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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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23 <u>Short title</u>: 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   <u>Keywords</u>: socio-ecology, systems model, *Colobinae*, geographical distribution, costs and

42   benefits of group living

43   **INTRODUCTION**

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45   The size of groups in which animals come together is a site- and species-specific trade-

46   off between the costs and benefits of group living (Alexander 1974; Clutton-Brock and

47   Harvey 1977; van Schaik *et al.* 1983; Terborgh and Janson 1986; Wrangham *et al.* 1993). A

48   major cost of living in a group is intra-group food competition (Dittus 1977; Whitten 1983;

49   Watts 1985; van Schaik and van Noordwijk 1988). An increase in intra-group food

50   competition with increasing group size can be recognized by an increase in the distance that

51   an animal travels each day to find sufficient food patches to meet its energetic requirements

52   and an increase in home range size (Clutton-Brock and Harvey 1977; Harvey and Clutton-

53   Brock 1981; Janson 1988; Wrangham *et al.* 1993; Janson and Goldsmith 1995; Lewis *et al.*

54   2001). Furthermore, feeding and foraging time may increase as per capita food quality

55   diminishes with increasing number of competitors, and per capita moving time may increase

56   as food patches get depleted (Caraco 1979; van Schaik *et al.* 1983; Janson and van Schaik

57   1988; Isbell 1991; Janson and Goldsmith 1995). In addition, in order to minimize the chance

58   that groups split up due to aggression within the group, animals need to invest time in

59   affiliating with other group members (Dunbar 1991). Thus, the costs of living in groups

60   should be reflected in the time that animals allocate to different activities during the day and

61   the distance they travel (Janson 1988; Dunbar 1992b; Dunbar 1992a; Janson and Goldsmith

62   1995). This direct relationship, however, is only expected to be detectable if there is no

63   difference in the quality and density of food between the area occupied by a larger group and

64   that occupied by a smaller group (Gillespie and Chapman 2001). Therefore, in order to

65   understand the relationships between group size and time allocations, we need to correct for

66   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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109   **METHODS**

110

111   **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, $T_{mo}SD$) and in mean

126   monthly rainfall (measured as Shannon's diversity index across the 12 calendar months,

127     $P_{mo}SH$), 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   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: $T_{mo}SD$, $P_{mo}SD$, *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 $T_{mo}SD$ 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 $T_{mo}SD$ (*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.

164

165   **The model**

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.

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

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):

215   *Social time(%) = 3.037+0.1597*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: *Group mass = 6.871*Group size* for

237   *Colobus* and *Group mass = 6.120*Group size* for *Piliocolobus*.

238

239   **Testing the models**

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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 WMCM 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 *Piliocolobus*, 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.

271

272   **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, $p > 0.1$, $n = 6\text{-}13$). 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.

289

290

291 **RESULTS**

292

293 **The basic models**

294   Feeding time correlated positively with group size in each genus separately

295 (*Colobus$_{excl.\ Nyungwe}$*: $n = 11$, $r = 0.550$, $p = 0.080$; *Colobus$_{incl.\ Nyungwe}$*: $n = 12$, $r = 0.700$, $p = $

296 0.011; *Piliocolobus*: $n = 6$, $r = 0.776$, $p = 0.070$, for biomass of group: $r = 0.892$, $p = 0.041$)

297 and when we look at the combined data for the three colobine genera (including olive colobus

298 from Taï; $r = 0.805$, $p < 0.001$, $n = 18$; Fig. 1). This suggests that foraging effort increases

299 with group size.

300   The best-fit multivariate equations are given in Table III and produce the models

301 depicted in Fig. 2a and 2b. For the basic model of *Colobus* (straight bold lines in Fig. 2a), we

302 used only the equations (identified as [a] in Table III) that were obtained while excluding the

303 extremely large group sizes of Nyungwe because this site was an extreme outlier (and hence

304 could easily distort equations). Feeding time increased with group size in both species, but

305 only in *Piliocolobus* did we have to include a climatic factor (i.e. rainfall variability/

306 seasonality) for the best result. In *Colobus* moving time was explained by rainfall variability

307 while in *Piliocolobus* both rainfall and group size had an important effect. This suggests that

308 *Colobus* do not move more as a result of increased intra-group food competition, while

309 *Piliocolobus* does. Temperature was an important variable for both species. Only in *Colobus*

310 did the relative moisture and evaporation play an important role.

