

Social and Ecological Correlates of Parasitic Infections in Adult Male Gray-Cheeked Mangabeys (*Lophocebus albigena*)

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19 **Abstract**

20 Intestinal parasites may constitute an important evolutionary and ecological force. Our aim
21 was to identify social, physiological, and environmental factors that correlate with intestinal
22 parasite infections in adult male gray-cheeked mangabeys (*Lophocebus albigena*). We
23 analyzed 102 fecal samples collected over 19 months from 18 adult males for the incidence
24 (proportions of samples with parasites) and intensity (total number of parasites per gram of
25 feces) of infection of nematodes relative to social status, fecal glucocorticoid and
26 testosterone metabolites, group size, and rainfall, all of which are factors that earlier studies
27 suggested can be important mediators of parasite load. Parasite incidence was greater in
28 immigrant males compared to low- and high-ranking males whereas parasite intensity was
29 greater in immigrant males and low-ranking males compared to high-ranking males. Fecal
30 samples with more parasites had higher concentrations of fecal glucocorticoid and
31 testosterone metabolites than fecal samples with fewer parasites. As immigrant males had a
32 greater incidence of parasites and higher concentrations of both metabolites than resident
33 males, this profile appears to fit immigrant males best. We also found higher nematode
34 intensities in mid-sized groups, and during periods with more rainfall. Our results suggest
35 that it will be fruitful for future studies to explore the role of immigrant males as spreaders
36 of intestinal parasites.

37

38 **Key words:** Nematodes, male rank, fecal glucocorticoids, fecal testosterone, immigrants,
39 helminths

40

41 **Introduction**

42 Parasitic diseases are known to play an important role in animal behavior, ecology,
43 and evolution (Huffman and Chapman 2009; Nunn and Altizer 2006). Intestinal parasites in
44 particular can be major mediators of animal overall body condition, as some are pathogenic
45 and reduce fitness (Huffman and Chapman 2009; Nunn and Altizer 2006). Within species
46 or social groups, parasite loads often vary systematically. Studies of marsupials (*Antechinus*
47 *stuartii*) (Bradley et al. 1980) and several other species of mammals (e.g., rodents: Jackson
48 and Farmer 1970; fur seals (*Arctocephalus forsteri*): Negro et al. 2010; yellow baboons
49 (*Papio cynocephalus*): Hausfater and Watson 1976; Muller-Graf et al. 1996; mandrills
50 (*Mandrillus sphinx*): Setchell et al. 2007, 2009) have shown that susceptibility to intestinal
51 parasites can correlate with the host's social and physiological condition. Parasitic
52 infections may be correlated, for example, with host social status, homeostatic imbalance
53 (stress), testosterone level, membership in particular groups, and group size.

54 The relationship between host social status and parasitic infection is complex
55 because these factors can also be influenced directly by the number of intraspecific contacts
56 and the effectiveness of immune defenses (Altizer et al. 2003; Muehlenbein 2009; Sapolsky
57 1993), which in turn may be influenced by diet and the nature of social contact. Usually,
58 social status is viewed as rank position within a hierarchy based on the outcome of
59 competition over desirable resources (Harcourt 1987; Pusey and Packer 1997; Whitten
60 1983) but it can also reflect the quality and quantity of previous interactions with others in
61 the group. Immigrants, for example, have a shorter history with their new groups and may
62 be especially challenged as they attempt to fit into the existing hierarchy. Variation in
63 parasitism is assumed to be strongly influenced by variation in social contact (Griffin and

64 Nunn 2012). Thus, if higher-ranking individuals experience more social contacts they may
65 be more exposed to parasites (Altizer et al. 2003; Møller et al. 1993; Nunn and Altizer
66 2006; Stuart and Strier 1995). Immigrants may also be more exposed to parasites as they
67 move from one group to another (Altizer et al. 2003; Møller et al. 1993). Whether high-
68 ranking individuals or immigrants are at greater risk of parasitic infections may also be
69 influenced by differential access to foods in their habitat. Higher-ranking individuals are
70 expected to have better access to high quality food that may help boost their immune
71 systems and thus their ability to fight parasitic infections whereas lower-ranking and
72 immigrant individuals may spend more time finding food, and may be more calorically
73 deprived (Sapolsky 2004), with immune systems less able to fight parasitic infections.

74 Challenging social interactions can be associated with long-term exposure to
75 stressors and coping mechanisms (McEwan and Stellar 1993; Sapolsky 2005), thus
76 affecting hormones that can also influence parasitic infections through their effects on the
77 immune system. Cortisol and testosterone are generally considered to suppress immune
78 function, making hosts less effective at controlling infections, including parasitic infections
79 (Bailey and Coe 1999; Braude et al. 1999; Friedman and Lawrence 2002; Muehlenbein
80 2006). In the case of cortisol, this may occur because although the stress response can be
81 adaptive for immediate threat, chronic stress is pathogenic (Munck et al. 1984). Thus, male
82 mandrills with higher glucocorticoids had a higher diversity of gastrointestinal parasites
83 (Setchell et al. 2010).

84 In the case of testosterone, while high testosterone levels may facilitate reproductive
85 effort by promoting competitive behavior and muscle anabolism (to aid in mate attraction
86 and competition with conspecifics), it also exhausts resources and inhibits immune

87 function, thus generating greater opportunities for parasitic infection and increasing
88 morbidity and mortality (Mougeot et al. 2006; Muehlenbein and Bribiescas 2005; Sheldon
89 and Verhulst 1996; Zuk 1996). Chimpanzees with higher testosterone levels had greater
90 parasite richness (number of species) (Muehlenbein 2006), and fur seals with high
91 testosterone levels had greater numbers of parasite eggs per gram of feces (Negro et al.
92 2010). In Grant's gazelles (*Nanger granti*), however, the relationship between testosterone
93 and parasitism varied depending on parasite species (Ezenwa et al. 2012).

