proceedings of the Royal Society of London Series B-Biological
- 781 Sciences.
- 782 Siex, K. S. & Struhsaker, T. T. 1999. Ecology of the Zanzibar red colobus monkey:
- 783 demographic variability and habitat stability. International Journal of
- 784 Primatology, 20, 163-192.

- Son, V. D. 2004. Time Budgets of *Macaca fascicularis* in a Mangrove Forest,
- 786 Vietnam. *Laboratory Primate Newsletter*, **43**, 1-4.
- 787 Stammbach, E. 1987. Desert, forest, and montane baboons: multi-level societies. In:
- 788 Primate Societies (Ed. by Smuts, B. B., Cheney, D. L., Seyfarth, R. M.,
- 789 Wrangham, R. W. & Struhsaker, T. T.), pp. 112-120.
- 790 Stanford, C. B. 1998. Chimpanzee and red colobus: The ecology of predator and
- 791 *prey.* Cambridge: Harvard University Press.
- 792 Starin, E. D. 1991. Socioecology of the red colobus monkey in The Gambia with
- particular reference to female-male differences and transfer patterns. pp. 406.
 New York: City University of New York.
- Stephan, H., Frahm, H. & Baron, G. 1981. New and revised data on volumes in brain
 structures in insectivores and primates. *Folia Primatologica*, **35**, 1-29.
- Struhsaker, T. T. 1979. Socioecology of five sympatric monkey species in the Kibale
 forest, Uganda. *Advances in the Study of Behavior*, 9, 159-228.
- Struhsaker, T. T. 1980. Comparison of the behaviour and ecology of red colobus and
 redtail monkeys in the Kibale Forest, Uganda. *Afr. J. Ecol.*, **18**, 33-51.
- Struhsaker, T. T. & Leland, L. 1979. Socioecology of five sympatric monkey species
 in the Kibale Forest, Uganda. *Advances in the study of Behavior*, 9, 159-228.
- Sugiyama, Y. 1976. Characteristics of the ecology of the Himalayan langurs. *Journal of Human Evolution*, 5, 249-277.
- 805 Sussmann, R. W. 1977. Feeding behaviour of *Lemur catta* and *Lemur fulvus*. In:
- 806 *Primate ecology* (Ed. by Cluttonbrock, T. H.), pp. 1-39. London: Academic
 807 Press.
- 808 Swedell, L. 2002. Affiliation among females in wild Hamadryas baboons (*Papio*809 *hamadryas hamadryas*). *International Journal of Primatology*, 23, 1205-1226.

810	Teas, J., Richie, T., Taylor, H. & Southwick, C. H. 1980. Population patterns and
811	behavioural ecology or rhesus monkeys (Macca mulatta) in Nepal. In: The
812	Maquaces (Ed. by Lindburg, D. G.), pp. 247-262. New York: Van Nostrand
813	Reinhold.
814	Teichroeb, J. A., Saj, T. L., Paterson, J. D. & Sicotte, P. 2003. Effect of group size on
815	activity budgets of Colobus vellerosus in Ghana. International Journal of
816	Primatology, 24, 743-758.
817	Tutin, C. E. G., McGrew, W. C. & Baldwin, P. J. 1983. Social organization of
818	savanna-dwelling chimpanzees, Pan troglodytes verus, at Mt. Assirik,
819	Senegal. Primates, 24, 154-173.
820	Van Noordwijk, M. A. 1985. The socioecology of sumatran long-tailed macaques
821	(Macaca fascicularis) II. The behaviour of individuals. Utrecht: University of
822	Utrecht.
823	van Schaik, C. P., van Noordwijk, M. A., de Boer, R. J. & den Tonkelaar, I. 1983. The
824	effects of group size on time budgets and social behaviour in wild long-tailed
825	macaques (Macaca fascicularis). Behavioral Ecology and Sociobiology, 13,
826	173-181.
827	White, F. J. 1992. Activity budgets, feeding behavior, and habitat use of pygmy
828	chimpanzees at Lomako, Zaire. American Journal of Primatology, 26, 215-
829	223.
830	White, F. J. & Chapman, C. A. 1994. Contrasting chimpanzees and bonobos - nearest-
831	neighbor distances and choices. Folia Primatologica, 63, 181-191.
832	Whiten, A. 1980. The Kloss Gibbon in Siberut Rain Forest. Cambridge: University of
833	Cambridge.

