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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

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

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

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

Methods

Data

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

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

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

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

2000). PGLS incorporates the expected covariance among species due to phylogeny into a statistical model using generalized least squares: the correlation between error terms is altered so that it reflects the degree of phylogenetic relatedness amongst the species to which they relate (see Shultz et al., 2005). The PGLS was implemented in R (Ihaka & Gentleman, 1996) using the Analysis of Phylogenetics and Evolution (APE) package (Paradis et al., 2004) and code written by R. P. Duncan. Phylogenies were derived from Purvis (1995). Because we did not know exact branch lengths in the phylogeny for all the species in our data, we used relative branch lengths, where branch lengths were set to be proportional to the number of taxa below each node in the phylogeny. PGLS allows us to add phylogenetic relationships to the full model, using λ as an indicator for the explanatory effect of phylogeny on the dependent 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.

Data were analysed in SPSS 13.0 and R.

Within-Taxon Analyses

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

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

Path Analysis

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

Observed and Predicted Values

Using the equation for the linear relationship between grooming and group size, we calculated the amount of time primates *ought* to spend grooming in their respective group sizes. Similarly, we calculated expected species-specific (cognitive) group sizes 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:

Prosimians: $\text{Log}_{10}(\text{group size}) = 0.419 + 4.688 * \log_{10}(\text{NCr})$

Monkeys: $\text{Log}_{10}(\text{group size}) = -0.221 + 4.135 * \log_{10}(\text{NCr})$

Apes: $\text{Log}_{10}(\text{group size}) = -1.683 + 6.527 * \log_{10}(\text{NCr})$

where NCr is neocortex ratio. Observed values were then expressed as percentage of predicted values for group sizes and for grooming time. This analysis identifies 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 grooming time; and these values were, in turn, used to determine the social and ecological pressure for each population.

RESULTS

Group Size and Grooming Across Species

To test whether grooming time increases linearly with group size or is traded against 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 groups because the demands of other activities such as foraging impose a natural ceiling on the time available.

Overall, the relationship between group size and grooming was better explained by a logarithmic equation ($r^2=0.46$) than by a linear relationship ($r^2=0.44$) (Table 2, Fig. 1); although the difference in overall r^2 values is marginal, the

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logarithmic model was the one selected by the stepwise regression procedure. This was especially true when the data set was split into terrestrial and arboreal species or 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. However, in one-male groups, the linear model provided a better fit and was chosen over the logarithmic model (Table 2), possibly reflecting the fact that one-male groups are usually smaller and grooming time may thus not reach its ecologically limited value.

In order to establish the group size at which the linear relation starts to flatten out in the multimale-grouping dataset, we progressively excluded large groups and assessed the amount of variance explained by a linear as compared to a logarithmic model in the residual dataset. This analysis also allows us to check whether the superior fit of the logarithmic model is solely driven by outliers that have unusually large group sizes. The difference between the two models only disappeared when 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 that it is only when group size exceeds 40 individuals that group members start to compromise on their grooming time (see Fig. 1) and are forced to trade grooming for 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

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

Constraints on Group Size

Since grooming is assumed to be essential to maintain group cohesion in primates, the amount of time that can be invested in grooming will inevitably limit group size in primates (Dunbar, 1996). We used path analysis to compare possible alternative models to assess the most likely causal links between the different variables that influence group size and grooming in primates. Because indirect relationships can be modelled using path analysis (but not by multivariate regression analysis or generalized linear models), we can estimate more accurately the effects of lifehistory and demographic variables on primate grooming time. Figure 2 depicts the best-fit model given by the AIC (solid lines). The most parsimonious causal model as based on the AIC is that neocortex ratio and predation pressure independently influence group size, which in turn affects grooming time. The model also includes an effect of body weight on neocortex ratio and assumes a correlated error term for body weight and predation risk. In addition, grooming time is affected by female dispersal and sex 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: $\chi^2 = 12.4$, df=13, p>0.5; BIC model: $\chi^2 = 19.0$, df=15, p>0.2).