311   The equation of forced resting time from our comparison of guenons and colobines was

312 strongly correlated to observed resting time ($r = 0.673$, $p = 0.033$, $n = 10$). In *Piliocolobus*,

313 however, it turned out that four observed values of resting time were lower than those

314 predicted by this equation (Wilcoxon Signed Ranks test, $n = 6$, $Z = -1.12$, ns). Therefore, we

315   first removed the intercept from the $Rest_{forced}$ equation and investigated what explained the

316   variation in 'extra' resting time ($Rest_{extra}$=observed resting time minus $Rest_{forced}$). 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 $Rest_{forced}$ and $Rest_{extra}$ 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.*

336

337   **Predicted and observed group sizes**

338   The predicted group sizes for *Colobus* correlated with maximum observed group sizes

339   ($n = 37$, $r = 0.467$, 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*: χ^2_1 = 69.1, *p* < 0.0001; *Piliocolobus*: χ^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%; χ^2_2 = 112.9, *p* <

439   0.0001); while for *Piliocolobus*, presence was best predicted using *T*, *Fac2,* and *Fac1* (total

17

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

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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.

468

469

470   **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

21

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).

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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), $10^{th}/ 90^{th}$

798 percentiles (whiskers), $5^{th}/ 95^{th}$ 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	*P*	*T*	*Fac1*	*Fac2*	$T_{mo}SD$	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	Taï	6.17	-4.33	90	1891.80	25.85	0.953	0.204	0.88	
DC_Oka	DRCongo	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); $T_{mo}SD$= 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]	*Satanas*	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]	*Polykomos*	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]	*Angolensis*	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]	*Guereza*	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]	*Angolensis*	5.00			9.68	7.57	33.45					66.70	49.90	27.40	21.00	6.40	5.90
Et_Bol[5]	*Guereza*	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]	*Satanas*	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]	*Vellerosus*	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]	*Guereza*	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]	*Guereza*	19.00	3.00	2.00	13.50	9.20	108.51	30.00						69.00			
Rw_Nyu[10]	*Angolensis*	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]	*Polykomos*	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]	*Guereza*	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$_{90}$[13]	*Guereza*	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. [1]

811 McKey *et al.* 1981; McKey and Waterman 1982; [2] Korstjens & Noë unpublished, Korstjens 2001; [3] Bocian 1997, some values are averages for

812 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; [8]

814 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]	*badius*	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]	*tholloni*	60.00			10.50	7.00						37.90		60.70	54.30	6.40	1.40
Ke_TR₈₀[3]	*ruformitratus*	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]	*ruformitratus*				9.67	7.21	190.96					35.90	25.30	46.90	24.00	5.40	8.70
SL_Tiw[5]	*badius*	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_Gom₉₀[6]	*tephrosceles*	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]	*kirkii*	26.95	10.10	2.03	5.80	5.46	104.83						2.85				
TG_Abu[8]	*temminckii*	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_Kib₉₀[9]	*tephrosceles*	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

820

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	R^2_{adj}	$_{(df)}F$	P
	Colobus			
Feed	[a] $2.455+9.075*\ln(N)$ *excluding Nyungwe*	0.364	$_{(9)}5.16$	0.049
	[b] $10.172+5.832*\ln(N)$ *including Nyungwe*	0.630	$_{(10)}17.02$	0002
Move	[a] $10.519+17.421*Fac2$ *excluding Nyungwe*	0.526	$_{(6)}6.66$	0.042
	[b] $11.484+18.238*Fac2$ *including Nyungwe*	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] $-53.265+2.544*T$ *including Nyungwe*	0.545	$_{(9)}10.79$	0.009
	Piliocolobus			
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$_{extra}$	$-50.383+41.597*T_{mo}SD$	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 left

831 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 (in

835 °C); $T_{mo}SD$= 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 $T_{mo}SD$ were estimated with regression equations based on information from

842 Willmott & Matsuura's database: '$T_{mo}SD=9.273-0.147*T-3.10e\text{-}03*P$', r^2adj=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^2adj=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.

