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2 **Time constraints limit group sizes and distribution in red and black-and-**
3 **white colobus monkeys**

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Short title: Colobine model

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25 **ABSTRACT**

26 Several studies have shown that, in frugivorous primates, a major constraint on group size is
27 within-group feeding competition. This relationship is less obvious in folivorous primates.
28 We investigated whether colobine group sizes are constrained by time limitations as a result
29 of their low energy diet and ruminant-like digestive system. We used climate as an easy to
30 obtain proxy for the productivity of a habitat. Using the relationships between climate, group
31 size and time budget components observed for *Colobus* and *Piliocolobus* populations at
32 different research sites, we created two taxon-specific models. In both genera, feeding time
33 increased with group size (or biomass). The models for *Colobus* and *Piliocolobus* correctly
34 predicted the presence or absence of the genus at, respectively, 86% of 148 and 84% of 156
35 African primate sites. Median predicted group sizes where the respective genera were present
36 were 19 for *Colobus* and 53 for *Piliocolobus*. We show that the differences between the two
37 genera are mainly due to intrinsic differences in the way each taxon's digestive physiology
38 interacts with climate variables to influence resting time requirements. The models may help
39 us explore these genera's responses to climatic change in both the past and the future.

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41 Keywords: socio-ecology, systems model, *Colobinae*, geographical distribution, costs and
42 benefits of group living

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INTRODUCTION

The size of groups in which animals come together is a site- and species-specific trade-off between the costs and benefits of group living (Alexander 1974; Clutton-Brock and Harvey 1977; van Schaik *et al.* 1983; Terborgh and Janson 1986; Wrangham *et al.* 1993). A major cost of living in a group is intra-group food competition (Dittus 1977; Whitten 1983; Watts 1985; van Schaik and van Noordwijk 1988). An increase in intra-group food competition with increasing group size can be recognized by an increase in the distance that an animal travels each day to find sufficient food patches to meet its energetic requirements and an increase in home range size (Clutton-Brock and Harvey 1977; Harvey and Clutton-Brock 1981; Janson 1988; Wrangham *et al.* 1993; Janson and Goldsmith 1995; Lewis *et al.* 2001). Furthermore, feeding and foraging time may increase as per capita food quality diminishes with increasing number of competitors, and per capita moving time may increase as food patches get depleted (Caraco 1979; van Schaik *et al.* 1983; Janson and van Schaik 1988; Isbell 1991; Janson and Goldsmith 1995). In addition, in order to minimize the chance that groups split up due to aggression within the group, animals need to invest time in affiliating with other group members (Dunbar 1991). Thus, the costs of living in groups should be reflected in the time that animals allocate to different activities during the day and the distance they travel (Janson 1988; Dunbar 1992b; Dunbar 1992a; Janson and Goldsmith 1995). This direct relationship, however, is only expected to be detectable if there is no difference in the quality and density of food between the area occupied by a larger group and that occupied by a smaller group (Gillespie and Chapman 2001). Therefore, in order to understand the relationships between group size and time allocations, we need to correct for confounding effects such as the density and quality of food sources.

67 Because it is often difficult to compare the quality and availability of food in different
68 areas, the effect of group size on time budgets or daily travel distances is not always apparent
69 in inter-specific comparisons. A failure to find clear evidence of increased foraging effort
70 with group size in folivores, who may rely more on non-contestable food sources, has
71 prompted some authors to conclude that group size in folivorous primates is not constrained
72 by food competition (Struhsaker 1978; Isbell 1983; Struhsaker and Leland 1987; Janson and
73 Goldsmith 1995; Treves and Chapman 1996). However, since these studies were conducted,
74 several elegant in-depth studies have shown clear evidence of direct or indirect food
75 competition in colobine monkeys: these include evidence for time constraints (Teichroeb *et*
76 *al.* 2003), increased foraging effort (Snaith and Chapman 2005), range size effects (Dunbar
77 and Dunbar 1974; Fashing 2001a; Steenbeek and van Schaik 2001), aggressive inter-group
78 interactions among females (Koenig 2000; Korstjens *et al.* 2005), intra-group contest
79 competition over food (Sterck and Steenbeek 1997; Koenig *et al.* 1998; Korstjens *et al.* 2002)
80 and a relationship between food availability and group size (Chapman and Chapman 2000).
81 Similarly, various studies of the relationship between folivore biomass and the quality of
82 leaves in a habitat have shown that folivorous primates can be food limited (Waterman *et al.*
83 1988; Oates *et al.* 1990; Chapman *et al.* 2002a).

84 In this paper, we were interested in determining the factors that explain the differences
85 in group size and geographical distribution between two colobine genera that are closely
86 related, largely overlap in diet choice and often share the same forest patches: the red colobus
87 (genus *Piliocolobus*, or alternatively *Procolobus*) and the black colobus group (genus
88 *Colobus*). A subsidiary question of interest was the controversial issue of whether folivore
89 group sizes are constrained by intra-group food competition.

90 Colobines have physiological adaptations that allow them to select leaves and seeds at
91 quantities that are toxic for other primates (Chivers 1994; Waterman and Kool 1994). The

92 best indicator of food quality for colobines is the protein-to-fiber ratio, which is highest in
93 fruit pulp and young leaves. Seeds can also have high protein levels, but often contain toxic
94 secondary components that can only be handled by specialized digestive systems (Waterman
95 and Kool 1994). There are, however, some differences in food selection between the red
96 colobus and the black-and-white colobus (Oates 1994). Roughly, *Colobus* is better able to
97 survive on a fallback diet consisting of high percentages of seeds and mature leaves, whereas
98 *Piliocolobus* has a more restricted diet of young leaves and fruit pulp.

99 The main goal of this paper is to investigate whether time constraints can explain both
100 the variation in group sizes between and within these taxa and the differences in their
101 geographical distribution (Oates 1994). In *Colobus*, average group sizes range between four
102 and twenty (the only exception being the large aggregations of several hundred individuals
103 observed in *Colobus angolensis*; Table IIa). In *Piliocolobus*, on the other hand, average group
104 sizes range between 15 and 75 individuals (Table IIb). Conversely, *Piliocolobus* has a more
105 limited range than species of the genus *Colobus*.

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METHODS

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The data

112 We conducted an extensive review of the literature on colobus monkeys in order to
113 locate all studies (≥ 10 months in length) that provide detailed quantitative data on diet,
114 ranging patterns and group sizes, as well as time budgets based on scan sampling procedures.
115 Because colobines rarely forage on insects, the component feeding time includes the almost
116 negligible amount of ‘food-searching/ handling’ time often categorized as foraging time. A

117 total of 14 studies on *Colobus* and 9 on *Piliocolobus* provided at least two of the variables
 118 required (see Tables I and II). For the populations for which data were available for several
 119 groups during the same time period, we averaged all variables over the sampled groups so as
 120 to ensure statistical independence. When data were available from the same population for
 121 different time periods (mainly the Kibale, Gombe and Tana River sites) we used the newest
 122 or the most complete dataset.

123 Climate variables used in the model were: average annual rainfall in mm (P), average
 124 annual mean temperature in °C (T), variation between calendar months in mean monthly
 125 temperature (measured as the standard deviation across the 12 months, T_{moSD}) and in mean
 126 monthly rainfall (measured as Shannon's diversity index across the 12 calendar months,
 127 P_{moSH}), number of months with less than 100 mm of rain per year ($P < 100$), and the plant
 128 productivity index $P2T$ (the number of months in the year in which rainfall [in mm] was more
 129 than twice the average monthly temperature [in °C](Le Houérou 1984). $P2T$ essentially
 130 defines the growing season in tropical habitats, and yields a very strong correlation with
 131 primary productivity. $P < 100$ provides an alternative measure of seasonality. These variables
 132 were important components of previous time budget models (Dunbar 1992a; Dunbar 1992b;
 133 Williamson and Dunbar 1999; Hill and Dunbar 2002; Korstjens et al. 2006; Lehmann et al. in
 134 press). In addition, we decided to use a third index of seasonality (Tuhkanen 1980):

$$135 \text{ Seasonality index} = (P_{mo\max} - P_{mo\min}) / P$$

136 where $P_{mo\max}$ and $P_{mo\min}$ stand for maximum and minimum mean monthly rainfall
 137 respectively, while P stands for average annual rainfall. We also used two measures for
 138 moisture derived from the Willmott and Feddema moisture indexes for the world (Willmott
 139 and Feddema 1992): average annual moisture index and average monthly moisture index.

140 To reduce the number of variables in our regression equations, we performed a
 141 Principle Components analysis using the variables: T_{moSD} , P_{moSD} , $P < 100$, $P2T$, Seasonality

142 index, and the two moisture variables. Two distinctive factors (*Fac1* and *Fac2*) came out of
143 this analysis that, roughly, correspond to moisture/temperature variability and number of dry
144 months (*Fac1*), and seasonality/rainfall variability (*Fac2*). Although we have used these two
145 climatic factors wherever possible, it had been established in previous models that T_{moSD} has
146 a very strong effect on colobine distribution. Therefore, we ran a multiple regression using
147 this equation instead of the climate factors when the climate factor that included most
148 variation in T_{moSD} (*Fac1*) had a strong but not-significant effect.

149 Wherever possible, we used the authors' own climate descriptions. If such data were
150 not available for the study site, we used data provided for the same site by other authors.
151 Since many studies only provide information on average annual rainfall and temperature, we
152 used data on monthly rainfall and temperature from Willmott and Matsuura (2001). Willmott
153 and Matsuura provide a global dataset of monthly and annual temperature and rainfall in
154 grids of 0.5 degrees latitude by longitude (v3.01)(Willmott and Matsuura 2001), based on a
155 combination of the Global Historical Climatology Network (GHCN version 2) and weather
156 station records of monthly and annual mean air temperature (T) and total precipitation (P)
157 (Legates and Willmott 1990b; Legates and Willmott 1990a). The time period evaluated was
158 1950-1999 inclusive.

159 For each research site and each independent control site (see below), we calculated the
160 average value of each climate variable for the data points in the Willmott and Matsuura and
161 the Willmott and Feddema datasets that fell within a radius of 0.5° longitude and latitude to
162 the site. In our analyses, we used the Willmott and Matsuura (2001) dataset unless data were
163 available from the field site itself.

