



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

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Social and ecological correlates of parasitic infections
in adult male gray-cheeked mangabeys (*Lophocebus albigena*)

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Abstract

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

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

Introduction

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Methods

Study area and subjects

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

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

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

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

Male status

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

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

Immigrant males

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

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

Collection of fecal samples for parasites and hormone analyses

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

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

Analysis of fecal samples for parasites

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

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

No fecal samples appeared watery or had a discoloration that would suggest illness. Like many previous studies, we assume that gastrointestinal helminth infection influences

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

Hormone extraction in the field

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

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

Hormone extraction in the laboratory

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

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

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

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

Statistical Analyses

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

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

Ethical Note

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

Results

Correlates of nematode incidence

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

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

Correlates of nematode intensity

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

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

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

Discussion

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

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

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

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

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

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

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

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

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

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References

- Alberts, S.C., Sapolsky, R.M., & Altmann, J. (1992). Behavioral, endocrine, and immunological correlates of immigration by an aggressive male into a natural primate group. *Hormones and Behavior* 26, 167-178.
- Altizer, S., Nunn, C.L., Thrall, P.H., Gittleman, J.L., Antonovics, J., Cunningham, A.A., Dobson, A.P., Ezenwa, V., Jones K.E., Pedersen, A.B., Poss, M., & Pulliam, J.R.C. (2003). Social organization and parasite risk in mammals: integrating theory and empirical studies. *Annual Review of Ecology, Evolution, and Systematics* 34, 517–547.

- 472 Arlet, M.E., Carey, J.R., & Molleman, F. (2009b). Species and sex differences in type and
473 frequencies of injuries and impairments among four arboreal primate species in
474 Kibale National Park, Uganda. *Primates* 50, 65-73.
- 475 Arlet, M.E., Grote, M.N., Isbell, L.A., Molleman, F., & Carey, J.R. (2009a). Reproductive
476 tactics influence cortisol levels in individual male mangabeys (*Lophocebus albigena*).
477 *Hormones and Behavior* 55, 210-216.
- 478 Arlet, M.E., & Isbell, L.A. (2009). Variation in behavioral and hormonal responses of adult
479 male mangabeys (*Lophocebus albigena*) to crowned eagles (*Stephanoaetus*
480 *coronatus*) in Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology*
481 63, 491-499.
- 482 Arlet, M.E., Isbell, L.A., Kaasik A., Molleman, F., Chancellor, R.L., Chapman, C.A.,
483 Mänd, R., & Carey, J.R. (2015). Determinants of reproductive performance among
484 female gray-cheeked mangabeys (*Lophocebus albigena*) in Kibale National Park,
485 Uganda. *International Journal of Primatology* 36, 55-73.
- 486 Arlet, M.E., Kaasik, A., Molleman, F., Isbell, L.A., Carey, J.R., & Mänd, R. (2011). Social
487 factors increase fecal testosterone levels in wild male gray-cheeked mangabeys
488 (*Lophocebus albigena*). *Hormones and Behavior* 59, 605-611.
- 489 Arlet, M.E., Molleman, F., & Chapman, C.A. (2008). Mating tactics in male grey-cheeked
490 mangabeys (*Lophocebus albigena*). *Ethology* 114, 841-852.
- 491 Bailey, M.T., & Coe, C.L. (1999). Maternal separation disrupts the integrity of the
492 intestinal microflora in infant rhesus monkeys. *Developmental Psychology* 35, 146-
493 155.