		Colobus Observed				*Piliocolobus* Observed		
		Absent	**Present**	*Overall*		**Absent**	**Present**	*Overall*
Predicted	**Absent** (*N* <3)	47	0		**Absent** (*N* <4)	64	1	
	Present (*N* ≥3)	33	68		**Present** (*N* ≥4)	60	31	
	Correct	58.8%	100%	77.7%	**Correct**	51.6%	96.9%	60.9%

849

850 Table Vb.

		Colobus Observed				*Piliocolobus* Observed		
		Absent	**Present**	*Overall*		**Absent**	**Present**	*Overall*
Predicted	**Absent** (*N* <7)	69	10		**Absent** (*N* <34)	105	6	
	Present (*N* ≥7)	11	58		**Present** (*N* ≥34)	19	26	
	Correct	86.3%	85.3%	85.8%	**Correct**	84.7%	81.3%	84.0%

851

852   **Fig. 1**.
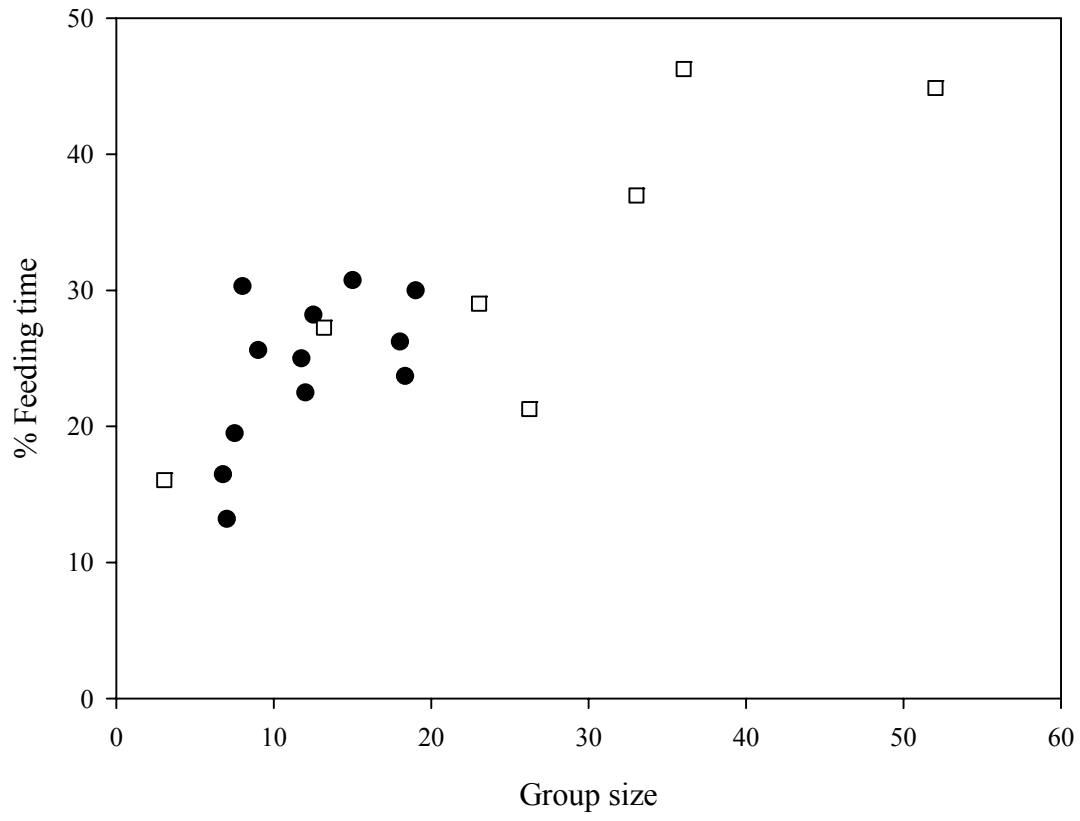
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854 **Fig. 2a**.