94 Higher levels of testosterone and cortisol are often related to increased levels of
95 aggression in high-rank males (e.g. Arlet et al. 2009a; Barrett et al. 2002; Bercovitch 1993;
96 Cavigelli 2000; Kraus et al. 1999). A positive association between rank and testosterone
97 level was found in male rhesus macaques (*Macaca mulatta*: Bercovitch 1993; Rose et al.
98 1975), Japanese macaques (*M. fuscata*: Barrett et al. 2002), gray-cheeked mangabeys (Arlet
99 et al. 2011), and chimpanzees (*Pan troglodytes*: Muehlenbein et al. 2004). Thus given the
100 effect of testosterone on immune system suppression, one might expect higher-ranking
101 males to have greater parasite loads than lower-ranking males. Overall, among male
102 vertebrates, this seems to hold true with regard to gastrointestinal helminths (Habig and
103 Archie 2015). Among primates, chimpanzees at Ngogo, Uganda, are consistent with the
104 vertebrate pattern: high-ranking males have higher parasite richness than low-ranking males
105 (Muehlenbein 2006). Yellow baboons (*P. cynocephalus*) are also consistent, but only
106 during periods of dominance stability (Hausfater and Watson 1976). When the dominance
107 hierarchy was unstable, high-ranking males had lower egg emissions than low-ranking
108 males (Hausfater and Watson 1976). However, no association was found between rank and
109 parasitic infection in a different population of chimpanzees (Seraphin 2000) or in

110 populations of olive baboons (Muller-Graf et al. 1996), rhesus macaques (Gordon et al.
111 1976) and bonobos (*P. paniscus*: Sannen et al. 2004). In orangutans (*Pongo pygmaeus*),
112 mandrills, and red jungle fowl (*Gallus gallus*) dominant males exhibited high testosterone
113 levels and *low* parasite loads (Thompson et al. 2012; Setchell et al. 2009; Zuk 1996). This
114 may be because testosterone can increase immunocompetence for certain phenotypes
115 (Peters 2000).

116 To further complicate matters, while testosterone affects behaviors that can cause
117 stress, stress can also influence testosterone levels (Sapolsky 2004). In olive baboons the
118 response of testosterone to stress differed by rank. Testosterone decreased in subordinate
119 males during stressful situations but increased in dominant males (Sapolsky 2005). Thus,
120 there appear to be complex interrelationships between social status, cortisol, testosterone,
121 and parasites, making it difficult to predict who is most vulnerable to parasitic infections.

122 Larger group size may also increase parasitic infections, the expectation being that
123 larger groups increase the number of social contacts (Griffin and Nunn 2012), but again, the
124 direction does not appear to be uniform. Positive associations have been found between
125 group size and 1) the number of intestinal protozoan species in gray-cheeked mangabeys
126 (*Lophocebus albigena*) (Freeland 1979), 2) nematode diversity in olive baboons (McGrew
127 et al. 1989) and 3) parasitic infection rate in several Amazonian primates (Davies et al.
128 1991) but no associations between group size and various measures of parasitism have been
129 found in other studies of primates (Chapman et al. 2009; Nunn 2002a, 2002b; Nunn et al.
130 2000; Semple et al. 2002; Snaith et al. 2008; Vitone et al. 2004, but see Rifkin et al. 2012).
131 A study of red colobus monkeys (*Procolobus rufomitratu*s) even found a negative
132 correlation between group size and parasite incidence (Snaith et al. 2008).

133 Finally, a positive relationship between humidity and parasite infection rate has
134 been suggested for chimpanzees (Huffman et al. 1997; McGrew et al. 1989), olive and
135 Guinea baboons (McGrew et al. 1989), muriquis (*Brachyteles arachnoides*) (Stuart et al.
136 1993), mantled howler monkeys (*Alouatta palliata*) (Stuart et al. 1990), and black howler
137 monkeys (*A. pigra*) (Eckert et al. 2006). Moist conditions appear to promote reinfection
138 and a higher incidence of infections, probably because eggs and larvae survive better in
139 humid environments than in dry ones (Hausfater and Meade 1982). However, some
140 nematode species (e.g., *Trichuris* spp., *Strongyloides* spp.) have not shown seasonal
141 variation in infections of primate populations (Huffman et al. 1997; McGrew et al. 1989).

142 Gray-cheeked mangabeys are phylogenetically closely related to the more widely
143 studied baboons (Burrell et al. 2009; Harris and Disotell 1998). Like most baboons, home
144 range overlap is extensive (Janmaat et al. 2009) and females reproduce aseasonally (Arlet et
145 al. 2015). However, they are more arboreal and live in smaller groups, making them
146 valuable for comparative analyses. Adult female gray-cheeked mangabeys usually remain
147 in their natal groups throughout life, whereas males disperse from their natal groups as
148 subadults (Olupot 1999; Olupot and Waser 2001a, 2005). Secondary (breeding) adult male
149 dispersers compete with other males for receptive females and rank as they attempt to join
150 other groups (Olupot and Waser 2001a, 2005). A study of fecal glucocorticoid metabolites
151 (fGCM) showed that immigrant males initially had a mean of 1.38 times higher fGCM
152 profiles than resident males, but over time their fGCM levels had declined and by the end
153 of 6 months were similar to those of resident males (Arlet et al. 2009a).

154 Our aim was to identify the social, physiological, and environmental factors that are
155 positively correlated with gastrointestinal nematode infections in adult male mangabeys.

156 We focus on nematodes because they can be noninvasively sampled through collection of
157 fecal samples and can have deleterious effects on health. Some more commonly observed
158 nematodes in wild primates include species of the genera *Physaloptera*, *Enterobius*,
159 *Trichuris*, and *Strongylus* (Nunn and Altizer 2006). Primates become infected with these
160 worms by the fecal-oral route, ingesting feces or contaminated substrates (soil, vegetation)
161 that contain third-stage larvae (Strongylidae spp.) or first-stage larvae in eggs (*Enterobius*,
162 *Trichuris*), through skin contact with infective larvae (Strongylidae spp.), or through
163 ingestion of infected arthropods (*Physaloptera*; Nunn and Altizer 2006). Although parasites
164 such as *Trichuris* are typically asymptomatic, heavy infections of *Strongyloides* are
165 associated with mucosal inflammation, ulceration, dysentery, weight loss, and death
166 (Chapman et al. 2006). Given that parasitic infections have variable associations with social
167 status, physiological condition, group size, and climatic conditions in other primates, we
168 did not establish predictions but conducted an exploratory study about the health of males
169 under different social, physiological, and environmental conditions.