834	Whitesides, G. H. 1989. Interspecific associations of Diana monkeys, Cercopithecus
835	diana, in Sierra Leone, West Africa: Biological significance or chance?
836	Animal Behaviour, 37, 760-776.
837	Wrangham, R. W. 1977. Feeding behaviour of chimpanzees in Gombe National Park,
838	Tanzania. In: Primate Ecology (Ed. by Clutton-Brock, T. H.), pp. 503-538.
839	London: London Academic Press.
840	Wrangham, R. W. 1980. An ecological model of female-bonded primate groups.
841	Behaviour, 75 , 262-300.
842	Yamakoshi, G. 1998. Dietary responses to fruit scarcity of wild chimpanzees in
843	Bossou, Guinea: Possible implications for ecological importance of tool use.
844	American Journal of Physical Anthropology, 106 , 283-295.
845	Yamakoshi, G. 2004. Food seasonality and socioecology in Pan: Are west african
846	chimpanzees another bonobo? African Study Monographs, 25, 45-60.
847	

Genus	Species	Dispersal	Predation	Weight	Terrestrial	OMG	NeoCr	Group	Groom	Time Budget References
			risk	(kg)				size	(%)	
Avahi	laniger	0	2	1.1	0	1	0.97	2	2	C. Hartcourt (from Dunbar, 1991)
Cercocebus	galeritus	0	2	7.4	1	0	2.38	27	5.5	Homewood, 1976
Cercopithecus	ascanius	1	3	3.5	0	0	2.46	26.75	3.45	Struhsaker, 1980; Cords, 1986
Cercopithecus	campbelli	1	3	3.6	0	1	2.21	9	2.8	Buzzard, 2004
Cercopithecus	diana	1	2	4.55	0	1	2.29	28.75	2.48	Whitesides, 1989; Buzzard, 2004
Cercopithecus	mitis	1	2	6	0	1	2.42	22.65	7.18	Struhsaker & Leland, 1979; Butynski, 1990; Lawes, 1991; Cords, 1995; Kaplin & Moermond, 2000; Cords, 2002
Chlorocebus	aethiops	1	3	4.05	1	0	2.17	19.7	9.17	Dunbar, 1974; Lee, 1981; Baldellou & Adan, 1997; Baldellou & Adan, 1998
Colobus	angolensis	1	2	9.85	0	0	2.25	18	5.25	Bocian, 1997
Colobus	guereza	1	1	9.9	0	1	2.32	9.04	5.52	Dunbar & Dunbar, 1974; Oates, 1977b; Oates, 1977a; Bocian, 1997; Fashing, 2001
Colobus	polykomos	1	2	9.4	0	0	2.27	12.5	3.49	Dasilva, 1989
Colobus	satanas	1	2	10.8	0	0	2.29	12	5.51	McKey & Waterman, 1982
Gorilla	gorilla	0	1	126.5	1	0	2.65	11	0.09	D. Doran pers. communication
Gorilla	g. beringei	1	1	126.5	1	0	2.65	6	1	Fossey & Harcourt, 1977
Hylobates	agilis	0	2	5.9	0	1	2.44	4.4	0	Gittins & Raemakers, 1980
Hylobates	klossii	0	2	5.8	0	1	2.35	3.8	0	Whiten, 1980
Hylobates	lar	0	2	5.5	0	1	2.08	3.4	2.1	Ellefson, 1974; Gittins & Raemakers, 1980
Indri	indri	0	1	10.5	0	1	1.24	4.3	1	Pollock, 1977

Table 1. Summary of data and references used for across species comparison of grooming time and group size