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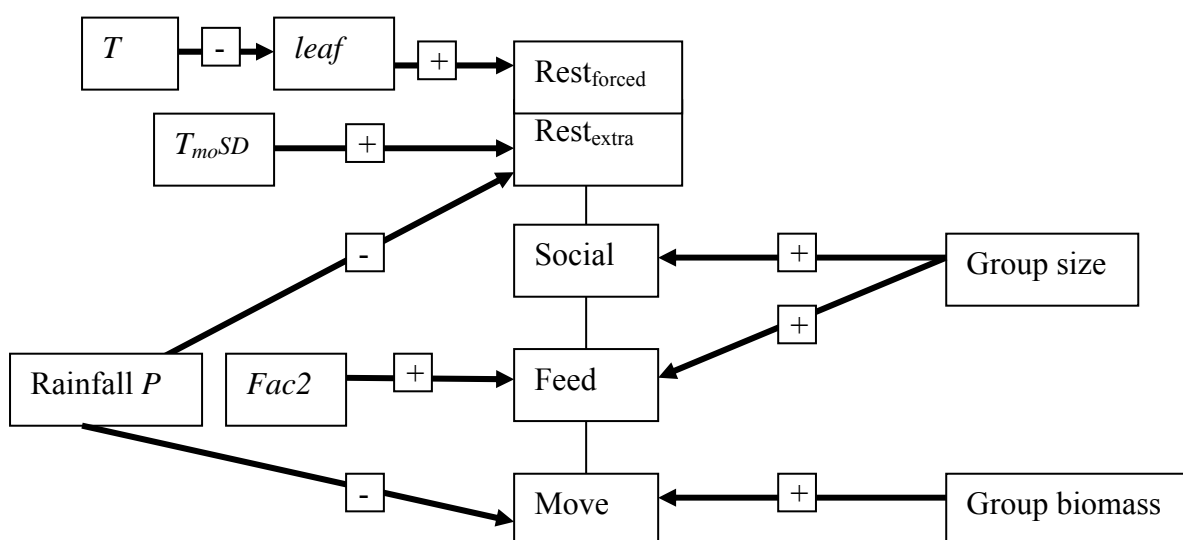860

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