- 494 Barrett, G.M., Shimizu, K., Bardi, M., Asaba, S., & Mori, A. (2002). Endocrine correlates
495 of rank, reproduction, and female-directed aggression in male Japanese macaques
496 (*Macaca fuscata*). *Hormones and Behavior* 42, 85-96.
- 497 Bercovitch, F.B. (1993). Dominance rank and reproductive maturation in rhesus macaques
498 (*Macaca mulatta*). *Journal of Reproduction and Fertility* 99, 113-120.
- 499 Bradley, A.J., McDonald, I.R., & Lee, A.K. (1980). Stress and mortality in a small
500 marsupial (*Antechinus stuartii*, Macleay). *General and Comparative Endocrinology*
501 40, 188-200.
- 502 Braude, S., Tang-Martinez, Z., & Taylor, G.T. (1999). Stress, testosterone and the
503 immunoredistribution hypothesis. *Behavioral Ecology* 10, 345-350.
- 504 Bribiescas, R.G. (2001). Reproductive ecology and life history of the human male.
505 *Yearbook of Physical Anthropology* 44, 148-176.
- 506 Burrell, A.S., Jolly, C.J., Tosi, A.J., & Disotell T.R. (2009). Mitochondrial evidence for the
507 hybrid origin of the kipunji, *Rungwecebus kipunji* (Primates: Papionini). *Molecular*
508 *Phylogenetics and Evolution* 51, 340-348.
- 509 Cavigelli, S.A., & Pereira, M.E. (2000). Mating season aggression and fecal testosterone
510 levels in male ring-tailed lemurs (*Lemur catta*). *Hormones and Behavior* 37, 246-278.
- 511 Chapman, C.A., Bowman, D.D., Ghai, R.R., Goldberg, T.L., Gogarten, J.F., Rothman,
512 J.M., Twinomugisha, D., & Walsh, C. (2012). Protozoan parasites in group-living
513 primates: Testing the biological island hypothesis. *American Journal of Primatology*
514 74, 510-517.

- 515 Chapman, C.A., Chapman, L.J., & Gillespie, T.R. (2002). Scale issues in the study of
516 primate foraging: red colobus of Kibale National Park. *American Journal of Physical*
517 *Anthropology* 117, 349–363.
- 518 Chapman, C.A., & Lambert, J.E. (2000). Habitat alteration and the conservation of African
519 primates: a case study of Kibale National Park, Uganda. *American Journal of*
520 *Primatology* 50, 169–186.
- 521 Chapman, C.A., Rothman, J.M., & Hodder, S.A.M. (2009). Can parasites be a selective
522 force influencing primate group size?: A test with red colobus. In M.A. Huffman &
523 C.A. Chapman, (Eds.) *Primate parasite ecology: The dynamics and study of host-*
524 *parasite relationships. Cambridge studies in biological and evolutionary*
525 *anthropology* (pp. 423-440). Cambridge: Cambridge University Press.
- 526 Chapman, C.A., Wasserman, M.D., Gillespie, T.R., Speirs, M.L., Lawes, M.J., Saj, T.L., &
527 Ziegler, T.E. (2006). Do food availability, parasitism, and stress have synergistic
528 effects on red colobus populations living in forest fragments? *American Journal of*
529 *Physical Anthropology* 131, 525–534.
- 530 Crockford, C., Wittig, R.M., Whitten, P.L., Seyfarth, R.M., & Cheney, D.L. (2008). Social
531 stressors and coping mechanisms in wild female baboons (*Papio hamadryas ursinus*).
532 *Hormones and Behavior* 53, 254-265.
- 533 Davies, C.R., Ayres, J.M., Dye, C., & Deane, L.M. (1991). Malaria infection rate of
534 Amazonian primates increases with body weight and group size. *Functional Ecology*
535 5, 655-662.

- 536 Eckert, K.A., Hahn, N.E., Genz, A., Kitchen, D.M., Stuart, M.D., Awerbeck, G.A.,
537 Stromberg, B.E., & Markowitz, H. (2006). Coprological surveys of *Alouatta pigra* at
538 two sites in Belize. *International Journal of Primatology* 27, 227-238.
- 539 Ezenwa, V.O. (2003). Habitat overlap and gastrointestinal parasitism in sympatric African
540 bovids. *Parasitology* 126, 379–388.
- 541 Ezenwa, V.O., Ekernas, L.S., & Creel, S. (2012). Unravelling complex associations
542 between testosterone and parasite infection in the wild. *Functional Ecology* 26, 123-
543 133.
- 544 Freeland, W.J. (1979). Primate social groups as biological islands. *Ecology* 60, 719-728.
- 545 Friedman, E.M., & Lawrence, D.A. (2002). Environmental stress mediates changes in
546 neuroimmunological interactions. *Toxicological Sciences* 67, 4-10.
- 547 Gillespie, T.R., Greiner, E.C., & Chapman, C.A. (2004). Gastrointestinal parasites of the
548 guenons of western Uganda. *Journal of Parasitology* 90, 1356-1360.
- 549 Griffin, R.H., & Nunn, C.L. (2012). Community structure and the spread of infectious
550 disease in primate social networks. *Evolutionary Ecology* 26, 779-800.
- 551 Gordon, T.P., Rose, R.M., & Bernstein, I.S. (1976). Seasonal rhythm in plasma testosterone
552 levels in the rhesus monkey (*Macaca mulatta*): a three-year study. *Hormones and*
553 *Behavior* 98, 168-175.
- 554 Gulland, F.M.D. (1992). The role of nematode parasites in Soay sheep (*Ovis aries* L.)
555 mortality during a population crash. *Parasitological Research* 105, 493–503.
- 556 Habig, B. & Archie, E.A. (2015). Social status, immune response and parasitism in males: a
557 meta-analysis. *Philosophical Transactions of the Royal Society B* 370, 20140109.