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The model

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166 We used a modeling approach to identify the factors that determine the differences
167 between the two genera. The model is based on the assumption that, because the amount of
168 daytime is fixed, an animal has to balance its nutritional intake and expenditure while trading
169 off the different time budget components (namely feeding, moving, resting and affiliative
170 social time). In addition, group size may have feedback consequences for most components
171 of the time budget. In effect, the model uses the observed relationships between climatic and
172 activity budget variables (mediated as appropriate by vegetation condition and relevant
173 behavioral ecology variables) to determine how much time a virtual colobus monkey ought to
174 invest in each time budget component at a specific location as group size increases. In
175 addition, primates are generally members of stable social units that require the investment of
176 time in affiliative interactions with group members to maintain an acceptable level of social
177 cohesion (with minimum levels of disruptive aggression). The model's principal aim is to
178 identify the maximum group size at which individual monkeys can meet the habitat-
179 determined demands on the individual time budget components without exceeding the gross
180 amount of time available during the day.

181 The data from the study sites were used in backwards multiple regression procedures to
182 determine the factors that influence the percentage of time that an average colobus monkey
183 invests in each component of its time budget. The aim was to find the multivariate equation
184 that accounted for the highest proportion of variance in the data. Following Dunbar (1992a),
185 we used basic biological considerations to decide which variables should be included as
186 potential independent variables at each stage. Thus, we assumed that feeding and moving
187 time are each independently determined by climate, diet and/or group size. Therefore, they
188 were not included as independent variables in the analysis when either of them was the
189 dependent variable.

190 Following Dunbar and Sharman (1984; Dunbar and Dunbar 1988), we view resting
191 time as composed of two components: 1) environmentally or otherwise enforced resting time
192 needed for thermoregulation, sheltering or digestion; and 2) ‘uncommitted time’ that can be
193 converted into more urgent activities when required. Previous models for Old World taxa
194 have suggested that there may be environmentally imposed limits to the amount of resting
195 time that animals can draw on (Dunbar 1992a). For example, some minimum level of resting
196 time may be imposed by ambient temperature: when animals may have to seek shade and rest
197 because other activities are, energetically or thermally, too costly. In addition, folivorous
198 primates require more time for digestion of their food than frugivorous primates. This is
199 reflected in a relatively high percentage of time spent resting in colobines relative to
200 cercopithecines (Dunbar 1988). Unfortunately, it is impossible to tease apart the two
201 components of resting time from the observed values reported by researchers. As a solution
202 to this problem, we derived a relationship between resting time and the percentage of leaves
203 in the diet that we obtained from an analysis of a dataset that contained both cercopithecines
204 and colobines (Korstjens, Lehmann and Dunbar, unpubl. data). From this interspecific
205 comparison we found that the percentage of time spent resting increases with the percentage
206 of leaves (*leaf*) in the diet according to the following equation:

$$207 \quad \text{Rest}_{\text{forced}} = 14.0753 + 0.6513 * \text{leaf} \quad (r^2 = 0.613, F_{14} = 20.04, p = 0.001)$$

208 Since, in primates, social bonding in some form seems to be crucial for group cohesion,
209 we also need to include a component for socializing time in the models. For these purposes,
210 we have assumed that these taxa are subject to the same principles of social bonding as other
211 Old World monkeys and apes. This allows us to use a general equation relating social time to
212 group size in Old World monkeys and apes, following Dunbar (1991, 1992a). For present
213 purposes, however, we use a new version of this equation based on new analyses of a larger
214 dataset (Lehmann et al, submitted):

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$$\text{Social time}(\%) = 3.037 + 0.1597 * \text{Group size}.$$

216 Note that we make no assumption that social time has to involve grooming, merely that it is
 217 dedicated to some form of affiliative interaction (e.g. sitting together). In effect, the model
 218 naturally allows us to test the validity of this assumption by evaluating the extent to which
 219 socializing time is a significant constraint on group size.

220 Backwards regression methods were used to obtain multivariate equations for each
 221 dependent variable of interest. We then used a linear program in Dbase to calculate maximum
 222 ecologically tolerable group size for the conditions at each location in the dataset based on
 223 the equations in Table III. For each combination of climate/habitat variables, we began with a
 224 group size of one animal. Group size was then allowed to increase in stepwise fashion by one
 225 individual, and the time budget was calculated for the new group size until it reached a size
 226 where the sum of feeding, moving, resting and “grooming” exceeded 100%. At this point,
 227 maximum group size was then set to the value for the previous cycle. All equations were set
 228 to reach a minimum value of 5% and a maximum value of 99%.

229 Since there is variation in body mass between the different species and subspecies of
 230 the two genera, we used biomass of the group rather than group size in several equations. For
 231 immature individuals we assumed body weight to be half that of an adult female (following
 232 Oates *et al.* 1990). Estimated body weight for a ‘group’ of one individual was that of an
 233 average adult (i.e. 9.84 kg for *Colobus* and 7.98 kg for *Piliocolobus*); for groups of two, we
 234 used 1.5 times the average body mass of an adult; while for groups of three we used 2.5 times
 235 the average adult body weight. For group sizes of >3, we used the relationship between group
 236 size and biomass of a group as obtained from the data: $\text{Group mass} = 6.871 * \text{Group size}$ for
 237 *Colobus* and $\text{Group mass} = 6.120 * \text{Group size}$ for *Piliocolobus*.

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Testing the models

240 We tested the validity of the models in three ways. First, we asked whether the
241 maximum group sizes predicted by the appropriate taxon-specific models correlated with
242 observed maximum and average group sizes. Second, we tested whether predicted group
243 sizes for the set of independent African primate sites were significantly larger at sites where
244 the species was known to occur than at sites where it did not. Third, in a more demanding
245 test, we asked whether the models could predict the biogeographic distribution of the two
246 genera in sub-Saharan Africa. Using these tests, we could then investigate whether we could
247 improve the performance of the models by changing one of the variables in the model.

248 In order to find sites where colobines occur, we screened the primate literature and
249 internet sites, especially the UNEP and WCMC World database on protected areas sites, and
250 we requested additional data directly from field researchers. For each site we established the
251 presence or absence of colobus monkeys and, when available, average group sizes for the
252 population. This dataset of forest and woodland sites allowed us to test the extent to which
253 our model could predict presence or absence of colobus monkeys at specific sites subject to a
254 range of climatic conditions. Since some of the sites in this database were close to each other,
255 we considered sites in the database as independent only if they were separated by at least 1-
256 degree of longitude and latitude. If the species was absent at one site but present at another
257 nearby site, we gave preference to the site where it was present, assuming that the chances
258 that a species has gone extinct at a site are higher than that the other site has a locally atypical
259 climate. This yielded a dataset containing 148 independent forest sites for *Colobus* and 156
260 sites for *Ptilocolobus*, respectively (including the study sites used for the model); the two
261 genera were recorded as being present at 68 and 32 of these, respectively, and absent at 80
262 and 124. For each of these sites we obtained climate variables as described above for the
263 study sites. We calculated the maximum group size predicted by our time budget models for
264 each of these sites based on the climate conditions at the site.

265 Finally, in order to check that the use of an intermediate step involving time budgets
266 was not introducing excessive error, we checked to see that these models produced the same
267 outcomes as direct climate-based logistic regression models. For the climatic models, we ran
268 a simple logistic regression using the backwards Likelihood Ratio method (SPSS 12.0.1) with
269 the principal climatic variables (*P*, *T*, *Fac1*, *Fac2*) as the independent variables and the
270 presence/ absence of the genus as dependent variable.

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Data analysis

273 The data for the variables in our dataset are given in Tables I and II. None of the
274 behavioral or environmental variables that were used in the model differed significantly from
275 a normal distribution (Kolmogorov-Smirnov test, $p > 0.1$, $n = 6-13$). We had two study
276 species of *Colobus* at Ituri forest, *C. guereza* and *C. angolensis*. Although the behavioral and
277 dietary data for these two studies are independent, the climatic variables for the site are not.
278 Therefore, we weighted each of these studies with 0.5 so that the site only accounted for one
279 datum in the analyses. Backwards regression methods were used to obtain multivariate
280 equations for each dependent variable of interest. We never included variables that correlated
281 significantly with each other. For each resulting equation, we looked at all partial plots and
282 the original scatter plots for the relevant variables to check that the model was not the result
283 of an outlier or an artifact of small sample sizes, and we checked that the residuals showed a
284 normal and homogeneous distribution.. Because of the small size of our samples, we never
285 included more than three variables in an equation. Our dataset on climate variables and
286 predicted party or community sizes did differ significantly from a normal distribution, and
287 when comparing group sizes at different sites, we used non-parametric tests. All correlations
288 were tested using the Pearson correlations.

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RESULTS

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The basic models

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Feeding time correlated positively with group size in each genus separately (*Colobus*_{excl. Nyungwe}: $n = 11$, $r = 0.550$, $p = 0.080$; *Colobus*_{incl. Nyungwe}: $n = 12$, $r = 0.700$, $p = 0.011$; *Piliocolobus*: $n = 6$, $r = 0.776$, $p = 0.070$, for biomass of group: $r = 0.892$, $p = 0.041$) and when we look at the combined data for the three colobine genera (including olive colobus from Tai; $r = 0.805$, $p < 0.001$, $n = 18$; Fig. 1). This suggests that foraging effort increases with group size.

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The best-fit multivariate equations are given in Table III and produce the models depicted in Fig. 2a and 2b. For the basic model of *Colobus* (straight bold lines in Fig. 2a), we used only the equations (identified as [a] in Table III) that were obtained while excluding the extremely large group sizes of Nyungwe because this site was an extreme outlier (and hence could easily distort equations). Feeding time increased with group size in both species, but only in *Piliocolobus* did we have to include a climatic factor (i.e. rainfall variability/seasonality) for the best result. In *Colobus* moving time was explained by rainfall variability while in *Piliocolobus* both rainfall and group size had an important effect. This suggests that *Colobus* do not move more as a result of increased intra-group food competition, while *Piliocolobus* does. Temperature was an important variable for both species. Only in *Colobus* did the relative moisture and evaporation play an important role.