Within-Taxon Analysis

For three taxa, papionins (baboons plus gelada), colobins, and apes (including gibbons), we have sufficient data to analyse how the amount of time spent grooming relates to group size across populations. Table 4 summarizes the results. Because it has previously been suggested that grooming time might be related to body size (due to the hygienic function of grooming: see Dunbar 1991), we also controlled for body weight using partial correlation analysis.

Apes

The best model, which explains 72% of the variance in grooming time, is a logarithmic relationship between time spent grooming and group size (Table 4, Figure 3a). Controlling for body weight only marginally improved the model.

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Papionins

As with the apes, the model which explains the most variance (and is selected by the stepwise procedure) is the logarithmic model, which accounts for 44% of the variance 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 individuals are considered, the linear model does equally well. Controlling for species body weight did not improve the model. Note that, in line with previous studies (see

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

Colobins

Across all colobins, there is no significant correlation between group size and grooming (Table 4). However, if we analyse the data for *Colobus* and *Piliocolobus* separately, we find a significant logarithmic relationship in *Piliocolobus*, while in *Colobus* the relationship is not significant. The fact that there is a significant logarithmic relation between grooming and group size in multi-male groups but not in one-male groups (see Table 5, Fig. 3c) is probably explained by the socio-demographic differences between *Piliocolobus* and *Colobus*: small one-male groups are more characteristic of the latter genus, whereas multimale groups are characteristic of the former. Controlling for species body weight did not improve the models. Note that, in line with the findings for baboons, the relationship between group size and grooming in *Piliocolobus* disappeared when we used social time rather than grooming time.

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

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

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

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

When species are distinguished by typical levels of predation risk (as defined by Nunn and van Schaik 2000), those that were classified as experiencing high predation pressure are found significantly more often on the right-hand side of the graph (i.e. in larger than expected groups), while those species with low predation risk are more likely to be found on the left-hand side of the graph (Kruskal Wallis Test: $\chi^2=10.2$, $df=2$, $n=40$, $p<0.01$). 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 ($\chi^2=1.70$, $df=2$, $n=40$, $p>0.4$).