170

171 **Methods**

172 Study area and subjects

173 We conducted the study from December 2005 to July 2007 in Kibale National Park,
174 Uganda (0°13' - 0°41'N and 30°19' - 30°32'E), near Makerere University Biological Field
175 Station, at Kanyawara. Kibale (795 km²) is a moist, evergreen, medium altitude forest with
176 a mosaic of swamp, grassland, thicket, and colonizing forest (Chapman and Lambert 2000;
177 Struhsaker 1975). Rainfall has a bimodal pattern, with rainy seasons typically in March–
178 May and August–November, and mean annual rainfall (1990–2001) of 1749 mm (Chapman

179 et al. 2002; Valtonen et al. 2013). We collected data on rainfall daily at the Makerere
180 University Biological Field Station.

181 The mangabey population in Kibale has been studied since the 1970s and multiple
182 groups are well habituated. We collected behavioral data and fecal samples from 18 adult
183 males in five groups (BT1, CC, LC1, LC2, and MK). Group size ranged from 9 to 23
184 individuals, with 1-9 adult males per group (Arlet et al. 2009a).

185 We considered an individual male as an adult when he was able to give “whoop-
186 gobble” calls, a characteristic call produced only by adult males (Waser 1977a). We
187 observed four adult males individually recognized by color collars from a previous study
188 (Olupot 1999) and 14 animals identified by relative size and distinguishing features (e.g.,
189 tail shape, scars, and fractures; Arlet et al. 2009b). Estimating the age of adult males and
190 thus the effect of age on parasite load was not possible because no visible physical markers
191 of male age are available for this species and most males immigrated into our study groups
192 from non-study groups. Nevertheless, we knew that all four collared males were at least 20
193 years old in 2015.

194

195 Male status

196 Earlier studies suggested that mangabey groups lack clear male dominance
197 hierarchies (Olupot and Waser 2005; Waser 1977b), perhaps because reduced visibility
198 between individuals, the complex three-dimensional structure of the forest canopy, and
199 wide group spread reduce both the actual and observed frequency of interactions. However,
200 we have collected sufficient behavioral data to demonstrate the existence of dominance
201 hierarchies in this species (Arlet and Isbell 2009; Arlet et al. 2011). Hierarchies are more

202 obvious in some smaller groups, while in larger groups two or three males usually have a
203 similar high dominance rank with a high number of reversals. Relative position in the male
204 dominance hierarchy within each group was determined from the outcome of dyadic
205 agonistic interactions, including chases, fights, and supplants during focal samples. This
206 was done for two study periods (December 2005-July 2006, and January-July 2007). We
207 observed 21–257 agonistic interactions per group. Dominance matrices were constructed
208 for each group with rank-order determined by placing winners above losers while
209 minimizing the number of reversals against the hierarchy (i.e., interactions below the
210 diagonal) (Arlet and Isbell 2009; Arlet et al. 2011). The percentage of reversals against the
211 hierarchy was 18.2–25.9% for four groups where we classified two males as high-ranking
212 (HR) and all other males as low-ranking (LR). In the fifth and largest group (LC1) 37.7-
213 46.1% of agonistic interactions were reversals. In this group we assigned high rank to three
214 males who won 20% more fights than other males and low rank to four males who lost
215 more than 33% fights to these high-ranking males. We measured linearity in five groups
216 using the Landau index h' (for 2006 and 2007, respectively): BT1 ($h=1$, $P=0.11$; $h=0.7$,
217 $P=0.37$), CC ($h=1$, $P=0.38$; $h=0.9$, $P=0.38$), LC1 ($h=0.77$, $P=0.003$; $h=0.75$, $P=0.24$), LC2
218 ($h=1$, $P=1.0$; $h=1$, $P=0.82$), MK ($h=1$, $P=0.38$; $h=1$, $P=1.0$). Values of h that are closer to 1
219 indicate greater linearity whereas values closer to 0 indicate the opposite. Landau h values
220 are high in these groups, but with such small group sizes it is not possible to confirm
221 linearity of most dominance hierarchies in most years. Given the high percentage of
222 reversals and the lack of statistically significant linearity, labelling males more precisely
223 than high- or low-rank seems unwarranted.

224

225 Immigrant males

226 Four males who joined groups during the study were regarded as immigrants.

227 Three immigrants remained in the study groups for the duration of the study, and one male
228 moved between two groups.

229

230 Collection of fecal samples for parasites and hormone analyses

231 We collected fecal samples from December 2005 to July 2007. We did not collect
232 fecal samples on the first observation day of each period because we did not know what
233 experiences males had during previous days when they were not under observation. After
234 the first day, when a focal individual defecated, the time was noted, the sample was
235 collected within minutes of defecation, placed in a sterile scintillation vial, and stored on
236 ice (for hormone analysis). Approximately 5 grams were placed into 10% formalin for
237 parasite analysis. At the end of the day, all samples designated for hormonal analyses were
238 placed in a $-20\text{ }^{\circ}\text{C}$ freezer until removed for hormone solubilization (Strier and Ziegler
239 1997; Whitten et al. 1999).

240 We collected one sample per male per particular day, with time intervals of at least
241 one day between samples from the same male. We aimed to collect samples from the same
242 individuals during both dry and wet seasons. We chose 102 samples from 18 adult males
243 for analysis (Table 1), considering the collection date (to compare the impact of rainfall)
244 and balancing the number of samples from high- and low-rank and immigrant males (for
245 rank and status factors). Two males, PL and MF, changed their status, thus their samples
246 were analysed separately based on their status at the time of fecal collection. The number of
247 fecal samples analyzed per individual adult male ranged from 2 to 10, with a median of 5.0.

248

249 Analysis of fecal samples for parasites

250 Samples (5 g of feces) were stored individually in 5.0 ml vials in a 10% formalin
251 solution. Preserved samples were transported to McGill University (Montreal, Canada),
252 where we examined 1 g of fecal material for helminth eggs and larvae using concentration
253 by sodium nitrate flotation and fecal sedimentation, primarily sedimentation that involved
254 examining the total sediment (Sloss et al. 1994; C.A. Chapman et al. unpublished data).
255 Parasites were identified on the basis of eggs or larvae color, shape, contents, and size
256 (Jessee et al. 1970). Our ability to identify parasite species from host fecal examination is
257 limited. Consequently, we present our findings at the level of genus when possible and
258 superfamily for the strongyle-type helminths. Measurements were made to the nearest 0.1
259 micron \pm SD using an ocular micrometer fitted to a compound microscope, and
260 representatives were photographed. Egg counts are dependent on a number of host factors,
261 including age and diet (e.g., Stear et al. 1995), limiting the conclusions we can draw using
262 this method. However, it is frequently used to describe infections (e.g., Chapman et al.
263 2006; Ezenwa 2003; Gulland 1992).