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The equation of forced resting time from our comparison of guenons and colobines was strongly correlated to observed resting time ($r = 0.673$, $p = 0.033$, $n = 10$). In *Piliocolobus*, however, it turned out that four observed values of resting time were lower than those predicted by this equation (Wilcoxon Signed Ranks test, $n = 6$, $Z = -1.12$, ns). Therefore, we

315 first removed the intercept from the $\text{Rest}_{\text{forced}}$ equation and investigated what explained the
 316 variation in ‘extra’ resting time ($\text{Rest}_{\text{extra}} = \text{observed resting time} - \text{Rest}_{\text{forced}}$). The best
 317 predictor of extra resting time was temperature variation. Thus, we calculated predicted
 318 resting time in *Piliocolobus* by adding up the two equations for $\text{Rest}_{\text{forced}}$ and $\text{Rest}_{\text{extra}}$ into
 319 Rest_{tot} . The resulting predicted resting time (Rest_{tot}) was positively, although not
 320 significantly, correlated with observed resting time ($r = 0.510$, ns, $n = 6$) and was lower than
 321 observed resting times for all cases (Wilcoxon Signed Ranks test, $n = 6$, $Z = -2.2$, $p = 0.03$).
 322 Considering that we need limiting resting time and not maximum resting time, a higher
 323 observed than predicted resting time suggests that our equations produce conservative values,
 324 and are thus quite adequate for our purposes.

325 Table IV gives the predicted maximum ecologically tolerable group sizes for *Colobus*
 326 and *Piliocolobus* monkeys living under different climatic regimes (simplified into a 2-way
 327 table using average annual temperature and rainfall). In effect, these distributions define the
 328 two taxa’s ecological niches. According to the model, neither genus copes well with low
 329 temperatures, unless rainfall is relatively high, and both fare best with high values for rainfall
 330 and temperature. The models suggest that, despite these similarities in their broad overall
 331 distributions within the climatic state space, the two genera in fact have rather different
 332 response curves: *Piliocolobus* has a more confined distribution in the lower right quadrant,
 333 but where it does occur it can do so at higher group sizes than can *Colobus*. Nonetheless, note
 334 that, at very high temperatures and rainfall values, predicted group sizes are even higher for
 335 *Colobus* than for *Piliocolobus*.

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Predicted and observed group sizes

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The predicted group sizes for *Colobus* correlated with maximum observed group sizes
 ($n = 37$, $r = 0.467$, $p = 0.004$) but not with average observed group sizes ($n = 40$, $r = -0.04$,

340 $p=0.8$). Predicted maximum group sizes were not significantly different from maximum
341 observed group sizes (Wilcoxon Signed Ranks test, $n = 37$, $Z = -0.248$, $p < 0.804$; Fig. 3a) but
342 they were significantly larger than average observed group sizes ($n = 40$, $Z = -2.9$, $p < 0.004$).
343 It is important to remember that the model is supposed to produce maximum and not actual
344 average group sizes at a site.

345 To simplify model development, we excluded the Nyungwe *Colobus angolensis*
346 population because it is an outlier in terms of group size. However, the fact this population
347 can live in extremely large groups needs to be explained. To investigate this, we reran our
348 model using equations that were derived from analyses of all populations, including
349 Nyungwe (equations [b] in Table III). The predicted forced resting time in Nyungwe (60%)
350 was well above the observed value (32%). Therefore, we did a multiple regression analysis
351 on the extra time (=observed resting time minus $Rest_{forced}$) for all sites including Nyungwe
352 (equation for $Rest_{extra}$ in Table III). The total resting time is then positively related to
353 temperature instead of being negatively related (combining $Rest_{extra}$ and $Rest_{forced}$). We
354 assume that social time in these large aggregations levels off, therefore, we let social time
355 increase only up to a maximum value associated with a social unit of 100 individuals. The
356 resulting predicted group sizes were much larger than those predicted using the basic model
357 (Wilkinson Signed Ranks Test $Z = -7.17$, $p < 0.001$, $n = 68$, where *Colobus* is present). This
358 model predicted a group size of 140 for Nyungwe. Predicted and observed maximum group
359 sizes were only significantly correlated when we included the value for Nyungwe ($r = 0.298$,
360 $p=0.073$, $n = 37$ excluding Nyungwe; $r = 0.590$, $p<0.0001$, $n = 38$ including Nyungwe) but
361 predicted group sizes were not significantly different from maximum observed group sizes
362 (Wilkinson Signed Ranks Test: $Z = -1.3$, $p < 0.17$, $n = 37$ excluding Nyungwe). This means
363 that, at Nyungwe, and possibly some other sites where observed maximum or average group
364 sizes exceed predicted group sizes shown in Fig. 3, some variable that is strongly positively

365 related to temperature may counterbalance the effect that leaf-feeding has on resting time.
366 The most likely candidate is the protein to fibre ratio in leaves, and a multi-site comparison
367 showed that the protein to fibre ratio at six sites was significantly negatively related to
368 average annual temperature (Table I and III). The protein:fibre ratio is particularly high in
369 Nyungwe (Fimbel *et al.* 2001), thus explaining why this site is so often an outlier. In
370 summary, it is just an unusually rich habitat for colobines.

371 Predicted group sizes for *Piliocolobus* compared well with average observed group
372 sizes ($Z = -0.80$, $p=0.42$, $n = 16$) but were smaller than maximum observed group sizes ($Z = -$
373 2.51 , $p=0.012$, $n = 16$) and correlated with both average and maximum observed group sizes
374 (Fig. 4; $r = 0.617$, $p = 0.011$, $r = 0.569$, $p = 0.021$, $n = 16$). This suggests that the right
375 climatic variables were used and that many populations of *Piliocolobus* have group sizes
376 close to their ecological maximum.

377

378 **Testing the models**

379 We test the validity of the models in three ways: first by determining whether or not
380 they correctly predict that each genus can support significantly larger group sizes at sites
381 where they occur than at sites where they do not in our African habitats database (and,
382 secondarily, that they also predict maximum group sizes ≈ 0 where the genus is absent),
383 second by asking whether the models can correctly predict the biogeographical distribution of
384 the two genera across sub-Saharan Africa, and third whether the climatic variables selected
385 by the time budget model are biologically significant. We regard the second test as a
386 particularly strong one, because it asks the model to tell us why each genus occurs where it
387 does and cannot occur where it is in fact absent.

388 *Group size.* The median predicted group sizes were significantly larger at sites where
389 *Colobus* or *Piliocolobus* were present (18.5 and 53.0 respectively) than where they were

390 absent (1.0 and 0.5 respectively; Mann Whitney U Tests: *Colobus*: $n = 68$, $n = 80$, $U = 390$, p
 391 < 0.001 ; *Piliocolobus*: $n = 32$, $n = 124$, $U = 438$, $p < 0.0001$). At sites where each genus is
 392 absent, mean predicted group sizes do approximate zero (and are certainly well below viable
 393 minimum group sizes).

394 *Biogeographic distribution.* As we noted earlier, a taxon can only occur at a site where
 395 its time-determined maximum predicted group size exceeds the minimum permissible size set
 396 by the predation risk at that site (Dunbar 1996). We have no way of determining what the
 397 minimum viable maximum ecologically tolerable group size might be in different sites, but as
 398 a first pass we set these at the minimum ever observed group size for each taxon (3 for
 399 *Colobus* and 4 for *Piliocolobus*). Table Va gives the results for each genus in the form of a
 400 contingency table comparing the number of sites where the models correctly or falsely
 401 predicted each genus's presence or absence. For both genera, the model provides a
 402 significantly better fit to the observed distribution than would be expected by chance
 403 (*Colobus*: $\chi^2_1 = 70.5$, $p < 0.0001$; *Piliocolobus*: $\chi^2_1 = 28.3$, $p < 0.0001$).

404 We can use this approach to give us some idea of the likely values for the minimum of
 405 maximum tolerable group sizes for each genus by examining the accuracy of the model as the
 406 minimum group size is allowed to vary from $0 \rightarrow N_{\max}$ (the maximum possible group size for
 407 that taxon). Fig. 5 shows how the accuracy of the model (in predicting presence/absence)
 408 changes as different minimum viable group sizes are used. The graph shows the cumulative
 409 percentage of cases for which the model correctly predicts presence/absence. If we take a
 410 minimum viable group size of 0, the model has an accuracy of 100% for sites where the
 411 species is present (because the genus is assumed to be able to live at every site where
 412 predicted group size is at least 0), but 0% accuracy for the sites where the genus is absent. As
 413 we increase the minimum viable group size, so these values reverse. The models have the
 414 highest overall accuracy close to where the two lines cross (highest accuracy is not where the

415 lines cross exactly because of different sample sizes for presence and absence), which is at a
 416 minimum viable group size of 7 individuals for *Colobus* and 34 for *Piliocolobus*. This does
 417 not necessarily imply that 7 and 34 individuals are the lowest viable group sizes for *Colobus*
 418 and *Piliocolobus* respectively, but rather that they are more likely to occur at sites for which
 419 our model predicts maximum ecologically tolerably group sizes of 7 and 34 or more. Table
 420 Vb gives the results for each genus comparing the number of sites where the models correctly
 421 or falsely predicted each genus's presence or absence when we use these minimum viable
 422 group sizes. Fig. 6a and b show how accurately the time budget model predicted presence and
 423 absence of the genera at all the independent sites when we use the above cut-off group sizes.
 424 The locations of the sites have been superimposed on a map of Africa that includes estimates
 425 of current distributions (grey regions) from the African Mammal Databank (AMD - IEA
 426 1998, <http://www.gisbau.uniroma1.it/amd>). For both genera, the model provides a
 427 significantly better fit to the observed distribution than would be expected by chance
 428 (*Colobus*: $\chi^2_1 = 69.1$, $p < 0.0001$; *Piliocolobus*: $\chi^2_1 = 72.1$, $p < 0.0001$). Using these taxon-
 429 specific minimum group sizes significantly improves the fit of the two models (compare
 430 Table Va to Table Vb).