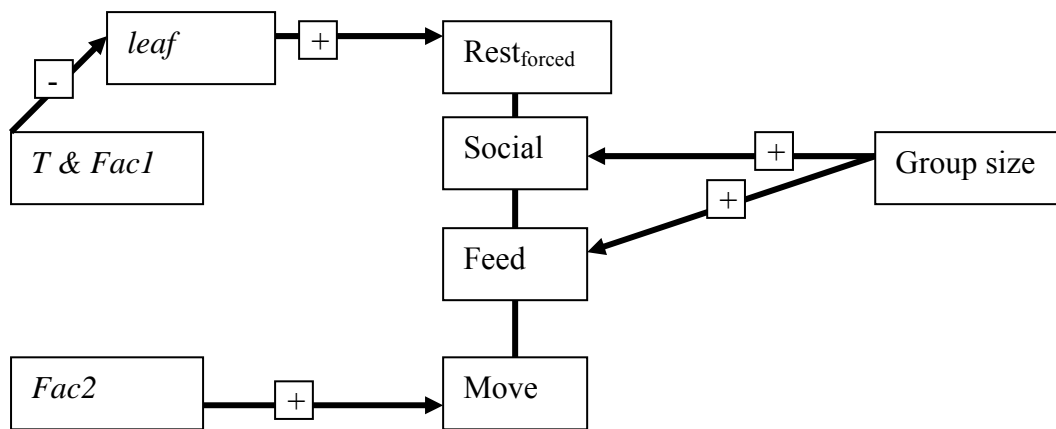
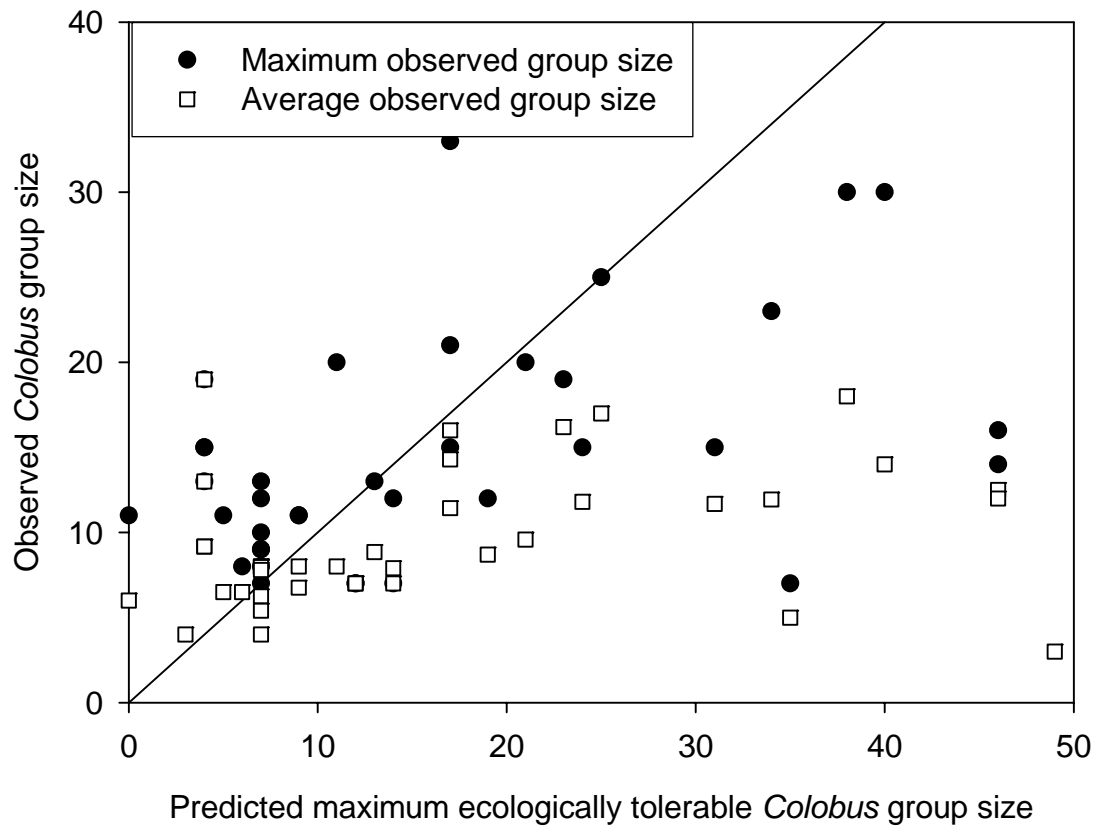864 **Fig. 2b**.