264 We used the term '*nematode incidence*', to describe the proportion of individuals
265 infected with *Physaloptera*, *Trichuris*, and *Strongyloidea* spp. We used the term '*nematode*
266 *intensity*' to describe the number of parasites (total numbers of eggs, larvae, and adult
267 stage) per gram of feces per male. In six cases a parasite egg was damaged or we were
268 unable to obtain a good image and these went unidentified.

269 No fecal samples appeared watery or had a discoloration that would suggest illness.

270 Like many previous studies, we assume that gastrointestinal helminth infection influences

271 overall condition (Chapman et al. 2006; Gillespie et al. 2004; Howells et al. 2010). We
272 conducted parasite analysis from the same fecal mass that was used for fGCM and fTM
273 analyses.

274

275 Hormone extraction in the field

276 The dry weight of each sample was calculated using the percent water of a sample
277 from the same homogenized fecal sample from which the hormones were extracted, by
278 drying these samples to constant weight in the field (Chapman et al. 2006). Our previous
279 study of fGCM (with the same sample set) showed that time of day did not have a
280 significant effect on cortisol concentration in adult male mangabeys (Arlet et al. 2009a).
281 Therefore we analyzed samples both from the mornings and afternoons.

282 Hormones were solubilized at the field station using the protocol employed for red
283 colobus (Chapman et al. 2006). A fecal sample was removed from the freezer, thawed, and
284 homogenized using a spatula. Then, 0.50 g was solubilized using a 5.0 pH citrate
285 buffer/95% ethanol solution (10 ml, 1:1) that was mixed for 21 – 27 hrs. After mixing,
286 samples were spun in a centrifuge for 30 min at 3200 rounds per minute to separate the
287 supernatant containing the hormones from the fecal pellet, and then 2 ml of the supernatant
288 was passed through a solid phase extraction cartridge (Alltech maxi-clean filter) for storage
289 and transport (Strier and Ziegler 2005) to the University of Wisconsin.

290

291 Hormone extraction in the laboratory

292 The samples were sent to the Wisconsin National Primate Research Center's
293 (WNRPC) Assay Services, where the method for measuring cortisol and testosterone

294 concentration was validated and samples analyzed. At the WNPRC, cortisol and
295 testosterone were extracted from the filters. The cartridges were washed with 1 ml of 20%
296 methanol and the columns were eluted with 2 ml methanol. This methanol was dried,
297 resuspended in 1 ml ethanol, and 50 μ l was taken for the enzyme immunoassay. The
298 WNPRC lab used the antibody R4866 for cortisol analysis which were developed by
299 Munro and Stabenfeldt (1984) and are well characterized. The antibody crossreacts 60%
300 with cortisone (a metabolite of cortisol), 2.5% with corticosterone and less than 1% with
301 other steroids (Ziegler et al. 1995). The WNPRC lab used the antibody R159 for
302 testosterone (Munro and Stabenfeldt 1984). The antibody crossreacts 92.4% with
303 dihydrotestosterone, 11.2% with 4-androsten-3beta, 17beta-diol, 5.4% with
304 dehydroandrosterone, 3.4% with androstenediol, 2.1% with androstenedione and less than
305 1% with other steroids (Ziegler et al.1995).

306 An assay comparing serial dilutions of pooled mangabey samples to cortisol
307 standards found no significant difference between the slopes ($t=-1.62$, $df=25$, $p>0.05$).
308 Accuracy was determined by superimposing values from pooled mangabey samples on a
309 standard curve. The mean accuracy over eight pooled samples was 109% with standard
310 deviation 2.9%. The inter-assay coefficients of variation were 13.6 and 12.8 for the low and
311 high pools, respectively, and the intra-assay coefficients of variation were 3.9 and 2.1 for
312 the low and high pools, respectively. An assay comparing serial dilutions of pooled
313 mangabey samples to testosterone standards found no significant difference between the
314 slopes ($t= 1.903$, $df=26$, $p=0.07$). The mean accuracy over eight pooled samples was
315 109.19% with standard deviation 2.17%. The inter-assay coefficients of variation were 10.6

316 and 11.7 for the low and high pools, respectively, and the intra-assay coefficients of
317 variation were 3.5 and 1.9 for the low and high pools, respectively.

318

319 Statistical Analyses

320 The data represent a count variable that can be described as a Poisson distribution: a
321 few samples had many parasites and 74% of the samples had no parasites at all. We
322 structured the data by group (N = 5) and by individual/status (N = 20; 18 males plus 1
323 change of status for 2 males). Group LC1 with its three HR males was included in the
324 analyses.

325 We performed all analyses using the statistical software R (R Development Core
326 Team 2011). We used Generalized Linear Mixed Models (GLMM), run with the lme4
327 package (Bates et al. 2011) to test with binomial distribution (with logit function) to
328 investigate nematode incidence (proportion of individuals infected) using social status (high
329 rank/low rank/immigrant), fecal glucocorticoid (fGCM) concentration, fecal testosterone
330 metabolite concentration (fTM), group size, and rainfall as predictor variables. We used
331 GLMM with a Poisson distribution (with log function) to investigate nematode intensity
332 (number of eggs, larvae, and adults per g fecal sample) using the same predictor variables
333 with centered values for fGCM and fTM. We performed post-hoc analyses using ANOVA
334 to investigate possible differences in parasite incidence and intensity among males of
335 different status.

336

337 Ethical Note

338 All fecal samples were collected from habituated, wild animals without interfering
339 with their activities. The research complied with with the laws of Uganda and the protocols
340 were approved by the Uganda Wildlife Authority and Uganda National Council for Science
341 and Technology at the time the field research was conducted.

342

343 **Results**

344 Correlates of nematode incidence

345 Overall, the model of nematode incidence was highly significant (likelihood ratio
346 test comparing full and null models: $\chi^2 = 57.02$, $df = 1$, $P < 0.001$). Nematode incidence
347 was significantly associated with male status, concentrations of fGCM, fTM, and group
348 size but not with rainfall (Table 2).