431 *Binary logistic models.* The time budget models differ from a more conventional
 432 regression model relating climate variables directly to presence/absence only in that they
 433 introduce an intermediate *behavioral* step (time budgets). All else equal, the two kinds of
 434 models should make exactly the same predictions from climate to presence/absence. The
 435 models based directly on climate alone (and using the complete database of presence and
 436 absence sites) selected the same independent variables as predictors for presence/absence as
 437 the time budget models did: the binary logistic analyses showed that *T* and *Fac1* were the
 438 main predictors of the presence of *Colobus* (total fit of this model 89.9%; $\chi^2_2 = 112.9$, $p <$
 439 0.0001); while for *Piliocolobus*, presence was best predicted using *T*, *Fac2*, and *Fac1* (total

440 fit of 82.7%; $\chi^2_3 = 59.1, p < 0.0001$). Thus the two approaches produce essentially the same
 441 results and we can be confident that the inclusion of an intermediate behavioral step in the
 442 time budgets models has not introduced any distortions.

443

444

Comparison between the two genera

445 We can now use our two models to investigate what determines the differences between
 446 the taxa. To do so, we can run an alternative variant of each model in which one of the
 447 equations has been exchanged for the corresponding equation of the other genus. This should
 448 tell us which of the time budget variables needs to change to cause *Colobus* to behave like
 449 *Piliocolobus*, and *vice versa*. For these purposes, we have focused on group sizes. To do so,
 450 we reran the basic models, altering the equations for feeding, moving and resting time one at
 451 a time. In each case, we simply used the equation for the other genus (as given in Table 3).
 452 Fig. 7 compares the average observed and predicted maximum ecologically tolerable group
 453 sizes for all genus-specific independent sites where each genus is present and absent in each
 454 variation of the models. Comparing the locations at which both species occur, both observed
 455 and predicted group sizes based on the basic model were significantly larger for *Piliocolobus*
 456 than for *Colobus* (Wilcoxon signed ranks test: Observed: $n = 6, Z = -2.2, p = 0.03$; Basic
 457 model: $n = 22, Z = -3.9, p < 0.0001$). The group sizes predicted by the models in which
 458 feeding, moving or resting time were altered differed significantly from those predicted by
 459 the respective basic models (Wilcoxon signed ranks test using locations where the genus is
 460 present: *Colobus*: $n = 68$, Feed: group sizes smaller than Basic, $Z = -5.1, p < 0.0001$, Move:
 461 group sizes smaller than Basic, $Z = -2.6, p = 0.009$, Rest: group sizes larger than Basic, $Z = -$
 462 $7.0, p < 0.0001$; *Piliocolobus*: $n = 32$, Feed: group sizes larger than Basic, $Z = -4.1, p <$
 463 0.0001 , Move: group sizes larger than Basic, $Z = -4.7, p < 0.0001$, Rest: group sizes smaller
 464 than Basic, $Z = -4.8, p < 0.0001$). However, it is obvious from Fig. 7 that the predicted group

465 sizes differ most strongly from those predicted by the basic model only when we use the
466 other genus's equation for resting time. This means that *Colobus* could live in larger
467 *Piliocolobus*-like groups if its resting time was less strictly constrained by leaf-feeding.

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DISCUSSION

471

472 We were interested in finding the behavioral and ecological constraints that explained
473 the differences between *Colobus* and *Piliocolobus* concerning group sizes and geographical
474 distribution. We used genus-specific systems models based on time constraints to do so.
475 Systems models of the kind developed here explicitly identify the biological pathways
476 through which purely ecological constraints produce their effects, and thus allow us to
477 identify the ecological chain of causes that influence a species' social system and
478 biogeography.

479 Although both models were significantly better than expected at predicting where
480 *Colobus* and *Piliocolobus* should and should not occur, both made errors. In some cases, false
481 predictions may be locations where colobines have (historically speaking) become extinct
482 only recently as a result of human disturbance. Alternatively, they may be a result of using
483 climate variables that are averaged across a long time span and/or across a relatively large
484 geographical area (note that a taxon's ability to survive in a habitat must depend on whether it
485 can cope with the worst years rather than the average or current year climatic conditions *per*
486 *se*). In addition, ground water and standing water, as well as soil quality, will always override
487 the relationships between climate and vegetation cover on the small scale even though on the
488 large (pan-African) scale they are subsumed within the error variance. Including them would
489 undoubtedly improve the predictive power of the models, but it would do so at the expense of

490 generalisability: it is not easy to illustrate (or, indeed, for us to understand) the output of
491 models that have more than a very small number of core driving variables.

492 The most important errors are the small number of cases where the model predicts
493 absence when the taxon is actually present (false negatives) and where the models predict
494 their presence (false positives) outside of their geographical range. Most false negatives
495 generated by the *Colobus* model were situated in East Africa: four were along the coast
496 (predicted group sizes 3-6) where moisture from the ocean probably influences vegetation;
497 three others (predicted group sizes 3-6) were at relatively high altitude locations in Ethiopia,
498 where climate predictions may not be precise enough to take into account the micro-climates
499 associated with individual mountains and, especially, sheltered valleys (*Colobus* used to be
500 widely distributed in the Ethiopian highlands, and in many of the areas where they do still
501 occur they tend to live in very small groups: Dunbar and Dunbar 1974; Dunbar 1987); three
502 other false negatives were in Kenya (predicted group sizes of 4-6). If predation levels are
503 low, viable group size may be smaller than 7 individuals, and the predicted maximum group
504 sizes of 3-6 for these false negatives may in fact be viable. Similarly, the *Piliocolobus* model
505 predicted the genus to be absent where they were actually present at only six locations. The
506 predicted maximum group sizes for these sites were 6-30.

507 More importantly, perhaps, most (8 of 11) of the false positives for *Colobus* were near
508 or inside their current, or most likely quite recent, distribution, and a 9th was on an island.
509 Note that two of our sites where *Colobus* is present fall outside of the distribution polygon
510 (obtained from the African Mammals Databank). The false positives produced by the
511 *Piliocolobus* model were again mostly within the geographical distribution of the species and
512 areas where they must have occurred previously, considering the isolation of some of the
513 small patches in which some populations are found today.

514 All things considered, the models did successfully predict a number of core aspects of
515 African colobine biogeography. The wider geographical distribution that we observe in
516 black-and-white colobus, for example, was supported by the models. Furthermore, despite the
517 use of relatively crude measures of climatic conditions to represent vegetation, these models
518 were extremely good at predicting the differences between these genera in both the typical
519 size of groups and the variability in group size.

520 Our analyses show that there are ecological constraints that limit maximum group sizes
521 in these two colobine genera. Comparison of observed maximum ecologically tolerable group
522 sizes with predicted maximum group sizes for individual populations suggested that
523 *Piliocolobus* live closer to, and more often exceed, their ecologically limiting group sizes
524 than *Colobus*. Bear in mind that these models simply specify the limiting group size within
525 which time budgets can be balanced, and that the actual average group size adopted by a
526 species is determined by the habitat-specific balance between predation risk and resource
527 defense, on the one hand, and time budget and other eco-physiological constraints on the
528 other (Dunbar 1996). One obvious reason why *Piliocolobus* might live closer to their
529 ecologically limiting group size is the high risk of predation that most populations of
530 *Piliocolobus* experience from chimpanzees (Boesch and Boesch 1989; Stanford 1995). The
531 largest observed groups of *Piliocolobus* (close to 100 individuals) are seen at Taï (Korstjens
532 2001), Kibale (Chapman pers comm), and Gombe (Clutton-Brock 1975), where they are
533 intensively hunted by chimpanzees. For reasons that are not entirely clear, *Colobus* seem to
534 be targeted much less often as prey by chimpanzees. In Taï, average annual capture rate
535 (percentage of individuals of the population that are captured each year by chimpanzees) is
536 3.2% for *Piliocolobus badius* and 1.4% for *Colobus polykomos* (Korstjens 2001).

537 These observations might tempt us to infer that reduced predation risk is the reason
538 why *Colobus* habitually live in smaller groups than *Piliocolobus*. However, our models

539 suggest that predation risk is not the only critical factor. To investigate the basis of the
540 differences between the genera, we developed alternative models for each genus in which we
541 manipulated only one of the time budget components at a time. The results showed that only
542 if we switch resting time around do maximum predicted group sizes for *Piliocolobus*
543 resemble those observed for *Colobus*, and vice versa. This analysis clearly shows that group
544 sizes of *Colobus* can be as large as those of *Piliocolobus* if they can reduce their required
545 resting time by feeding on more easily digestible foods. Thus, it is not just predation risk that
546 explains the difference in group sizes between these genera, but also resting-time constraints
547 as a result of food selection, presumably due to differences in digestive physiology. In
548 support of this conclusion we take the example of Nyungwe, where extremely large
549 aggregations of *Colobus* are observed, and where resting time is very low. Our analyses
550 indicate that the amount of forced resting time is strongly reduced here thanks to a high
551 protein to fiber ratio (Fimbel *et al.* 2001).

552 Body size may play a part in explaining the slight differences in diet between
553 *Piliocolobus* and *Colobus*. Indeed, the smallest extant colobine, the *Procolobus verus*,
554 depends entirely on carefully selected young leaves from a limited number of tree species
555 (Korstjens 2001; Oates and Korstjens in press). Body size further reduces predation risk and
556 directly affects thermoregulatory needs. The wider geographical distribution of *Colobus*
557 compared to *Piliocolobus* is related to the same effect: they can rely on less easily digested
558 fall-back foods by a simple increase in resting time at the cost of reduced group size.

559 In summary, it seems that time constraints do limit colobine group sizes and that the
560 differences between the genera are explained by the amount of resting time they require to
561 digest their fall-back foods. These system models, therefore, provide a powerful tool that
562 allows us to estimate maximum group sizes under current, past and future climate conditions

563 – something that may be of value both to palaeontologists and to conservationists (see
564 Cowlishaw & Dunbar 2000).

565

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566

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- 780

781 **Figure captions**

782

783 **Fig. 1.** Feeding time plotted against group size for *Colobus* (●) and *Pilio/ Procolobus* (□)
 784 [data from Table IIb].

785 **Fig. 2.** Flowchart for (a) the *Colobus* and (b) the *Piliocolobus* time budget models.

786 **Fig. 3.** Predicted versus observed average and maximum group sizes for *Colobus*.