- 558 Harcourt, A.H. (1987). Dominance and fertility among female primates. *Journal of*
559 *Zoology, London* 213, 471-487.
- 560 Harris, E.E., & Disotell, T.R. (1998). Nuclear gene trees and the phylogenetic relationships
561 of the mangabeys (Primates: Papionini). *Molecular Biology and Evolution* 15, 892-
562 900.
- 563 Hausfater, G., & Meade, B.J. (1982). Alternation of sleeping groves by yellow baboons
564 (*Papio cynocephalus*) as a strategy for parasite avoidance. *Primates* 23, 287-297.
- 565 Hausfater, G., & Watson, D.F. (1976). Social and reproductive correlates of parasite ova
566 emissions by baboons. *Nature* 262, 688-689.
- 567 Higham, J.P., Heistermann, M., & Maestriperi, D. (2013). The endocrinology of male
568 rhesus macaque social and reproductive status: a test of the challenge and social stress
569 hypotheses. *Behavioral Ecology and Sociobiology* 67, 19-30.
- 570 Howells, M.E., Pruett, J., & Gillespie, T.R. (2010). Patterns of gastro-intestinal parasites
571 and commensals as an index of population and ecosystem health: the case of
572 sympatric western chimpanzees (*Pan troglodytes verus*) and Guinea baboons (*Papio*
573 *hamadryas papio*) at Fongoli, Senegal. *American Journal of Primatology* 71, 1-7.
- 574 Huffman, M.A. (1997). Current evidence for self-medication in primates: A
575 multidisciplinary perspective. *Yearbook of Physical Anthropology* 40, 171–200.
- 576 Huffman, M.A., & Chapman, C.A. (2009). *Primate parasite ecology: the dynamics and*
577 *study of host-parasite relationships*. Cambridge: Cambridge University Press.
- 578 Jackson, L.A., & Farmer, J.N. (1970). Effect of host fighting behavior on the course of
579 infection of *Trypanosoma duttoni* in mice. *Ecology* 51, 672-679.

- 580 Janmaat, K.R., Olupot, W., Chancellor, R.L., Arlet, M.E., & Waser, P.M. (2009). Long-
581 term site fidelity and individual home range shifts in grey-cheeked mangabeys.
582 *International Journal of Primatology* 30, 443-466.
- 583 Jessee, M.T., Schilling, P.W., & Stunkard, J.A. (1970). Identification of intestinal helminth
584 eggs in Old World primates. *Laboratory Animal Care* 20, 83-87.
- 585 Kraus, C., Heistermann, M., & Kappeler, P.M. (1999). Physiological suppression of sexual
586 function of subordinate males: a subtle form of intrasexual competition among male
587 sifakas (*Propithecus verreauxi*)? *Physiology and Behavior* 66, 855-861.
- 588 McGrew, W.C., Tutin, C.E.G., Collins, D.A., & File, S.K. (1989). Intestinal parasites of
589 sympatric *Pan troglodytes* and *Papio* spp. at two sites: Gombe (Tanzania) and Mt.
590 Assirik (Senegal). *American Journal of Primatology* 17, 147-155.
- 591 Møller, A., Dufva, R., & Allander, K. (1993). Parasites and the evolution of host social
592 behavior. *Advances in the Study of Behavior* 22, 65–102.
- 593 Mougeot, F., Redpath, S.M., & Piertney, S. (2006). Elevated spring testosterone increases
594 parasite intensity in male red grouse. *Behavioral Ecology* 17, 117–125.
- 595 Muehlenbein, M.P. (2006). Intestinal parasite infections and fecal steroid levels in wild
596 chimpanzees. *American Journal of Physical Anthropology* 130, 546-550.
- 597 Muehlenbein, M.P. (2009). The application of endocrine measures in primate parasite
598 ecology. In M.A. Huffman & C.A. Chapman CA (Eds.), *Primate parasite ecology:
599 the dynamics and study of host-parasite relationships*. Cambridge: Cambridge
600 University Press.
- 601 Muehlenbein, M.P., & Bribiescas, R.G. (2005). Testosterone-mediated immune functions
602 and male life histories. *American Journal of Human Biology* 17, 527–558.