349 There was no significant difference in parasite incidence between low- and high-
350 ranking males (ANOVA: $F=1.52$, $df=1$, $P=0.22$). However, a greater proportion of
351 immigrant males had parasites than low-ranking (ANOVA: $F=3.92$, $df=1.0$, $P=0.05$) and
352 high-ranking males (ANOVA: $F=13.72$, $df=1.0$, $P<0.001$; Figure 1). Samples with parasites
353 had higher fGCM and fTM levels than those without parasites (Table 2, Figures 2, 3).
354 Higher than mean (93.9 ng/g) concentrations of fGCM were observed for 63.9% of infected
355 samples but only 25.7% of samples with no parasites. Similarly, higher than mean (62.3
356 ng/g) concentrations of fTM were observed for 54.4% of infected samples but only 36.9%
357 of samples with no parasites. Half of the infected samples came from medium-sized groups
358 (14-16 individuals), whereas the remaining came from larger (18-22 individuals) and
359 smaller groups (fewer than 13 individuals; Figure 4).

360

361 Correlates of nematode intensity

362 Overall, the model of nematode intensity was significant (likelihood ratio test
363 comparing full and null models: $\chi^2 = 453.2$, $df = 1$, $P < 0.001$). Nematode intensity (total
364 number of parasites at all life stages/g feces/male) was significantly related to male status,
365 concentrations of fGCM and fTM, group size, and rainfall (Table 3).

366 Fecal samples from low-ranking and immigrant males were not significantly
367 different in parasite intensity (ANOVA: $F=3.73$, $df=1$, $P=0.06$) but fecal samples from each
368 had significantly greater nematode intensities than those from high-ranking males
369 (ANOVA: immigrant males $F=11.62$, $df=1.69$, $P=0.001$; low-ranking males: $F=3.85$,
370 $df=1.71$, $P=0.05$; Figure 5).

371 Nematode intensity was significantly related to concentrations of both fGCM and
372 fTM and there was a significant interaction between these two hormone metabolites (Table
373 3): when fTM was higher, then the positive effect of fGCM on parasite intensity was not as
374 strong as predicted by the two combined main effects. Qualitatively, higher fGCM was
375 associated with higher parasite intensity both for samples with low fTM and for samples
376 with high fTM levels (Figure 6). Furthermore, nematode intensity was greatest at
377 intermediate group sizes of 14 to 18 individuals within the group (Table 3, Figure 7).
378 Finally, samples collected during rainy season months had greater nematode intensities than
379 those from dry season months (Table 3, Figure 8).

380

381 **Discussion**

382 Our results show that low-ranking or immigrant status, physiological stress (as
383 measured by fGCM), high concentration of testosterone (as measured by fTM), living in
384 mid-sized groups, and the rainy season all contribute to high nematode infections in adult
385 male gray-cheeked mangabeys. Prolonged stressful conditions can suppress the immune
386 system (Munck et al. 1984), making it easier for parasites to establish themselves. In fact,
387 psychological stress has been shown to increase vulnerability specifically to parasitic
388 infection (Bailey and Coe 1999). Negative associations between cortisol and immune
389 measures have also been found in chimpanzees (Muehlenbein and Watts 2010), yellow and
390 olive baboons (Alberts et al. 1992; Sapolsky and Spencer 1997), and red colobus (Chapman
391 et al. 2006). Conditions for low-ranking males may indeed be stressful. They are, by
392 definition, males who lose more often in competitive interactions with others. Under stable
393 conditions, low-ranking males have higher cortisol levels than high-ranking males in
394 yellow baboons (Sapolsky et al. 1997) and mandrills (Setchell et al. 2010). While we were
395 able to construct dominance hierarchies we also note the high percentage of reversals
396 against the hierarchy in large groups, suggesting that male dominance hierarchies in gray-
397 cheeked mangabeys are relatively fluid or unstable over time. Such conditions have been
398 shown to increase cortisol levels for those being challenged in, for example, olive baboons
399 (Sapolsky 1992) and rhesus macaques (Higham et al. 2013).

400 Elsewhere we have shown that immigrant male gray-cheeked mangabeys have
401 higher cortisol levels than resident males (i.e., both high-and low-ranking males), and that
402 this may last for up to six months after males have transferred into a new group (Arlet et al.
403 2009a). Stressful conditions may manifest early on in the dispersal process. Although
404 dispersing males do not incur increased aggression before leaving their groups (Olupot and

405 Waser 2001a), traveling apart from groups appears to increase males' risk of mortality,
406 most likely from crowned eagle (*Stephanoaetus coronatus*) predation (Olupot and Waser
407 2001b). Males traveling alone or entering a new group may also lack social support, which
408 is an important mechanism for coping with stressful conditions (Crockford et al. 2008;
409 Wingfield and Sapolsky 2003). Finally, the dispersal phase may expose males to more
410 parasites as the males come into contact with unfamiliar conspecifics harboring different
411 parasites (Chapman et al. 2012; Freeland 1979; VanderWaal et al. 2014a).

412 We also found that greater nematode incidence and intensity were associated with
413 higher concentrations of fTM. Similar results have been reported for other species (e.g.,
414 mandrills: Setchell et al. 2009, chimpanzees: Muehlenbein 2006). Testosterone can have an
415 immunosuppressive effect (Prall and Muehlenbein 2013; Salvador et al. 1996; Weatherhead
416 et al. 1993). However, although dominant males had the highest concentrations of fTM,
417 they had the lowest nematode intensities. It is unclear why, if dominant males have high
418 testosterone, and higher testosterone is associated with higher parasite loads, dominant
419 males did not have high parasite loads. It is possible that in dominant males testosterone
420 has an immunocompetence effect (Peters 2000). Our data suggest that the testosterone
421 signal in parasitic infections might be coming from immigrant males. They had higher
422 mean values of fTM (51.6) and nematode intensity (23.8; Table 1) than low-ranking males
423 (testosterone: 46.6; nematode intensity: 7.3; Table 1). The trend is similar if outlier
424 immigrant male KK, with the highest nematode load, is removed.