787 **Fig. 4.** Predicted versus observed average and maximum group sizes for *Piliocolobus*.

788 **Fig. 5.** Accuracy of the models in predicting presence and absence (cumulative percentage
 789 correct) plotted against predicted group sizes for the African primate sites.

790 **Fig. 6.** Accuracy of the model in predicting presence where present (●) or where absent (false
 791 positive: ○) and absence where absent (▲) or actually present (false negative: △) for (a)
 792 *Colobus* and (b) *Piliocolobus*.

793 **Fig. 7.** Maximum group sizes at independent sites where the genera are present or absent
 794 predicted by the basic model (Basic) compared both with models in which the equations for
 795 Feed, Move or Rest have been exchanged between the genera and with observed group sizes
 796 for (a) *Colobus* and (b) *Piliocolobus*. In each case, only one equation is exchanged at a time.
 797 The plots give the median (line inside boxes), 25th - 75th percentiles (box), 10th/ 90th
 798 percentiles (whiskers), 5th/ 95th percentiles (dots)

799

800 **Table I.** Location and climate for the different field sites from which behavioral ecological information was obtained

Label	Country	Study site	Lat	Lon	Alt	<i>P</i>	<i>T</i>	<i>Fac1</i>	<i>Fac2</i>	<i>T_{moSD}</i>	P/F
Ca_DE	Cameroon	Lombe, Douala-Edea	3.48	9.83	10	4000.00	25.50	1.183	-0.224	0.90	0.20
CI_Tai	Ivorycoast	Tai	6.17	-4.33	90	1891.80	25.85	0.953	0.204	0.88	
DC_Oka	DR Congo	Okapi WR, Ituri Forest	1.53	28.53	790	1802.00	23.33	1.551	0.523	0.36	0.51
DC_Sal	DR Congo	Botsima, Salonga	-1.25	22.00	525	1774.00	24.50	1.399	0.100	0.19	
Et_Bol	Ethiopia	Bole valley	9.42	38.55	1700	1105.00	19.50	0.381	-0.205	1.34	
Ga_lope	Gabon	Makande	0.67	11.90	275	1531.00	25.50	0.911	-0.098	1.15	
Gh_BF	Ghana	Boabeng-Fiema	7.72	-1.70	350	1250.00	26.30	0.428	0.007	1.22	
Ke_Kak	Kenya	Kakamega	0.32	34.87	1580	1859.00	22.00	1.541	0.024	0.67	
Ke_Nai	Kenya	Lake Naivasha	-0.75	36.33	1890	600.00	17.50	0.663	0.295	1.10	
Ke_TR	Kenya	Tana River	-1.92	40.83	30	466.00	27.20	-0.609	-0.0002	1.08	
Rw_Nyu	Rwanda	Nyungwe	-2.53	29.29	2297	1744.00	15.25	1.300	0.0474	0.54	0.91
Se_Fat	Senegal	Fathala	13.65	-16.83	21	1050.00	28.00	-1.058	-1.326	1.23	
SL_Tiw	Sierra Leone	Tiwai	7.52	-11.33	103	2708.00	27.50	0.855	-0.365	1.46	0.35
Ta_Gom	Tanzania	Gombe	-4.67	29.65	1524	1390.36	23.50	0.416	-0.294	0.62	
Ta_Zan	Tanzania	Zanzibar	-6.27	39.42	13	1400.00	26.00	-0.084	-0.068	1.42	
TG_Abu	The Gambia	Abuko	13.40	-16.50	10	1124.00	25.00	-1.020	-1.271	1.24	
Ug_Cho	Uganda	Chobe, Kabalega NP	2.25	32.15	945	1200.00	24.45	0.706	0.209	0.87	
Ug_Kib	Uganda	Kibale	0.22	30.40	1500	1702.92	20.18	.99742	-0.0483	0.70	0.51
Ca_KL	Cameroon	Kilum-Ljim	6.25	10.43	2506	2910	18.70	1.12	-0.424	1.06	0.69
Mw_Zom	Malawi	Zomba	-15.33	35.32	1800	2014	23.20	0.052	-0.567	2.41	0.42

801

802 For sources see Table II; climate values also came from Willmottt and Matsuura's global climate dataset as described in the methods

803 section. Lat = Latitude; Lon= longitude; *T/ P* = average annual Temperature (in °C) and Rainfall (in mm); P/F=protein to fiber ratio (Fimbel *et*804 *al.* 2000; Beeson and Lea 1994); *T_{moSD}*= variation in monthly temperature; *Fac1/Fac2*=climate factors extracted using principal component

805 analysis (see methods).

806 **Table IIa.** Behavioral ecology information for *Colobus*

Site	Species	N	AF	AM	BM	BF	BN	Feed	Move	Rest	Social	Frt tot	Seed	Lf tot.	Ly	Lm	Flower
Ca_DE ¹	<i>Satanas</i>	12.00	6.00	2.30	10.40	7.42	95.17	22.49	3.63	54.19	13.60	51.02	51.02	43.10	20.40	19.70	
CI_Tai ²	<i>Polykomos</i>	15.00	5.00	1.00	9.90	8.30	85.53	30.75	13.31	54.85	6.29	48.30		48.50	28.30	19.90	2.70
DC_Oka ³	<i>Angolensis</i>	18.00	7.00	3.50	9.68	7.57	125.68	26.23	24.26	43.61	5.25	24.60	22.00	57.90	26.20	3.80	2.90
DC_Oka ³	<i>Guereza</i>	7.50	2.50	1.50	13.50	9.20	64.53	19.50	21.97	51.80	5.25	27.50	22.10	51.10	23.50	2.40	7.20
DC_Sal ⁴	<i>Angolensis</i>	5.00			9.68	7.57	33.45					66.70	49.90	27.40	21.00	6.40	5.90
Et_Bol ⁵	<i>Guereza</i>	6.76	1.81	1.27	13.50	9.20	52.97	16.47	9.42	70.74	3.29	28.33		70.40			1.30
Ga_Lop ⁶	<i>Satanas</i>	11.75	6.00	3.33	10.40	7.42	105.36	25.00				47.53	34.63	39.95	28.90	3.00	9.03
Gh_BF ⁷	<i>Vellerosus</i>	18.33	5.83	4.33	8.50	6.90	112.37	23.70	14.60	59.10	2.60	16.00	8.00	74.00	40.00	34.00	6.00
Ke_Kak ⁸	<i>Guereza</i>	9.00	4.00	1.00	13.50	9.20	75.84	25.60	2.30	63.35	7.80	38.55	1.20	52.75	20.40	6.60	.14
Ke_Nai ⁹	<i>Guereza</i>	19.00	3.00	2.00	13.50	9.20	108.51	30.00						69.00			
Rw_Nyu ¹⁰	<i>Angolensis</i>	300.0			9.68	7.57	2006	42.00	20.00	32.00	5.00	17.00		72.00	30.90	39.80	5.00
SL_Tiw ¹¹	<i>Polykomos</i>	12.50	4.00	3.00	9.90	8.30	91.34	28.20	9.00	61.40	1.00	36.00	33.00	57.00	30.00	27.00	3.00
Ug_Cho ¹²	<i>Guereza</i>	7.00	4.00	1.00	13.50	9.20	70.16	13.20		70.10		9.05		69.45	32.40	19.00	13.95
Ug_Kib ¹³	<i>Guereza</i>	8.00	3.37	1.18	13.50	9.20	69.59	30.31	7.32	55.93	12.20	15.20		85.53	72.60	3.60	2.17

807

808 Note: For site labels see Table I. *N* = group size; AF/AM = number of adult females/ males in the study group; BM/BF=body mass of AM/AF;809 *BN* = biomass of study group; Feed/Move/Rest/Social = % of daytime individuals spent feeding/moving/resting/ socializing. Frt tot/ Seed/ Lf tot/810 Ly/ Lm/ Flower = % of feeding time spent consuming fruits (incl. seeds)/ seeds only/ leaf material/ young leaves/ mature leaves/ or blossom. ¹811 McKey *et al.* 1981; McKey and Waterman 1982; ² Korstjens & Noë unpublished, Korstjens 2001; ³ Bocian 1997, some values are averages for812 two groups for each species; ⁴ Maisels *et al.* 1994; ⁵ Dunbar and Dunbar 1974; ⁶ Oates 1994; Tutin *et al.* 1997; Fleury and Gautier-Hion 1999,813 averages for five groups studied in and around the Lope reserve; ⁷ Teichroeb *et al.* 2003, P. Sicotte pers. comm., averages for three groups; ⁸814 Fashing 2001b, 2001a, pers. comm., averages for two groups; ⁹ Rose 1978; ¹⁰ Fimbel *et al.* 2001; ¹¹ Dasilva 1989; Whitesides 1989; Oates 1994,

815 averages for two study groups; ¹² Oates 1977b; Oates 1977a; ¹³ Onderdonk and Chapman 2000; Rode *et al.* 2003, C. Chapman pers. comm.,
 816 averages for 5 groups at sites near and in Kibale National Park.