DISCUSSION

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

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

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

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

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

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

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

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

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

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- 847

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

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

| | | | | | | | | | | |
|---------------------------|-------------------------|---|---|-------|---|---|------|-------|-------|--------------------------------------------------------------------------------------------------------------|
| <i>Lemur</i> | <i>catta</i> | 1 | 3 | 2.7 | 1 | 0 | 1.18 | 12.2 | 7.18 | Sussmann, 1977 |
| <i>Lemur</i> | <i>fulvus</i> | 0 | 2 | 2.2 | 0 | 0 | 1.23 | 15.33 | 7.98 | Sussmann, 1977 |
| <i>Lophocebus</i> | <i>albigena</i> | 1 | 2 | 7.7 | 0 | 0 | 2.39 | 15 | 5.8 | Struhsaker, 1979 |
| <i>Macaca</i> | <i>fascicularis</i> | 1 | 2 | 5 | 1 | 0 | 2.23 | 82.45 | 7.98 | van Noordwijk, 1985; Son, 2004 |
| <i>Macaca</i> | <i>fuscata</i> | 1 | 2 | 13.45 | 1 | 0 | 2.45 | 36.5 | 10.7 | Maruhashi 1881; Seth & Seth 1986 ¹ |
| <i>Macaca</i> | <i>mulatta</i> | 1 | 2 | 4.6 | 1 | 0 | 2.6 | 32 | 15 | Teas et al., 1980 |
| <i>Pan</i> | <i>paniscus</i> | 0 | 1 | 39.1 | 1 | 0 | 3.02 | 27.8 | 5.7 | White, 1992 |
| <i>Pan</i> | <i>t. schweinfurthi</i> | 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 |
| <i>Pan</i> | <i>t. verus</i> | 0 | 1 | 40.9 | 1 | 0 | 3.22 | 40.33 | 8.27 | Tutin et al., 1983; Yamakoshi, 1998; Boesch & Boesch-Achermann, 2000; Yamakoshi, 2004 |
| <i>Papio</i> ² | <i>anubis</i> | 1 | 3 | 16.5 | 1 | 0 | 2.76 | 58.8 | 8.3 | Nagel 1973; Eley et al., 1989 |
| <i>Papio</i> ² | <i>ursinus</i> | 1 | 3 | 18.6 | 1 | 0 | 2.81 | 28.07 | 12.64 | Henzi et al., 1997b; Barrett et al., 1999; Barrett et al., 2000 |
| <i>Papio</i> ² | <i>hamadrayas</i> | 0 | 3 | 15.5 | 1 | 1 | 2.59 | 51 | 13.5 | Nagel, 1973 |
| <i>Piliocolobus</i> | <i>badius</i> | 0 | 3 | 8.15 | 0 | 0 | 2.22 | 42.5 | 4.5 | Noe R & Korstjens AH pers. communication |
| <i>Piliocolobus</i> | <i>ruformitratus</i> | 0 | 3 | 6 | 0 | 1 | 2.22 | 16.16 | 0.83 | Decker, 1994 |
| <i>Piliocolobus</i> | <i>temminckii</i> | 0 | 3 | 6.5 | 0 | 0 | 2.22 | 26.2 | 5.4 | Starin, 1991 |
| <i>Piliocolobus</i> | <i>tephrosceles</i> | 0 | 3 | 8.75 | 0 | 0 | 2.22 | 51.67 | 4.99 | Clutton-Brock, 1974; Clutton-Brock, 1975; Struhsaker & Leland, 1979; Stanford, 1998; Chapman & Chapman, 2000 |
| <i>Pongo</i> | <i>pygmaeus</i> | 0 | 1 | 53 | 0 | 1 | 3.17 | 1 | 0 | Mackinnon, 1974 |
| <i>Presbytis</i> | <i>entellus</i> | 0 | 2 | 14.9 | 1 | 0 | 2.56 | 33 | 4.4 | Sugiyama, 1976 |
| <i>Presbytis</i> | <i>rubicunda</i> | 0 | 1 | 6.3 | 0 | 1 | 2.36 | 7 | 0 | Davies, 1984 |
| <i>Procolobus</i> | <i>verus</i> | 0 | 2 | 3.7 | 0 | 1 | 2.15 | 3 | 3.58 | Noe R & Korstjens AH pers. communication |

| | | | | | | | | | | |
|-----------------------|----------------------|---|---|------|---|---|------|-------|-------|------------------------|
| <i>Propithecus</i> | <i>verreauxi</i> | 1 | 2 | 3.6 | 0 | 0 | 1.1 | 5.1 | 4.7 | Howarth et al., 1986 |
| <i>Trachypithecus</i> | <i>leucocephalus</i> | 0 | 1 | 7.5 | 0 | 1 | 2.22 | 10 | 11.71 | Li & Rogers, 2004 |
| <i>Theropithecus</i> | <i>gelada</i> | 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

| | n | linear | | logarithmic | |
|-------------|----|----------------|---------------|----------------|---------------|
| | | r ² | p | r ² | p |
| 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.

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

| | TR | OMG | Phylo (λ) | Neo Cortex | Group size (lg) | Sex ratio | Fem disp | Pred ation | Weight (lg) | AIC |
|----------|----------------------------------------------------------------------------------------------------------------------------------------|------|------------------------|---------------|--------------------|--------------|-------------|---------------|----------------|-----------|
| 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) |
| Best fit | $\text{Log}_{10}(\text{groom}) = 0.05 + 0.56 * \text{log}_{10}(\text{group size}) - 0.06 * \text{sex ratio} + 0.24 * \text{dispersal}$ | | | | | | | | | |
| Linear | $\text{Groom} = 1.5 + 0.24 * \text{group size} - 0.45 * \text{sex ratio} + 2.4 * \text{dispersal}$ | | | | | | | | | |

Values given for parameters represent effect sizes (partial squared η); TR=terrestriality; OMG=one-male group; Phylo=phylogeny; group size (lg)= \log_{10} -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)= \log_{10} -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.