Lemur	catta	1	3	2.7	1	0	1.18	12.2	7.18	Sussmann, 1977
Lemur	fulvus	0	2	2.2	0	0	1.23	15.33	7.98	Sussmann, 1977
Lophocebus	albigena	1	2	7.7	0	0	2.39	15	5.8	Struhsaker, 1979
Macaca	fascicularis	1	2	5	1	0	2.23	82.45	7.98	van Noordwijk, 1985; Son, 2004
Macaca	fuscata	1	2	13.45	1	0	2.45	36.5	10.7	Maruhashi 1881; Seth & Seth 1986 ¹
Macaca	mulatta	1	2	4.6	1	0	2.6	32	15	Teas et al., 1980
Pan	paniscus	0	1	39.1	1	0	3.02	27.8	5.7	White, 1992
Pan	t. schweinfurthi	0	1	38.9	1	0	3.13	59.2	11.67	Wrangham, 1977; Nishida, 1990; White & Chapman, 1994: Matsumoto-Oda & Oda, 1998;
										Fawcett, 2000
Pan	t. verus	0	1	40.9	1	0	3.22	40.33	8.27	Tutin et al., 1983; Yamakoshi, 1998; Boesch & Boesch-Achermann, 2000; Yamakoshi, 2004
Papio ²	anubis	1	3	16.5	1	0	2.76	58.8	8.3	Nagel 1973; Eley et al., 1989
Papio ²	ursinus	1	3	18.6	1	0	2.81	28.07	12.64	Henzi et al., 1997b; Barrett et al., 1999; Barrett et al., 2000
2										Nagel 1073
Papio [∠]	hamadrayas	0	3	15.5	1	1	2.59	51	13.5	Nagel, 1975
Papio ² Piliocolobus	hamadrayas badius	0 0	3 3	15.5 8.15	1 0	1 0	2.59 2.22	51 42.5	13.5 4.5	Noe R & Korstjens AH pers. communication
Papio ² Piliocolobus Piliocolobus	hamadrayas badius ruformitratus	0 0 0	3 3 3	15.5 8.15 6	1 0 0	1 0 1	2.59 2.22 2.22	51 42.5 16.16	13.5 4.5 0.83	Noe R & Korstjens AH pers. communication Decker, 1994
Papio ² Piliocolobus Piliocolobus Piliocolobus	hamadrayas badius ruformitratus temminckii	0 0 0 0	3 3 3 3	15.5 8.15 6 6.5	1 0 0 0	1 0 1 0	2.59 2.22 2.22 2.22	51 42.5 16.16 26.2	13.5 4.5 0.83 5.4	Noe R & Korstjens AH pers. communication Decker, 1994 Starin, 1991
Papio ² Piliocolobus Piliocolobus Piliocolobus Piliocolobus	hamadrayas badius ruformitratus temminckii tephrosceles	0 0 0 0	3 3 3 3 3	15.5 8.15 6 6.5 8.75	1 0 0 0 0	1 0 1 0 0	2.59 2.22 2.22 2.22 2.22 2.22	51 42.5 16.16 26.2 51.67	13.5 4.5 0.83 5.4 4.99	Noe R & Korstjens AH pers. communication Decker, 1994 Starin, 1991 Clutton-Brock, 1974; Clutton-Brock, 1975; Strubeckor & Leland, 1970; Starford, 1989;
Papio ² Piliocolobus Piliocolobus Piliocolobus Piliocolobus	hamadrayas badius ruformitratus temminckii tephrosceles	0 0 0 0	3 3 3 3 3	15.5 8.15 6 6.5 8.75	1 0 0 0	1 0 1 0 0	2.59 2.22 2.22 2.22 2.22 2.22	51 42.5 16.16 26.2 51.67	13.5 4.5 0.83 5.4 4.99	Noe R & Korstjens AH pers. communication Decker, 1994 Starin, 1991 Clutton-Brock, 1974; Clutton-Brock, 1975; Struhsaker & Leland, 1979; Stanford, 1998; Chapman & Chapman, 2000
Papio ² Piliocolobus Piliocolobus Piliocolobus Piliocolobus Pongo	hamadrayas badius ruformitratus temminckii tephrosceles pygmaeus	0 0 0 0 0	3 3 3 3 3	15.5 8.15 6 6.5 8.75 53	1 0 0 0 0	1 0 1 0 0	2.59 2.22 2.22 2.22 2.22 2.22 3.17	51 42.5 16.16 26.2 51.67 1	13.5 4.5 0.83 5.4 4.99 0	Noe R & Korstjens AH pers. communication Decker, 1994 Starin, 1991 Clutton-Brock, 1974; Clutton-Brock, 1975; Struhsaker & Leland, 1979; Stanford, 1998; Chapman & Chapman, 2000 Mackinnon, 1974
Papio ² Piliocolobus Piliocolobus Piliocolobus Piliocolobus Pongo Presbytis	hamadrayas badius ruformitratus temminckii tephrosceles pygmaeus entellus	0 0 0 0 0	3 3 3 3 3 1 2	15.5 8.15 6 6.5 8.75 53 14.9	1 0 0 0 0	1 0 1 0 0	2.59 2.22 2.22 2.22 2.22 3.17 2.56	51 42.5 16.16 26.2 51.67 1 33	13.5 4.5 0.83 5.4 4.99 0 4.4	Noe R & Korstjens AH pers. communication Decker, 1994 Starin, 1991 Clutton-Brock, 1974; Clutton-Brock, 1975; Struhsaker & Leland, 1979; Stanford, 1998; Chapman & Chapman, 2000 Mackinnon, 1974 Sugiyama, 1976
Papio ² Piliocolobus Piliocolobus Piliocolobus Piliocolobus Pongo Presbytis Presbytis	hamadrayas badius ruformitratus temminckii tephrosceles pygmaeus entellus rubicunda	0 0 0 0 0 0 0	3 3 3 3 3 1 2 1	15.5 8.15 6 6.5 8.75 53 14.9 6.3	1 0 0 0 0 1 0	1 0 1 0 0 1 0	2.59 2.22 2.22 2.22 2.22 3.17 2.56 2.36	51 42.5 16.16 26.2 51.67 1 33 7	13.5 4.5 0.83 5.4 4.99 0 4.4 0	Noe R & Korstjens AH pers. communication Decker, 1994 Starin, 1991 Clutton-Brock, 1974; Clutton-Brock, 1975; Struhsaker & Leland, 1979; Stanford, 1998; Chapman & Chapman, 2000 Mackinnon, 1974 Sugiyama, 1976 Davies, 1984