817

818

819 **Table IIb.** Behavioral ecology information for *Piliocolobus*

Site	Species	Grpsz	AF	AM	BM	BF	BN	Feed	Move	Rest	Social	Frt tot	Seed	Lf tot.	Ly	Lm	Flower
CI_Tai ¹	<i>badius</i>	52.00	18.50	10.50	8.36	8.21	334.89	44.90	18.90	29.90	6.30	28.80	30.80	49.60	46.00	3.50	19.50
DC_Sal ²	<i>tholloni</i>	60.00			10.50	7.00						37.90		60.70	54.30	6.40	1.40
Ke_TR ₈₀ ³	<i>ruformitratus</i>	13.15	5.83	1.00	9.67	7.21	79.45	27.28	22.23	48.50	1.98	22.68		59.35	53.48	1.98	16.65
Se_Fat ⁴	<i>ruformitratus</i>				9.67	7.21	190.96					35.90	25.30	46.90	24.00	5.40	8.70
SL_Tiw ⁵	<i>badius</i>	33.00	13.00	7.00	8.30	8.20	232.76	37.00	5.00	55.00	3.00	31.30		51.90	31.70	20.20	16.10
Ta_Gom ₉₀ ⁶	<i>tephrosceles</i>	23.00	11.20	6.00	10.50	7.00	166.80	29.05	13.11	48.20	10.14	24.63		72.20			
Ta_Zan ⁷	<i>kirkii</i>	26.95	10.10	2.03	5.80	5.46	104.83						2.85				
TG_Abu ⁸	<i>temminckii</i>	26.20	10.75	2.00	6.50	6.50	125.45	21.30	12.50	52.10	12.60	41.65		46.86	34.90	11.40	8.70
Ug_Kib ₉₀ ⁹	<i>tephrosceles</i>	36.00			10.50	7.00	222.06	46.29	13.57	35.57		7.22	30.80	86.08	75.03	8.40	2.18

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821 ¹ McGraw 1998; Korstjens 2001; ² Maisels *et al.* 1994; ³ Decker 1994, average for three groups; ⁴ Gatinot 1978; ⁵ Oates 1994; Davies *et al.*
 822 1999; ⁶ Stanford 1998; ⁷ Siex and Struhsaker 1999; ⁸ Starin 1991; ⁹ Chapman and Chapman 2000; Onderdonk and Chapman 2000; Gillespie and
 823 Chapman 2001; Chapman and Chapman 2002; Chapman *et al.* 2002b; Rode *et al.* 2003, averages for 2 groups at Kanyawara,

824

825 **Table III.** The equations used in the time budget models

	Equation	R²_{adj}	(df)F	P
<i>Colobus</i>				
Feed	[a] $2.455+9.075*\ln(N)$ <i>excluding Nyungwe</i>	0.364	(9)5.16	0.049
	[b] $10.172+5.832*\ln(N)$ <i>including Nyungwe</i>	0.630	(10)17.02	0002
Move	[a] $10.519+17.421*Fac2$ <i>excluding Nyungwe</i>	0.526	(6)6.66	0.042
	[b] $11.484+18.238*Fac2$ <i>including Nyungwe</i>	0.458	(7)5.92	0.045
Leaf	$134.195-2.361*T-21.668*Fac1$	0.427	(2,10)5.48	0.025
Rest_{extra}	[b] $-53.265+2.544*T$ <i>including Nyungwe</i>	0.545	(9)10.79	0.009
<i>Piliocolobus</i>				
Feed	$-7.752 + 13.653*\ln(N) + 11.759*Fac2$	0.822	(2,3)12.52	0.035
Move	$20.202+0.0570*BN-0.0110*P$	0.839	(2,3)14.00	0.030
Rest_{extra}	$-50.383+41.597* T_{moSD}$	0.709	(4)9.74	0.036
Leaf	$175.424-4.609*T$	0.730	(7)16.25	0.007
Generic				
Rest_{forced}	$14.0753+0.6513*Leaf$			
Social	$3.037+0.159*N$			
Prot/Fibre	$1.630-0.0509*T$	0.848	(5)27.8	0.003

826

827 Feed/Move/Social=average % time spent feeding/moving/socializing in the annual time

828 budget; Rest_{forced}=resting time enforced on animals purely as a result of eating leaves, this

829 equation is based on a inter-generic comparison that included colobines and their closest

830 relatives guenons (see methods); Rest_{extra}=the part of the observed resting time that is left831 after deducting Rest_{forced} from observed resting time; the equation for social time is based on

832 an inter-generic analysis of social time in old-world primates (see methods); Leaf=average %

833 of feeding time spent on foraging for leaves; Prot/ Fibre=protein to fibre ratio. *N*=group size;834 *BN*=group biomass; *P*=average annual rainfall (in mm); *T*= average annual temperature (in835 °C); *T_{moSD}*= variation in monthly temperature; *Fac1/Fac2*=climate factors extracted using

836 principal component analysis (see methods).

837 **Table IV.** Predicted maximum group sizes according to the *Colobus* (a) and *Piliocolobus* (b)
 838 model under different combinations of core climatic variables (average annual rainfall and
 839 temperature)^a

Rainfall (mm)	Temperature (°C)								
	0	5	10	15	20	25	30	35	40
100	0	0	0	0	0	1	2	5	9
500	0	0	0	0	1	3	5	9	15
900	0	0	0	1	3	5	9	15	25
1300	0	0	1	3	5	9	16	25	38
1700	0	1	3	5	10	16	26	38	54
2100	1	3	5	10	16	26	39	55	74
2500	3	6	10	17	27	40	56	75	96
2900	6	10	17	27	40	56	75	97	120

840

Rainfall (mm)	Temperature (°C)								
	0	5	10	15	20	25	30	35	40
100	0	0	0	0	0	0	0	0	1
500	0	0	0	0	0	0	0	4	38
900	0	0	0	0	0	0	8	51	64
1300	0	0	0	0	0	15	65	70	70
1700	0	0	0	0	23	76	76	76	76
2100	0	0	0	34	78	83	83	83	83
2500	0	3	44	63	85	90	90	90	90
2900	5	23	49	69	92	96	96	96	96

841 ^a The values for T_{moSD} were estimated with regression equations based on information from
 842 Willmott & Matsuura's database: ' $T_{moSD}=9.273-0.147*T-3.10e-03*P$ ', $r^2_{adj}=0.585$, $F_{(2,$
 843 $11668)}=8221$, $p<0.0001$. *Fac1* was estimated from information from the African primate sites:
 844 ' $Fac1=-0.552+0.00104*P-0.0291*T$ ', $r^2_{adj}=0.542$, $F_{(2,317)}=189.9$, $p<0.0001$. *Fac2* could not
 845 be predicted from rainfall and temperature so its median value (-0.174) was used.

846 **Table V.** Fit of the models when we use minimum viable group sizes (N) of 3 for *Colobus*
 847 and 4 for *Piliocolobus* (Va) and when we use 7 for *Colobus* and 34 for *Piliocolobus* (Vb)
 848 Table Va.

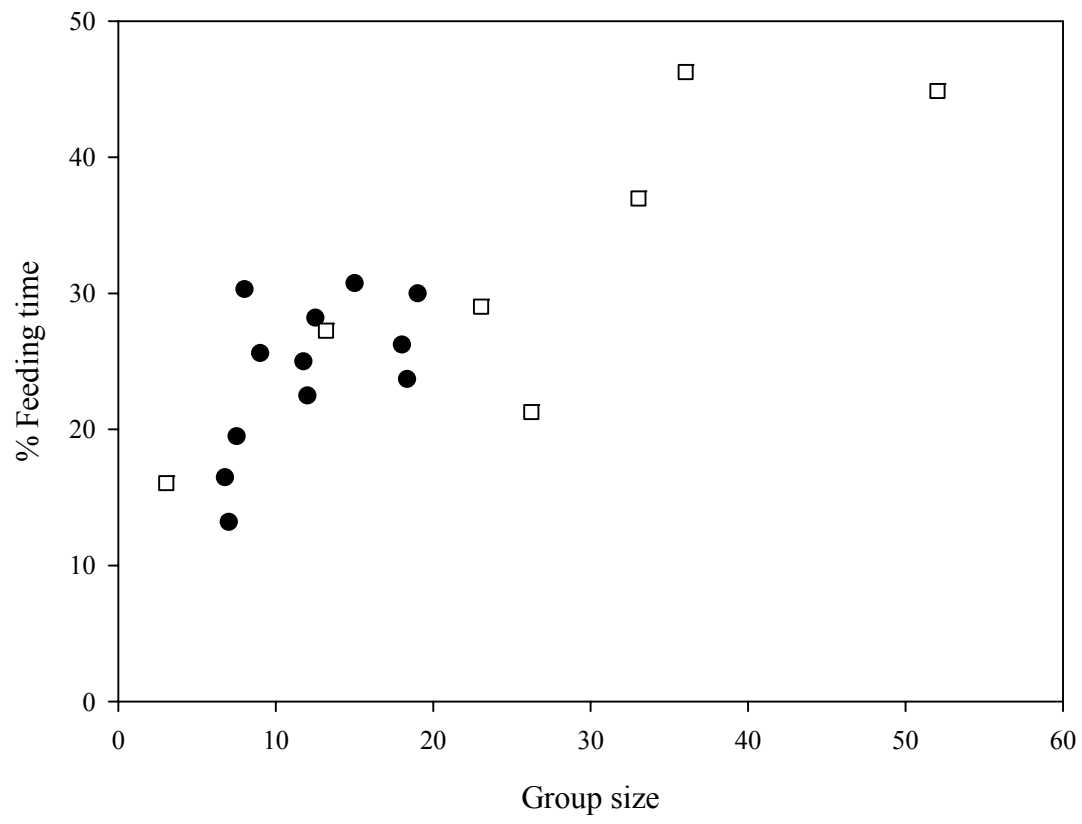
		<i>Colobus</i> Observed			<i>Piliocolobus</i> Observed		
		Absent	Present	<i>Overall</i>	Absent	Present	<i>Overall</i>
Predicted	Absent ($N < 3$)	47	0		Absent ($N < 4$)	64	1
	Present ($N \geq 3$)	33	68		Present ($N \geq 4$)	60	31
	Correct	58.8%	100%	77.7%	Correct	51.6%	96.9%

849
 850 Table Vb.