- 603 Muehlenbein, M.P., & Watts, D.P. (2010). The costs of dominance: testosterone, cortisol
604 and intestinal parasites in wild male chimpanzees. *BioPsychoSocial Medicine* 4, 21
- 605 Muehlenbein, M.P., Watts, D.P., & Whitten, P.L. (2004). Dominance rank and fecal
606 testosterone in adult male chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo,
607 Kibale National Park, Uganda. *American Journal of Primatology* 64, 71-82.
- 608 Muller-Graf, C.D.M., Collins, D.A., & Woolhouse, M.E.J. (1996). Intestinal parasite
609 burden in five troops of olive baboons (*Papio cynocephalus anubis*) in Gombe
610 Stream National Park, Tanzania. *Parasitology* 112, 489–497.
- 611 Munck, A., Guyre, P., & Holbrook, N. (1984). Physiological functions of glucocorticoids
612 during stress and their relation to pharmacological actions. *Endocrine Reviews* 5, 25-
613 47.
- 614 Munro, C., & Stabenfeldt, G. (1984). Development of cortisol enzyme immunoassay in
615 plasma. *Clinical Chemistry* 31, 985.
- 616 Negro, S.S., Caudron, A.K., Dubois, M., Delahaut, P., & Gemmell, N.J. (2010). Correlation
617 between male social status, testosterone levels, and parasitism in a dimorphic
618 polygynous mammal. *PLoS ONE* DOI: 10.1371/journal.pone.0012507.
- 619 Nunn, C.L. (2002a). A comparative study of leukocyte counts and disease risk in primates.
620 *Evolution* 56, 177–190.
- 621 Nunn, C.L. (2002b). Spleen size, disease risk and sexual selection: a comparative study in
622 primates. *Evolutionary Ecology Research* 4, 91–107.
- 623 Nunn, C.L., & Altizer, S.M. (2006). *Infectious diseases in primates: behavior, ecology and*
624 *evolution*. Oxford: Oxford University Press.

- 625 Nunn, C.L., Gittelman, J.L., & Antonovics, J. (2000). Promiscuity and the primate immune
626 system. *Science* 290, 1168-1170.
- 627 Olupot, W. (1999). *Mangabey dispersal and conservation in Kibale Forest National Park,*
628 *Uganda*. Dissertation. Indiana: Purdue University.
- 629 Olupot, W., & Waser, P.M. (2001a). Correlates of intergroup patterns in male grey-cheeked
630 mangabeys. *International Journal of Primatology* 22, 169-187.
- 631 Olupot, W., & Waser, P.M. (2001b). Activity patterns, habitat use and mortality risks of
632 mangabey males living outside social groups. *Animal Behaviour* 61, 1227-1235.
- 633 Olupot, W., & Waser, P.M. (2005). Patterns of male residency and inter-troop transfer in
634 mangabeys (*Lophocebus albigena*). *American Journal of Primatology* 66, 331-349.
- 635 Peters, A. (2000). Testosterone treatment is immunosuppressive in superb fairy-wrens, yet
636 free-living males with high testosterone are more immunocompetent. *Proceedings of*
637 *the Royal Society of London, B: Biological Sciences* 267, 883–889.
- 638 Prall, S.P., & Muehlenbein, M.P. (2013). Testosterone and immune function in primates: A
639 brief summary with methodological considerations. *International Journal of*
640 *Primatology* 35, 805-824.
- 641 Pusey A., & Packer, C. (1997). The ecology of relationships. In J.R. Krebs & N.B. Davies
642 (Eds.), *Behavioural ecology: an evolutionary approach*, 4th ed. (pp. 254-284). New
643 York: Blackwell.
- 644 Rifkin, J.L., Nunn, C.L., & Garamszegi, L.Z. (2012). Do animals living in larger groups
645 experience greater parasitism? A meta-analysis. *American Naturalist* 180, 70-82.
- 646 Rose, R.M., Bernstein, I.S., & Gordon, T.P. (1975). Consequences of social conflict on
647 plasma testosterone levels in rhesus monkeys. *Psychosomatic Medicine* 37, 50-60.