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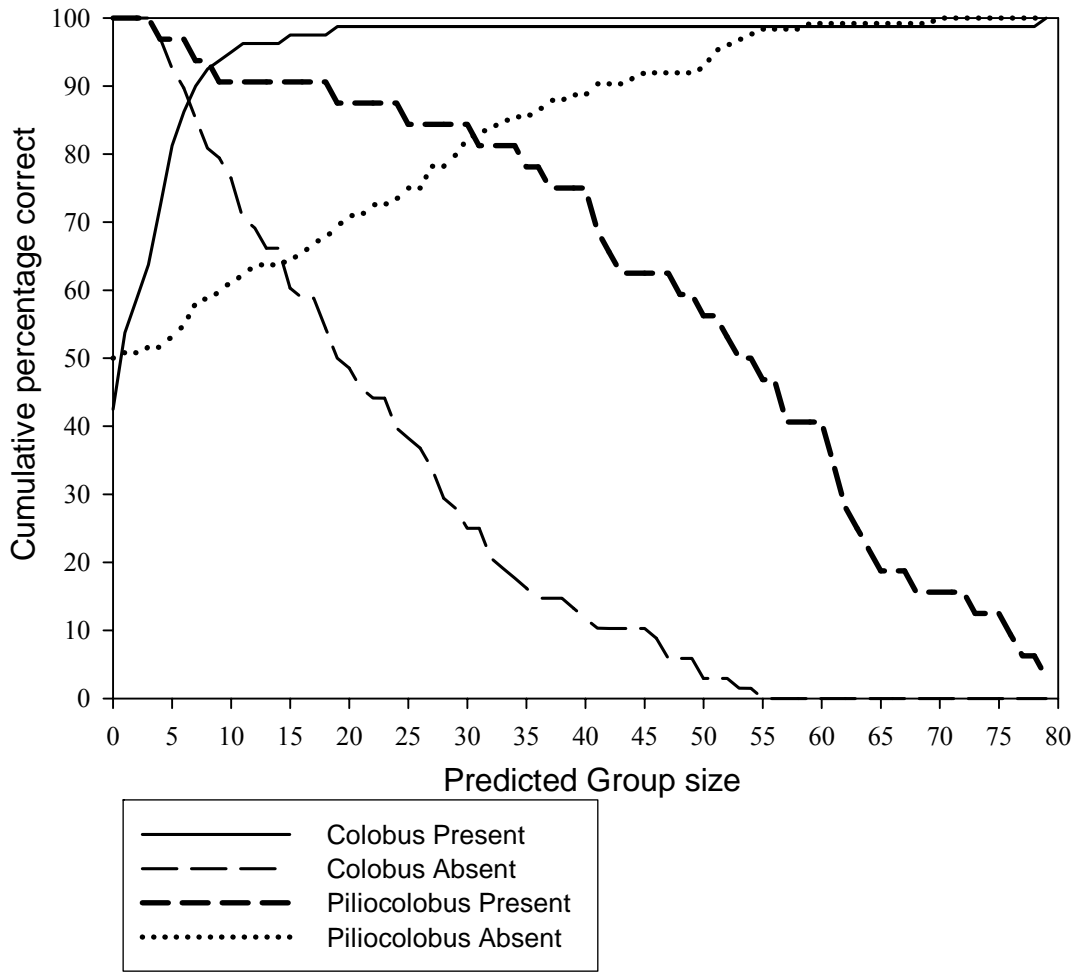
867
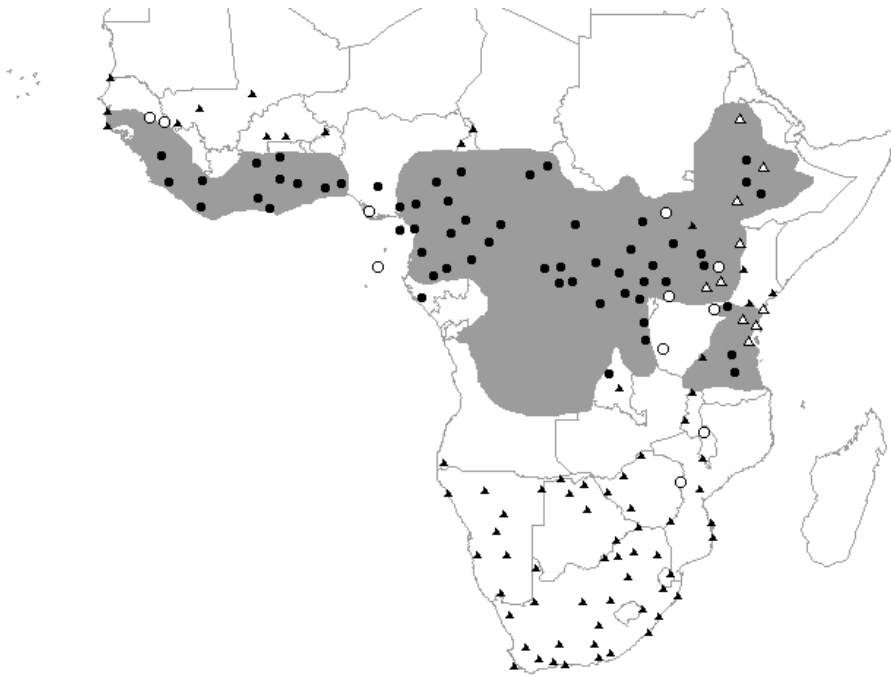
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876 **Fig. 3**.