		<i>Colobus</i> Observed			<i>Piliocolobus</i> Observed		
		Absent	Present	<i>Overall</i>	Absent	Present	<i>Overall</i>
Predicted	Absent ($N < 7$)	69	10		Absent ($N < 34$)	105	6
	Present ($N \geq 7$)	11	58		Present ($N \geq 34$)	19	26
	Correct	86.3%	85.3%	85.8%	Correct	84.7%	81.3%

851

852 **Fig. 1.**



854 **Fig. 2a.**

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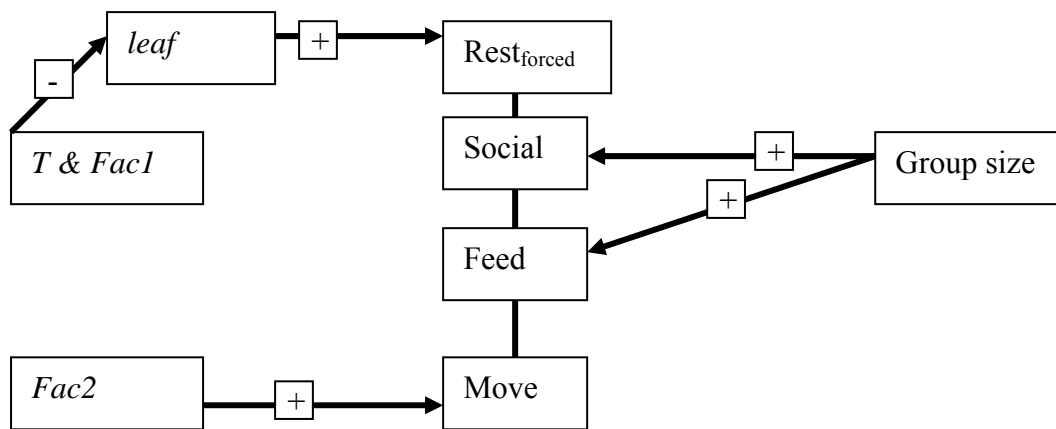
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864 **Fig. 2b.**

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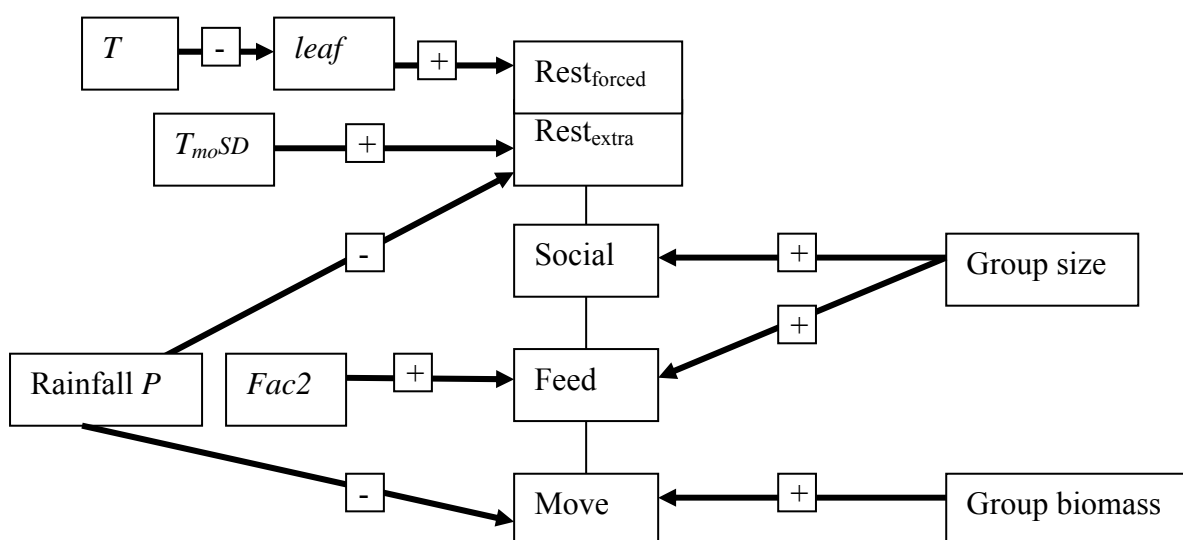
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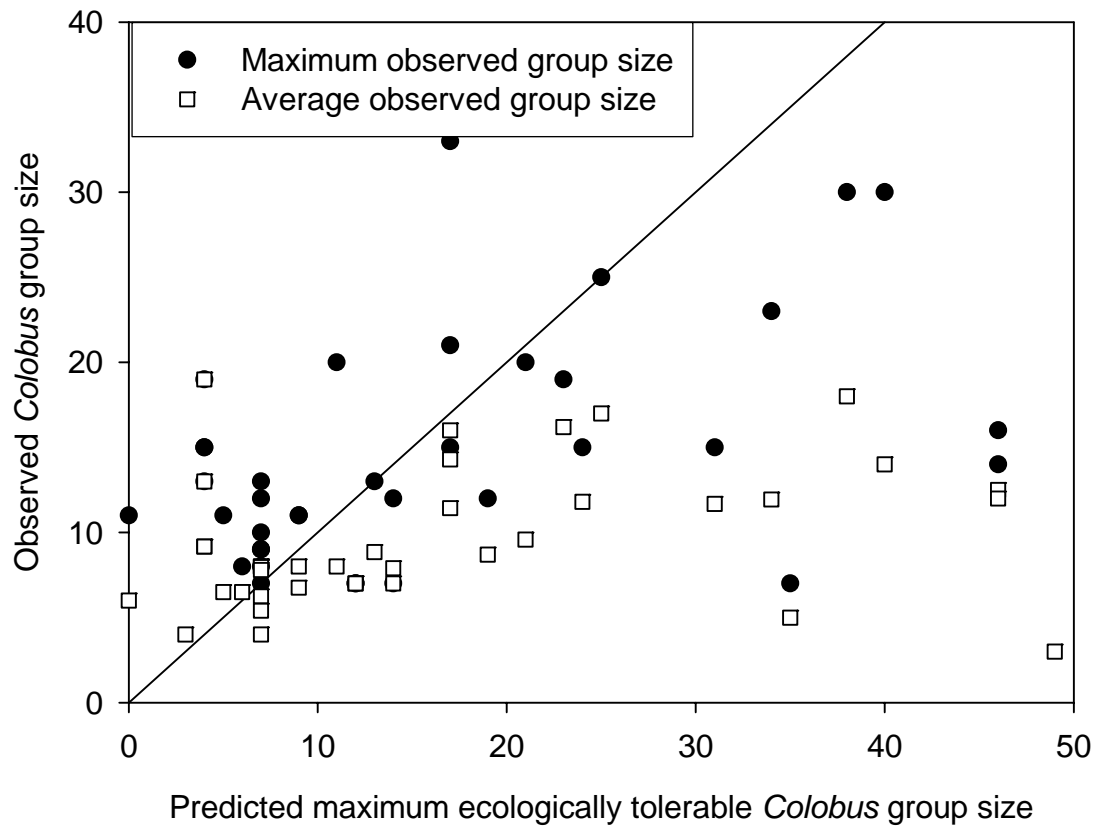
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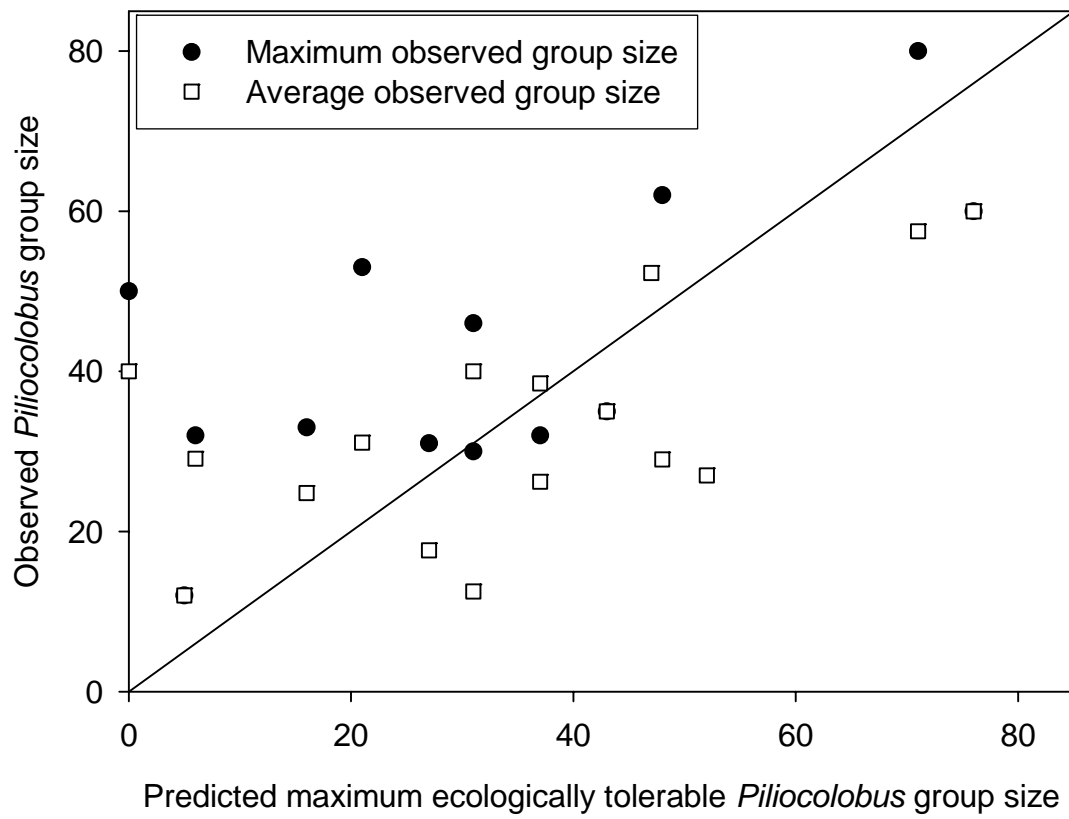
876 **Fig. 3.**