- 648 Salvador, A., Veiga, J.P., Martin, J., Lopez, P., Abelenda, M., & Puerta, M. (1996). The
649 cost of producing a sexual signal: testosterone increases the susceptibility of male
650 lizards to ectoparasite infestation. *Behavioral Ecology* 7, 145–150.
- 651 Sannen, A., van Elsacker, L., Heistermann, M., & Eens, M. (2004). Urinary testosterone-
652 metabolite levels and dominance rank in male and female bonobos (*Pan paniscus*).
653 *Primates* 45, 89-96.
- 654 Sapolsky, R.M. (1992). Cortisol concentrations and the social significance of rank
655 instability among wild baboons. *Psychoneuroendocrinology* 17, 701-709.
- 656 Sapolsky, R.M. (1993). Neuroendocrinology of the stress-response In J.B. Becker, S.M.
657 Breedlove, & D. Crews (Eds.), *Behavioral endocrinology* (pp. 287-324). Cambridge:
658 The MIT Press.
- 659 Sapolsky, R.M. (2004). Social status and health in humans and other animals. *Annual*
660 *Review of Anthropology* 33, 393-418.
- 661 Sapolsky, R.M. (2005). The influence of social hierarchy on primate health. *Science* 5722,
662 648-652.
- 663 Sapolsky, R.M., Alberts, S.C., & Altmann, J. (1997). Hypercortisolism associated with
664 social subordination or social isolation among wild baboons. *Archives of General*
665 *Psychiatry* 54, 1137-1143.
- 666 Sapolsky, R.M., & Spencer, E.M. (1997). Insulin-like growth factor I is suppressed in
667 socially subordinate male baboons. *American Journal of Physiology* 273, 1347-1351.
- 668 Semple, S., Cowlshaw, G., & Bennett, P.M. (2002). Immune system evolution among
669 anthropoid primates: parasites, injuries and predators. *Proceedings of the Royal*
670 *Society of London, B: Biological Sciences* 269, 1031–1037.

- 671 Seraphin, S.B. (2000). *The reproductive ecology and stress physiology of free-ranging male*
672 *chimpanzees in Budongo Forest, Uganda*. Master's thesis. Oxford: Oxford
673 University.
- 674 Setchell, J.M., Bedjabaga, I.B., Goossens, B., Reed, P., Wicking, E.J., & Knapp, L.A.
675 (2007). Parasite prevalence, abundance, and diversity in a semi-free-ranging colony of
676 *Mandrillus sphinx*. *International Journal of Primatology* 28, 1345-1362.
- 677 Setchell, J.M., Charpentier, M., Abbott, K.A., Wickings, E.J., & Knapp, L.A. (2009). Is
678 brightest best? Testing the Hamilton-Zuk hypothesis in mandrills. *International*
679 *Journal of Primatology* 30, 825-844.
- 680 Setchell, J.M., Smith, T., Wickings, E.J., & Knapp, L.A. (2010). Stress, social behaviour,
681 and secondary sexual traits in a male primate. *Hormones and Behavior* 58, 720-728.
- 682 Sheldon, B.C., & Verhulst, S. (1996). Ecological immunology: costly parasite defenses and
683 trade-offs in evolutionary ecology. *Trends in Ecology and Evolution* 11, 317-321.
- 684 Sloss, M.W., Kemp, R.L., & Zajac, A.M. (1994). *Veterinary clinical parasitology (6th ed.)*.
685 Ames: Iowa State University Press.
- 686 Snaith, T.V., Chapman, C.A., Rothman, J.M., & Wasserman, M.D. (2008). Bigger groups
687 have fewer parasites and similar cortisol levels: a multi-group analysis in red colobus
688 monkeys. *American Journal of Primatology* 70, 1072-1080.
- 689 Stear, M.J., Bairden, K., Bishop, S.C., Duncan, J.L., Karimi, S.K., McKellar Q, & Murray,
690 M. (1995). Different patterns of faecal egg output following infection of Scottish
691 blackface lambs with *Ostertagia circumcincta*. *Veterinary Parasitology* 59, 29-38.