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

| taxon | subgroup | linear | | | logarithmic | | partial (BW) | | |
|-----------------------------|---------------------|--------|----------------|-------|----------------|--------------|----------------|------|----|
| | | n | r ² | p | r ² | p | r ² | p | df |
| APES¹ | | 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 |
| COLOBINS³ | | 24 | 0.06 | 0.17 | 0.02 | 0.4 | 0.08 | 0.16 | 21 |
| COLOBINS: | <i>Colobus</i> | 10 | -0.1 | 0.88 | -0.1 | 0.88 | 0.0 | 0.97 | 7 |
| | <i>Piliocolobus</i> | 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 |

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); Cowlshaw, 1993; Bronikowski & Altmann, 1996; Barrett et al., 2000 (2 populations); Swedell, 2002; ³ Clutton-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

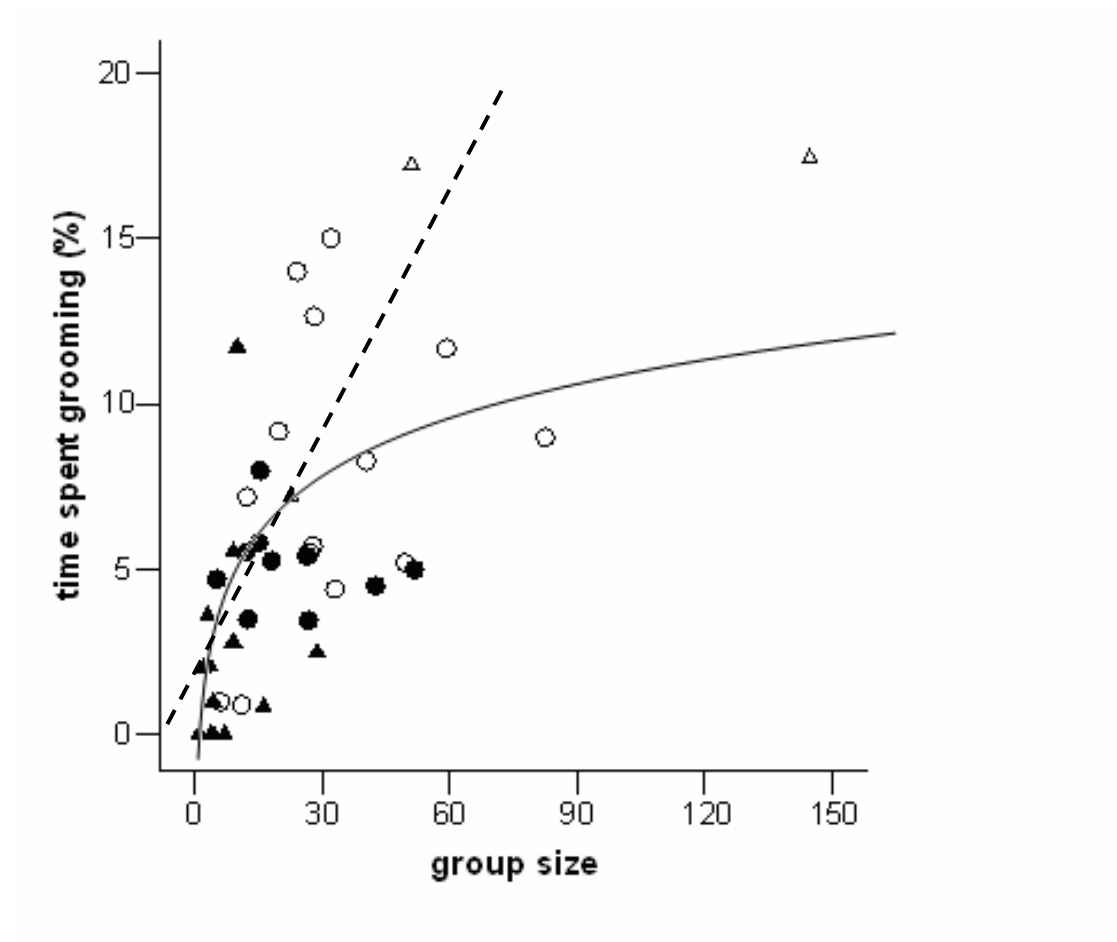


Fig. 2

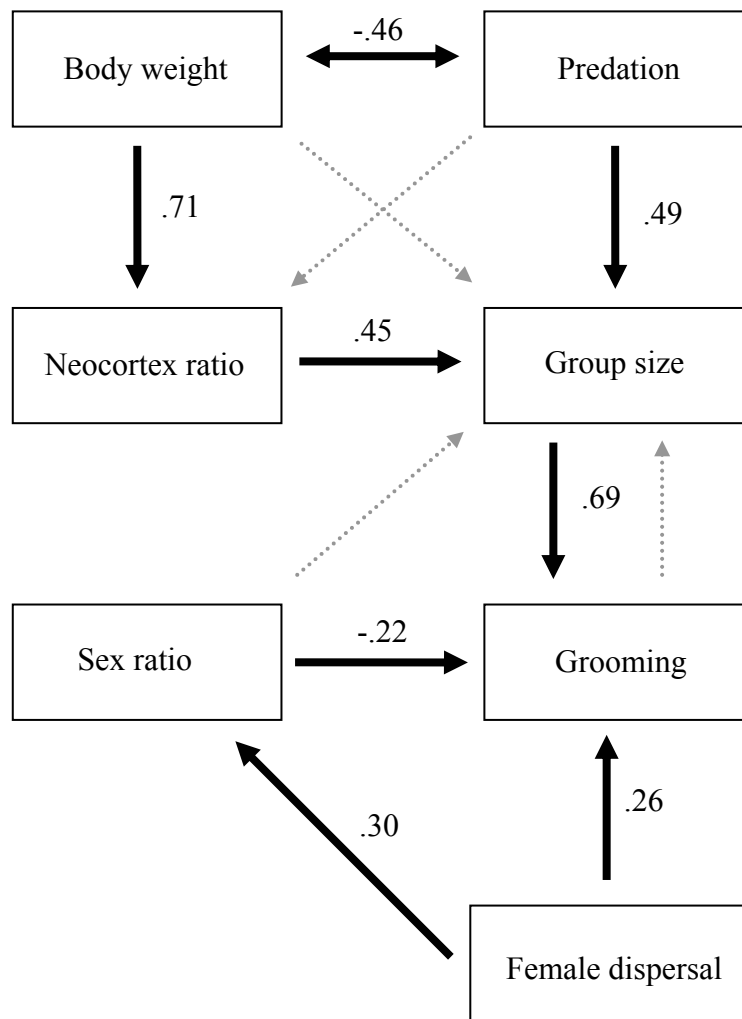
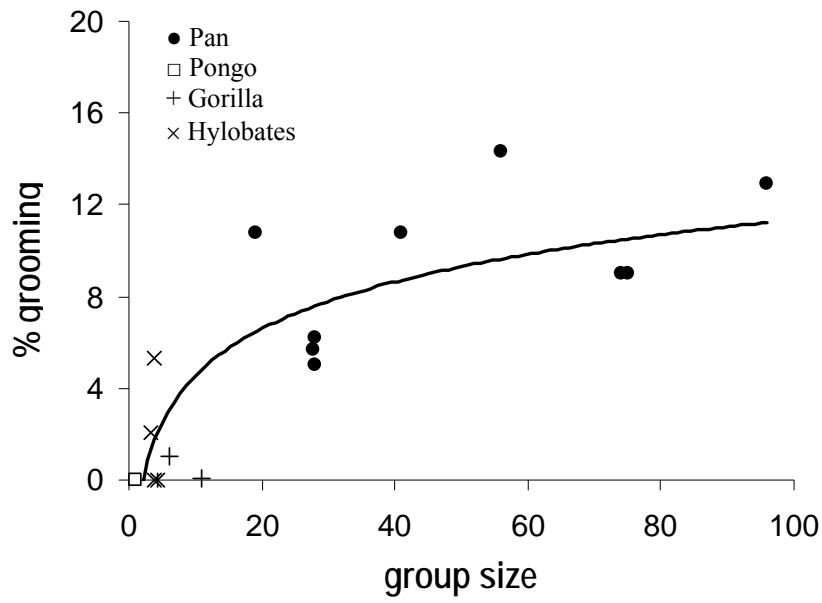