877

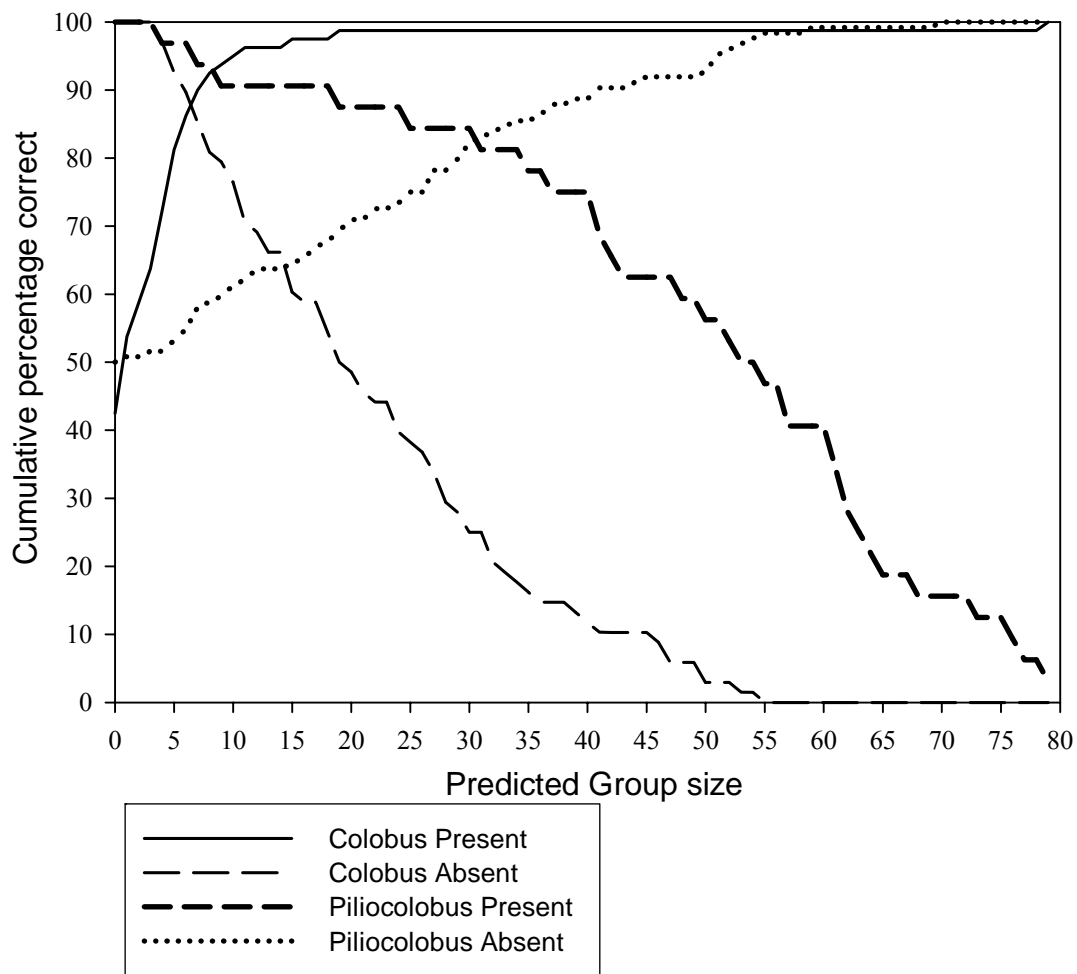
878

879 **Fig. 4.**



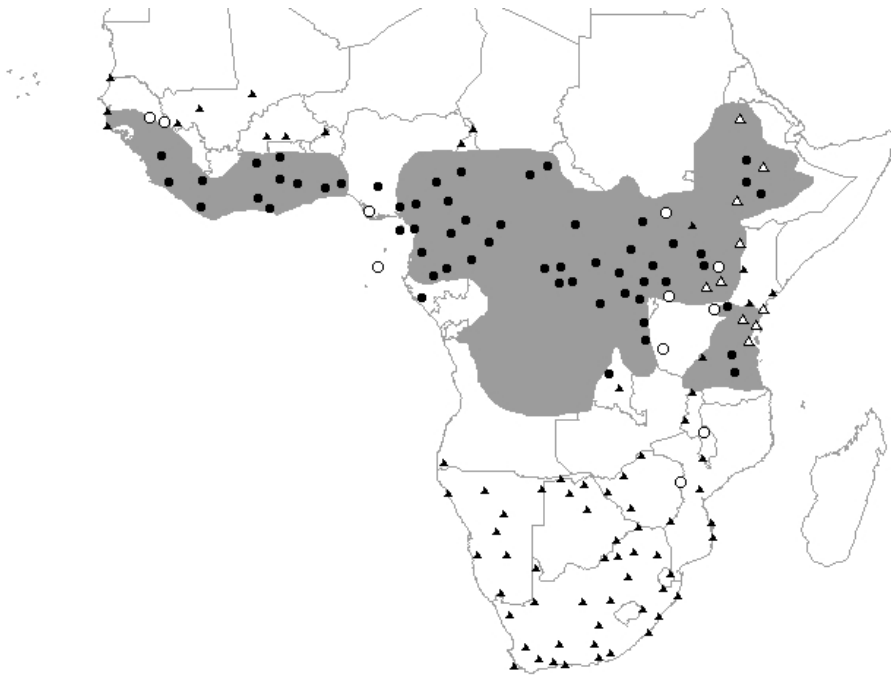
880

881 Fig. 5:

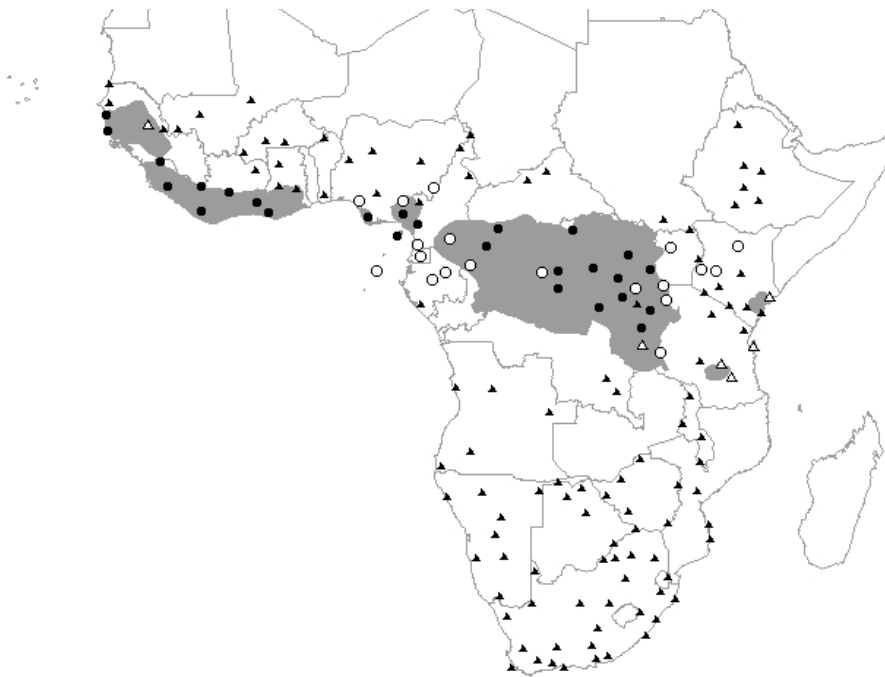


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883 Fig. 6a:



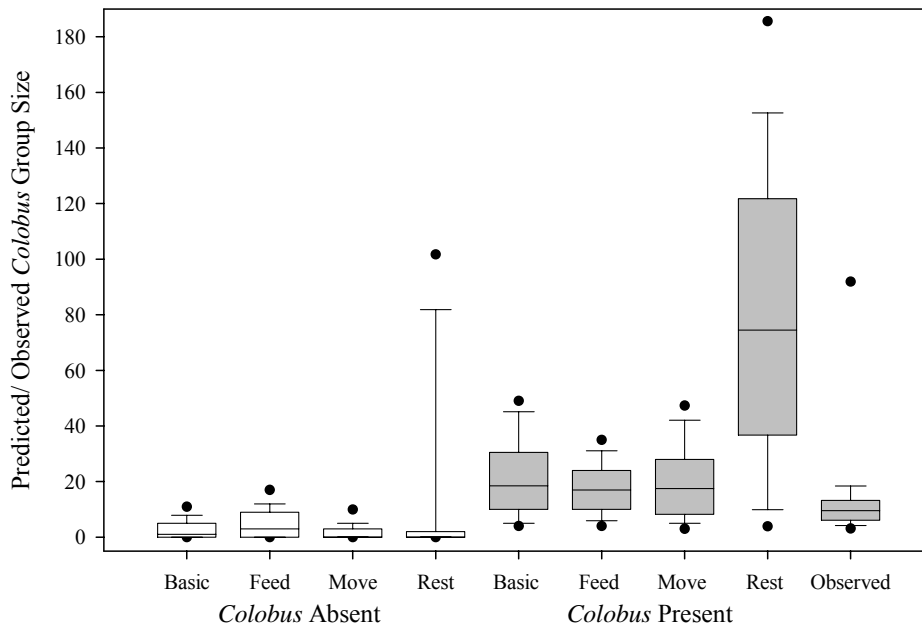
884
885 Fig. 6b.



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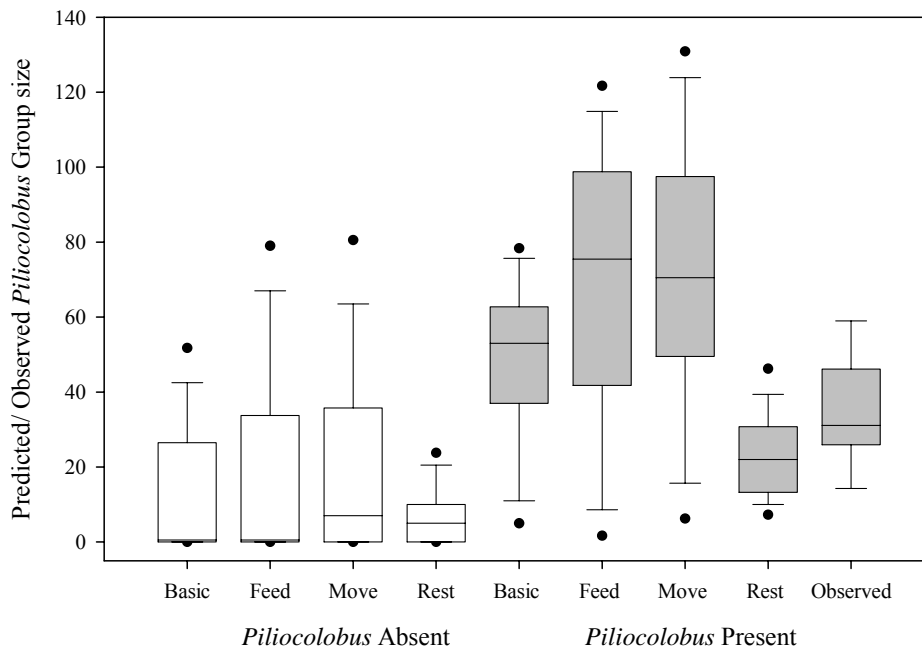
887

888 **Fig. 7a.**



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890 **Fig. 7b.**



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