425 We also found that both parasite incidence and intensity were related to group size,
426 as reported in an earlier study of gray-cheeked mangabeys at Kibale (Freeland 1979),
427 however, the mid-sized groups of 14-16 individuals were most infected with nematodes

428 during our study. We suggest that this pattern is also related to male movements and social
429 interactions. Immigrant males are attracted to groups with more estrous females (Arlet et al.
430 2008; Olupot and Waser 2001a), and the chance of finding fertile females generally
431 increases in larger groups. However, the largest groups may also include more competitors
432 such that immigrant males may be deterred from transferring to them. Thus, mid-sized
433 groups may be ‘optimal’ for male immigration. In giraffe (*Giraffa camelopardalis*), which
434 have a fission-fusion social organization structured around social cliques (VanderWaal et
435 al. 2014b), individuals that interact with others outside their social clique have higher
436 parasite loads (VanderWaal et al. 2014a). Our study suggests the same for immigrant male
437 gray-cheeked mangabeys. The high frequency of social interactions between immigrant
438 males and estrous females may also make such males parasite spreaders, exposing members
439 of their new groups to parasites obtained from their former groups.

440 Finally, we found that parasite intensity was positively correlated with rainfall. Our
441 results are thus consistent with what is known about the effects of climatic conditions on
442 parasites (e.g., Huffman et al. 1997; McGrew 1989; Stuart et al. 1993).

443 In summary, our results repeatedly point to immigrant males as important vessels
444 for nematode infection in gray-cheeked mangabey populations. In the future it would be
445 beneficial to investigate the social aspects of parasite transmission. Social networks
446 analyses have recently been employed to document that gut bacteria can be socially
447 transmitted in yellow baboons (Tung et al. 2015) and to identify who is most likely to
448 spread bacterial and helminth infections in giraffes (VanderWaal et al. 2014a). This
449 approach may be especially fruitful in elucidating in greater detail the role of immigrant

450 male gray-cheeked mangabeys specifically, and immigrants in general, in parasite
451 transmission.

452

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462

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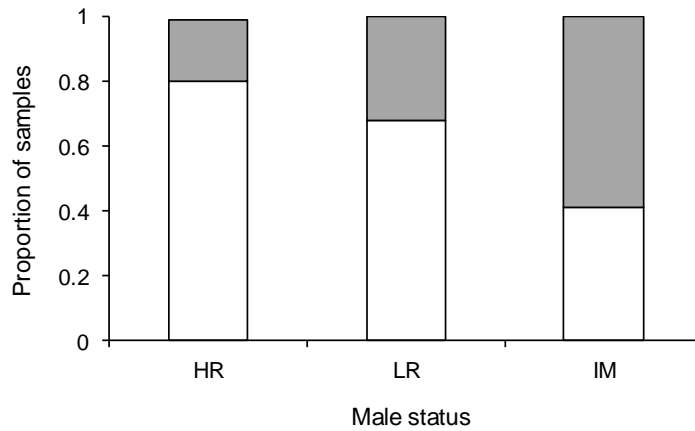
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746 Figure Legends

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749 **Fig.1** Nematode incidence (proportion of samples with parasites) in male gray-cheeked

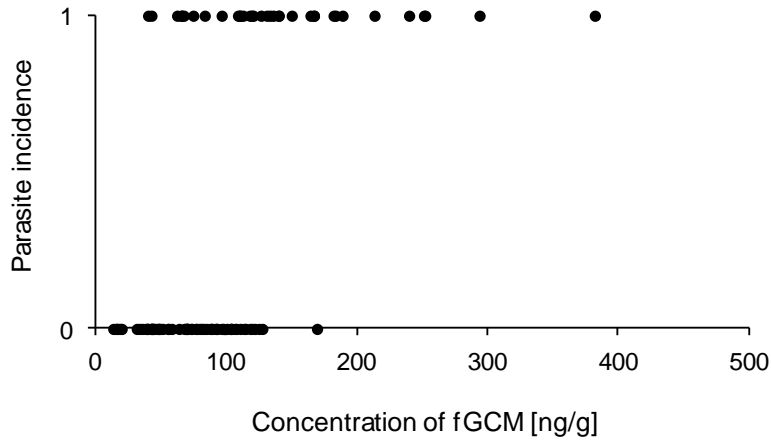
750 mangabeys relative to male status (HR/LR/M) in Kibale National Park, Uganda, 2006-

751 2007. Shaded proportions are those with parasites; white proportions are those without

752 parasites. HR = high-ranking males, LR = low-ranking males, IM = immigrant males.

753 Shaded proportions are those with parasites; white proportions are those without parasites

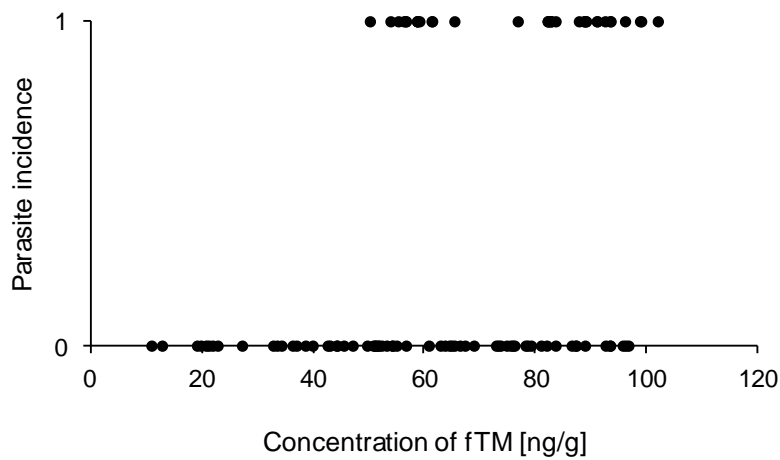
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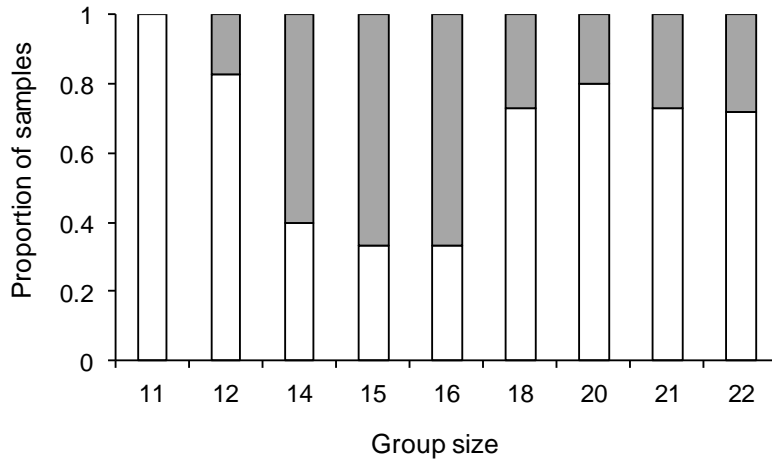
756 **Fig. 2** Samples with and without parasites in male gray-cheeked mangabeys relative to
 757 concentrations of fecal glucocorticoid metabolite in Kibale National Park, Uganda, 2006-
 758 2007