Fig. 3 a)



b)

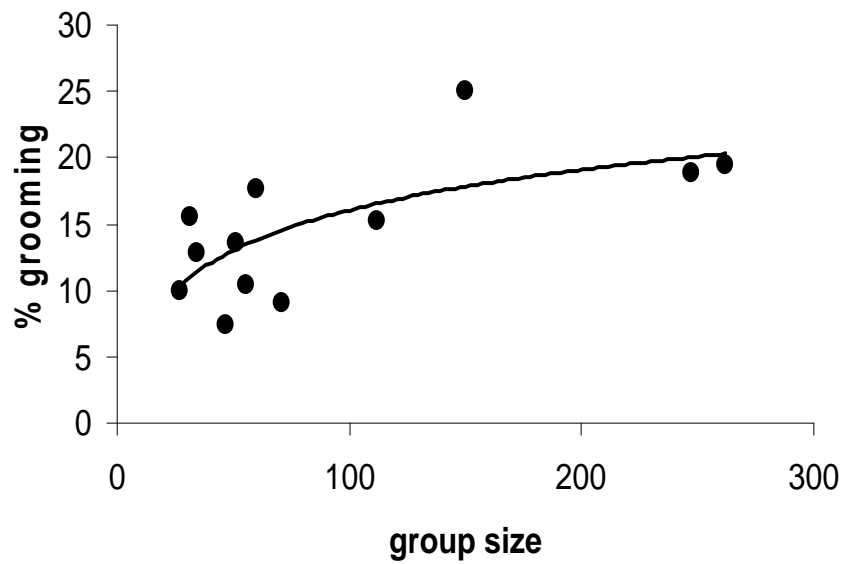


Fig. 3 c)

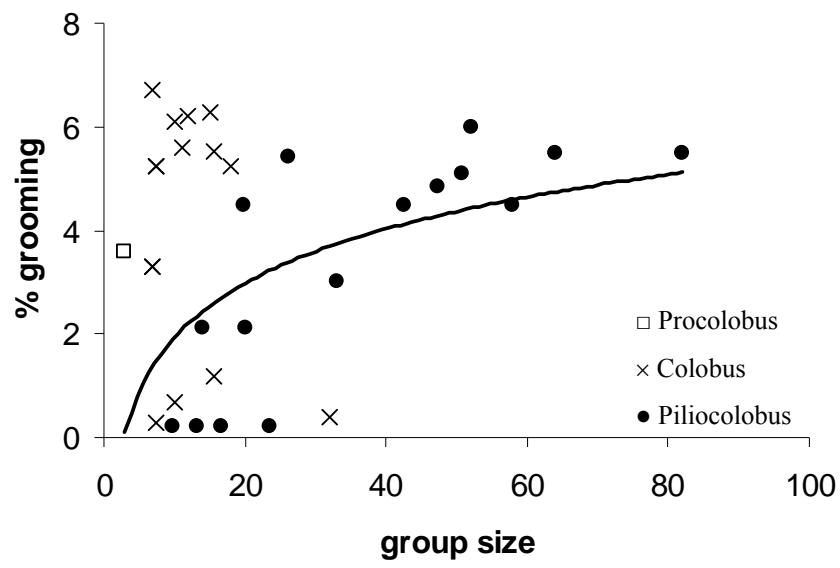


Fig. 4