Propithecus	verreauxi	1	2	3.6	0	0	1.1	5.1	4.7	Howarth et al., 1986
Trachypithecus	leucocephalus	0	1	7.5	0	1	2.22	10	11.71	Li & Rogers, 2004
Theropithecus	gelada	1	3	17.1	1	1	2.55	144.7	17.4	Iwamoto & Dunbar, 1983

Dispersal: 1=female philopatry, 0=female dispersal; predation: 1=low risk, 2=medium risk, 3=high risk; weight = average weight of males and females; terrestrial: 1=terrestrial, 0=arboreal; OMG=one male group: 1=OMG, 0=multi-male groups; NeoCr=neocortex size in relation to the rest of the brain (see Dunbar 1992a): data in italics indicate that values were estimated using the equation provided by Kudo and Dunbar (2001), while all other data are calculated from brain measures (Stephan et al., 1981); group size: as recorded in those studies that provided data on grooming time; % groom=percentage of time per day spend grooming; ¹ the strongly provisioned temple group was not included; ²due to significant variation in social system, group size and ecology, we distinguish between the several *Papio* (sub-)species.

Table 2. Relationship between grooming and group size using linear and logarithmic models across all primate species, and within terrestrial versus arboreal and multi-male versus one-male groups

		linear		logarithmic			
	n	r ²	р	r ²	р		
All	40	0.44	0.0001	0.46	0.0001		
Arboreal	24	0.10	0.14	0.22	0.02		
Terrestrial	16	0.40	0.01	0.50	0.002		
Multi male	24	0.16	0.05	0.24	0.02		
Single male	16	0.62	0.0001	0.58	0.001		

Values for linear and logarithmic models are depicted. Numbers in bold indicate the best models, i.e. significant models with the highest explanatory value.

	TR	OMG	Phylo	Neo	Group	Sex	Fem	Pred	Weight	AIC
			(λ)	Cortex	size (lg)	ratio	disp	ation	(lg)	
M_max	0.001	0.02	0	0.122	0.321	0.293	0.14	0.064	0.302	11.5
M_min	-	-	-	-	0.27	-	-	-	-	7.5
M_best	-	-	-	(0.02)	0.33	0.16	0.11	-	-	3.0 (2.6)

Table 3. Model selection for grooming time based on effect sizes (partial η) and AIC

Best fit $Log_{10}(groom) = 0.05 + 0.56*log_{10}(group size) - 0.06*sex ratio + 0.24*dispersal$

Linear Groom= 1.5 + 0.24*group size - 0.45*sex ratio + 2.4*dispersal

Values given for parameters represent effect sizes (partial squared η); TR=terrestriality; OMG=one-male group; Phylo=phylogeny; group size (lg)= log₁₀-transformed average group sizes; sex ratio = number of females/number of males; fem. disp = female dispersal (females disperse: disp=0 and females philopatric: disp=1), predation=predation risk (high=3, medium=2, low=1); weight (lg)= log₁₀-transformed average weights for males and females; M_max indicates the fully parameterized model; parameters were gradually removed depending on effect sizes and the AIC was calculated; M-min gives the AIC for the minimal model and M_best indicates the best model. Neocortex ratio is in parenthesis because the AIC is smallest when neocortex ratio is included into the model; however as the AIC changed only little when removing neocortex ratio from the model, we chose the model with the fewest parameters as the best. Best fit gives the equation for the best model; linear fit gives the equation derived from groups of less than 40 individuals, which allows us to calculate what primates *ought* to do if time was unlimited.