877

878

879 **Fig. 4**.

880   Predicted maximum ecologically tolerable *Piliocolobus* group size
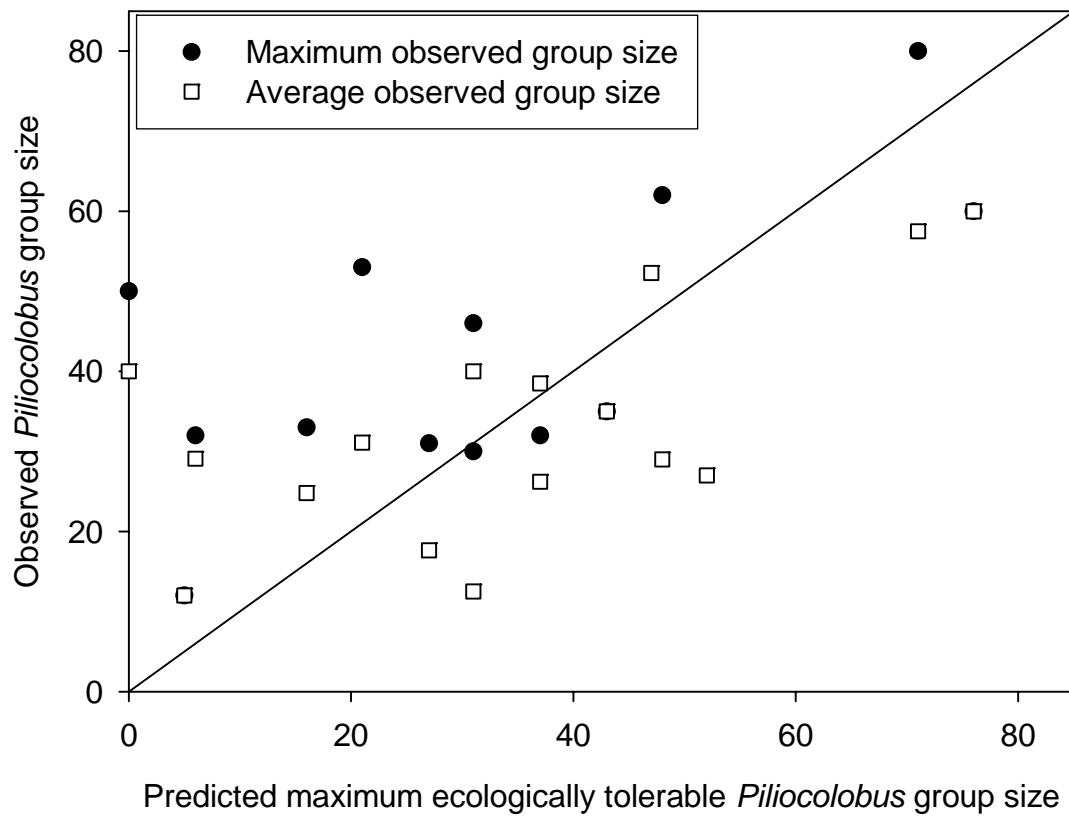
881   **Fig. 5**:
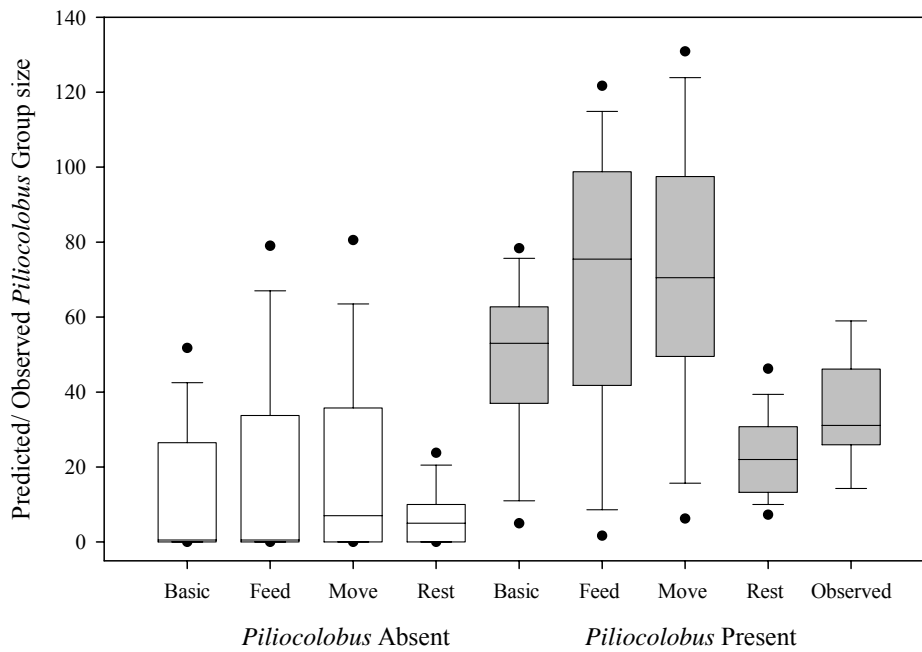

882

883   Fig. 6a:

884
885   **Fig.** 6b.

886

887

888   **Fig. 7a**.

889   *Colobus* Absent   *Colobus* Present

890   **Fig. 7b**.

891   *Piliocolobus* Absent   *Piliocolobus* Present

892

47