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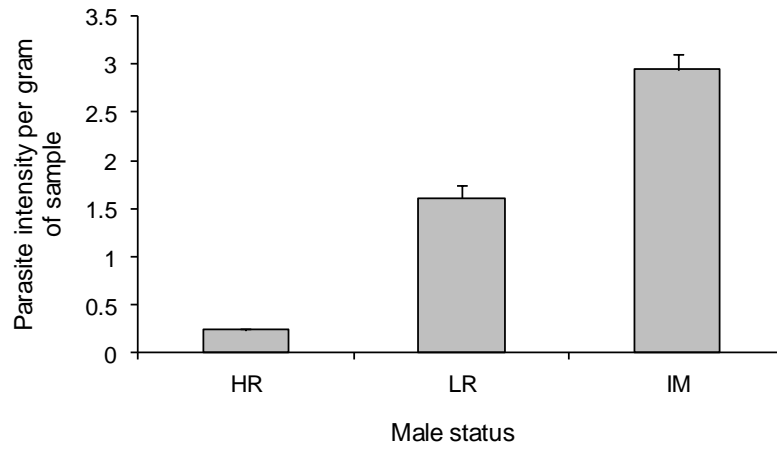
761 **Fig. 3** Samples with and without parasites in male gray-cheeked mangabeys relative to
 762 concentrations of fecal testosterone metabolite in Kibale National Park, Uganda, 2006-2007



763 **Fig.4** Nematode incidence (proportion of samples with parasites) in male gray-cheeked
 764 mangabeys relative to group size in Kibale National Park, Uganda, 2006-2007. Shaded
 765 proportions are those with parasites; white proportions are those without parasites

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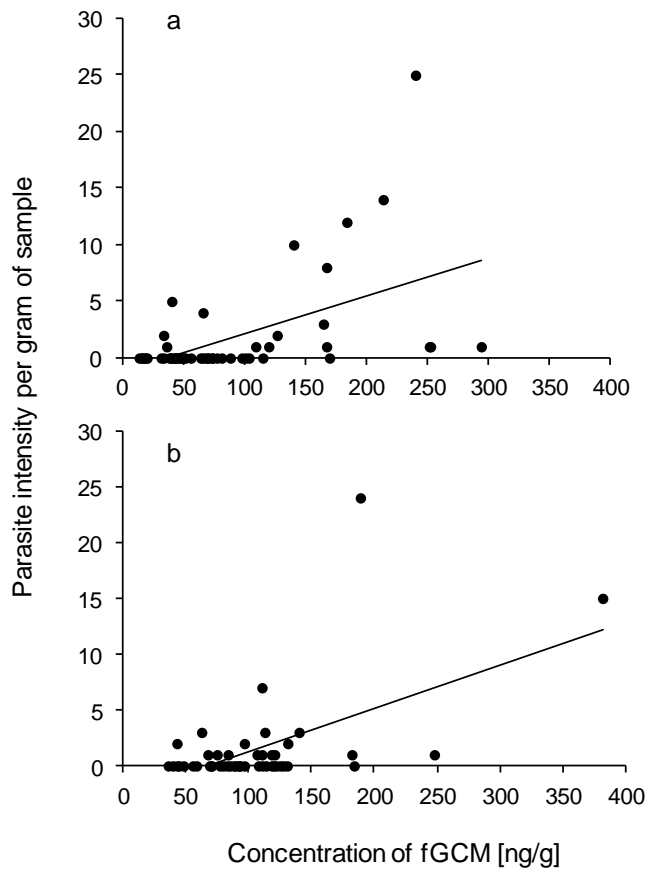
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769 **Fig. 5** Nematode intensity (abundance of parasites per gram fecal sample) in male
770 gray-cheeked mangabeys relative to male status in Kibale National Park, Uganda, 2006-
771 2007. HR = high-ranking males, LR = low-ranking males, IM = immigrant males

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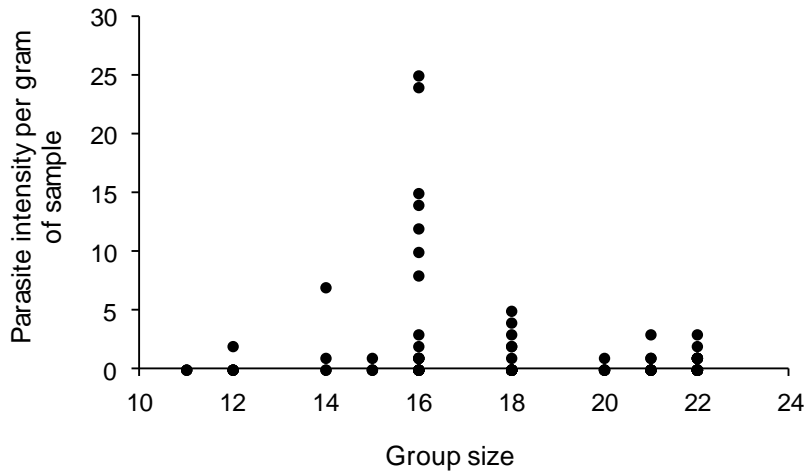
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776 **Fig. 6** Nematode intensity (abundance of parasites per gram fecal sample) in male gray-
 777 cheeked mangabeys relative to fecal glucocorticoid metabolites: a) when fTM was below
 778 the mean of 62.3 ng/g and b) when fTM was above the mean of 62.3 ng/g