taxon	subgroup		linear		logari	thmic	partial (BW)		
		n	r ²	р	r ²	р	r ²	р	df
APES ¹		16	0.64	0	0.72	0	0.72	0	13
PAPIONINS ²		12	0.42	0.022	0.44	0.019	0.3	0.08	9
COLOBINS ³		24	0.06	0.17	0.02	0.4	0.08	0.16	21
COLOBINS:	Colobus	10	-0.1	0.88	-0.1	0.88	0.0	0.97	7
	Piliocolobus	12	0.48	0.005	0.60	0	0.21	0.13	10
COLOBINS:	Multi-male	14	0.19	0.07	0.26	0.04	0.31	0.05	11
	Single male	10	0.02	0.32	-0.1	0.53	0.32	0.12	7

Table 4. Relationships between grooming and group size in individual primate taxa

Values for linear and logarithmic models are depicted. Partial(BW) indicates results for partial correlations (using the best model), which were used to control for possible effects of body weight. Bold numbers indicate the best models, i.e. significant models with the highest explanatory value. Data were averaged if grooming time was available for more than one group. Data were obtained from ¹ Chivers, 1974; Ellefson, 1974; Mackinnon, 1974; Fossey & Harcourt, 1977; Wrangham, 1977; Gittins & Raemakers, 1980; Whiten, 1980; Tutin et al., 1983; Nishida, 1990; White, 1992; White & Chapman, 1994; Matsumoto-Oda & Oda, 1998; Yamakoshi, 1998; Boesch & Boesch-Achermann, 2000; Fawcett, 2000; Yamakoshi, 2004; ² Nagel, 1973 (2 species); Sharman, 1981; Iwamoto & Dunbar, 1983 (3 populations, group size = band size, which is the social unit); Eley et al. 1989 (time budgets for adults only); Cowlishaw, 1993; Bronikowski & Altmann, 1996; Barrett et al., 2000 (2 populations); Swedell, 2002; ³Clutton-Brock, 1974; Dunbar & Dunbar, 1974; Clutton-Brock, 1975; Oates, 1977b; Oates, 1977a; Marsh, 1979;

Struhsaker & Leland, 1979; Struhsaker, 1980; Marsh, 1981; McKey et al., 1981; Dasilva,

1989; Whitesides, 1989; Starin, 1991; Decker, 1994; Maisels et al., 1994; Oates et al.,

1994; Bocian, 1997; Stanford, 1998; Davies et al., 1999; Onderdonk & Chapman, 2000;

Fashing, 2001; Fimbel et al., 2001; Teichroeb et al., 2003, Noe & Korstjens, pers. com (3

species)., P. Fasching, pers. com., P. Sicott, pers. com.

Figure Legends

Figure 1. Relationship between time spent grooming and group size across 40 different primate species; the dashed line indicates the linear fit for groups with less than 40 individuals, while the black line depicts the logarithmic relationship for groups of all sizes. Triangles represent species with single-male social systems, circles represent multi-male social systems, open symbols indicate terrestrial species and solid symbols indicate arboreal species.

Figure 2. Path diagram indicating causal relationships between socio-ecological variables, neocortex ratio, group size and grooming. Arrows indicate presumed causal relationships, rectangles indicate observed variables; numbers on arrows represent standardized regression weights for the whole model. Solid arrows represent the best model based on the AIC statistic, grey dotted arrows represent relationships that were included in the analysis but which were not selected in the best model.

Figure 3. Relation between grooming and group size in (a) apes, (b) papionins and (c) the African colobins. Fitted lines follow logarithmic models.

Figure 4. Classification of primate species/populations according to their deviation from expected grooming times and group sizes; observed values are expressed as percentage of predicted values; lines at 100 demarcate lines of equality (observed = expected). Symbols indicated predation risk (open circle=low predation risk, black cross=intermediate risk, filled squares=high predation risk); individuals should aim at living in the upper left corner (i.e. in smaller groups with more grooming then necessary) or around the 100%/100% intersection. Deviations from this range indicate strong ecological constraints.

Fig. 1







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Fig. 3 a)







Fig. 3 c)





Fig. 4