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783 **Fig. 7** Nematode intensity (abundance of parasites per gram fecal sample) in adult male

784 gray-cheeked mangabeys relative to group size in Kibale National Park, Uganda, 2006-

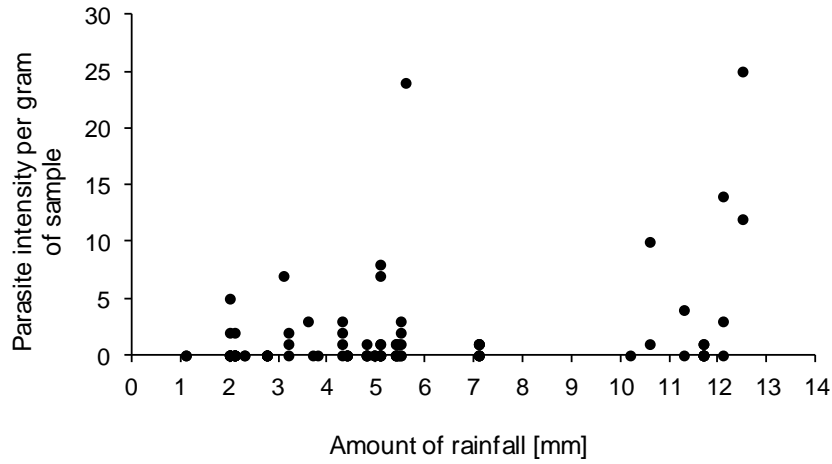
785 2007

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793 **Fig. 8** Nematode intensity (abundance of parasites per gram fecal sample) in adult male

794 gray-cheeked mangabeys relative to monthly rainfall (mm) in Kibale National Park,

795 Uganda, 2006-2007. Each point represents one fecal sample (N=102)

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807 Table 1. Individual identity, social status (high-ranking male (HR), low-ranking male (LR),
 808 or immigrant male (M)), group identity, group size, nematode incidence and intensity, and
 809 fecal glucocorticoid (fGCM) and testosterone metabolite (fTM) concentrations among adult
 810 male gray-cheeked mangabeys in Kibale National Park, Uganda, 2006-2007.

Male	Status	Group	Group size	Incidence (mean±SD)	<i>Physaloptera sp.</i>	<i>Trichuris sp.</i>	<i>Strongyloidea sp.</i>	Unknown sp.	Intensity	fGCM ng/g (mean±SD)	fTM ng/g (mean±SD)	Sample size
PL	HR	BT1	18	0.0 ± 0.0	0	0	0	0	0	76.2 ± 28.4	63.0 ± 8.9	6
LM	HR	BT1	18	0.4 ± 0.6	0	3	0	1	4	71.1 ± 16.1	78.8 ± 3.8	5
PL	LR	BT1	18	1.0 ± 0.0	3	1	3	0	7	36.5 ± 4.7	60.2 ± 1.6	2
BG2	LR	BT1	18	0.4 ± 0.5	7	0	0	0	7	53.8 ± 9.8	51.8 ± 7.7	7
KR	HR	CC	15	0.3 ± 0.6	0	0	0	1	1	67.8 ± 25.3	63.3 ± 3.1	3
MF	HR	CC	18	0.3 ± 0.5	2	0	0	0	2	82.8 ± 13.5	74.8 ± 17.3	4
KJ	LR	CC	16	0.6 ± 0.6	25	0	0	1	26	68.7 ± 69.4	47.2 ± 25.7	5
KK	M	CC	16	0.7 ± 0.5	51	0	12	3	66	137.4 ± 57.2	50.8 ± 11.3	10
MF	M	CC	16	0.7 ± 0.5	18	0	8	0	18	220.5 ± 107.6	59.1 ± 23.4	4
MG	HR	LC1	22	0.0 ± 0.0	0	0	0	0	0	110.1 ± 15.9	93.0 ± 14.5	7
R	HR	LC1	21	0.0 ± 0.0	0	0	0	0	0	132.6 ± 29.7	101.5 ± 5.6	5
YM	HR	LC1	21	0.5 ± 0.6	0	0	2	0	2	115.3 ± 47.8	88.7 ± 8.9	4
MR	LR	LC1	22	0.0 ± 0.0	0	0	0	0	0	28.7 ± 15.2	43.5 ± 8.7	6
NK	LR	LC1	22	0.4 ± 0.6	1	0	3	0	4	70.2 ± 37.7	45.7 ± 27.8	5
BW	M	LC1	22	0.4 ± 0.5	2	1	4	0	7	98.6 ± 29.3	60.7 ± 26.0	8
HL	M	LC1	21	0.6 ± 0.5	2	0	2	0	4	183.1 ± 29.3	47.6 ± 26.1	7
IB	HR	LC2	12	0.2 ± 0.5	1	1	0	0	2	41.8 ± 4.7	77.9 ± 13.3	5
NY	LR	LC2	12	0.0 ± 0.0	0	0	0	0	0	33.7 ± 13.1	19.8 ± 10.3	4
KY	HR	MK	15	0.3 ± 0.6	0	0	1	0	1	71.0 ± 3.0	74.5 ± 9.3	3
KC	LR	MK	14	0.5 ± 0.7	5	0	2	0	7	82.8 ± 38.7	65.9 ± 15.4	2

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813 Table 2. Results of a GLMM with binomial distribution examining factors associated with
 814 parasite incidence in adult male gray-cheeked mangabeys in Kibale National Park, 2006-
 815 2007.

	Estimate	SE	P
Intercept	-5.30	2.20	0.022
Status	4.75	3.09	0.002
fGCM	0.03	0.01	0.001
fTM	0.09	0.02	0.001
Group size	-0.43	0.12	0.001
Rainfall	0.08	0.09	0.351

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818 Table 3. Results of a GLMM with Poisson distribution examining factors associated with
 819 parasite intensity in adult male gray-cheeked mangabeys in Kibale National Park, 2006-
 820 2007.

	Estimate	SE	P
Intercept	1.080	0.720	0.140
Status	3.940	3.970	<0.001
fGCM	0.010	0.001	<0.001
fTM	0.060	0.009	<0.001
Group size	-0.280	0.040	0.011
Rainfall	0.130	0.030	0.003
821 fGCM x fTM	-0.003	<0.001	<0.001

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