- 692 Strier, K.B., & Ziegler, T.E. (1997). Behavioral and endocrine characteristics of the
693 reproductive cycle in wild muriqui monkeys, *Brachyteles arachnoides*. *American*
694 *Journal of Primatology* 67, 1-4.
- 695 Struhsaker, T.T. (1975). *The red colobus monkey*. Chicago: University of Chicago Press.
- 696 Stuart, M.D., Greenspan, L.L., Glander, K.E., & Clarke, M.R. (1990). Coprological survey
697 of parasites of wild mantled howling monkeys, *Alouatta palliata palliata*. *Journal of*
698 *Wildlife Diseases* 26, 547-549.
- 699 Stuart, M.D., & Strier, K.B. (1995). Primates and parasites: A case for a multidisciplinary
700 approach. *International Journal of Primatology* 16, 577–593.
- 701 Stuart, M.D., Strier, K.B., & Pierberg, S.M. (1993). A coprological survey of parasites of
702 wild muriquis *Brachyteles arachnoides* and brown howling monkeys *Alouatta fusca*.
703 *Journal of the Helminthological Society of Washington* 60, 111–115.
- 704 Thompson, M.E., Zhou, A., & Knott, C.D. (2012). Low testosterone correlates with
705 delayed development in male orang-utans. *PLoS ONE* 7: e47282.
706 doi:10.1371/journal.pone.0047282.
- 707 Tung, J., Barreiro, L.B., Burns, M.B., Grenier, J.-C., Lynch, J., Grieneisen, L.E., Altmann,
708 J., Alberts, S.C., Blekhman, R., & Archie, E.A. (2015). Social networks predict gut
709 microbiome composition in wild baboons. *eLife* 10.7554/eLife.05224.
- 710 Valtonen, A., Molleman, F., Chapman, C.A., Carey, J.R., Ayres, M.P., & Roininen, H.
711 (2013). Tropical phenology: bi-annual rhythms and interannual variation in an
712 Afrotropical butterfly assemblage. *Ecosphere* 4, 1–28.

- 713 VanderWaal, K.L., Atwill, E.R., Isbell, L.A., & McCowan, B. (2014a). Linking social and
714 pathogen transmission networks using microbial genetics in giraffe (*Giraffa*
715 *camelopardalis*). *Journal of Animal Ecology* 83, 406-414.
- 716 VanderWaal, K.L., Wang, H., McCowan, B., Fushing, H., & Isbell, L.A. (2014b). Multi-
717 level social organization and space use in reticulated giraffe (*Giraffa camelopardalis*).
718 *Behavioral Ecology* 25, 17-26.
- 719 Vitone, N.D., Altizer, S.M., & Nunn, C.L. (2004). Body size, diet and sociality influence
720 the species richness of parasitic worms in anthropoid primates. *Evolutionary Ecology*
721 *Research* 6, 1–17.
- 722 Waser, P.M. (1977a). Individual recognition, intragroup cohesion and intergroup spacing:
723 evidence from sound playback to forest monkeys. *Behaviour* 60, 27-74.
- 724 Waser, P.M. (1977b). Feeding, ranging and group size in the mangabey, *Cercocebus*
725 *albigena*. In T.H. Clutton-Brock (Ed.), *Primate ecology* (pp. 183-222). London:
726 Academic Press.
- 727 Weatherhead, P.J., Metz, K.J., Bennett, G.F., & Irwin, R.E. (1993). Parasite faunas,
728 testosterone and secondary sexual traits in male red-winged blackbirds. *Behavioral*
729 *Ecology and Sociobiology* 33, 13–23.
- 730 Welle, S., Jozefowicz, R., Forbes, G., Riggs, R.C. (1992). Effect of testosterone on
731 metabolic rate and body composition in normal men and men with muscular
732 dystrophy. *Journal of Clinical Endocrinology and Metabolism* 74, 332–335.
- 733 Whitten, P.L. (1983). Diet and dominance among female vervet monkeys (*Cercopithecus*
734 *aethiops*). *American Journal of Primatology* 5, 139-159.

- 735 Whitten, P.L., Brockman, D.K., & Stavisky, R.C. (1998). Recent advances in noninvasive
736 techniques to monitor hormone-behavior interactions. *Yearbook of Physical*
737 *Anthropology* 41, 1-23.
- 738 Wingfield, J.C., & Sapolsky, R.M. (2003). Reproduction and resistance to stress: when and
739 how. *Journal of Neuroendocrinology* 15, 711-724.
- 740 Ziegler, T.E., Scheffler, G., & Snowdon, C.T. (1995). The relationship of cortisol levels to
741 social environment and reproductive functioning in female cotton-top tamarins
742 *Saguinus oedipus*. *Hormones and Behavior* 29, 407–424.
- 743 Zuk, M. (1996). Disease, endocrine–immune interactions, and sexual selection. *Ecology* 7,
744 1037–1042.
- 745

Figure Legends

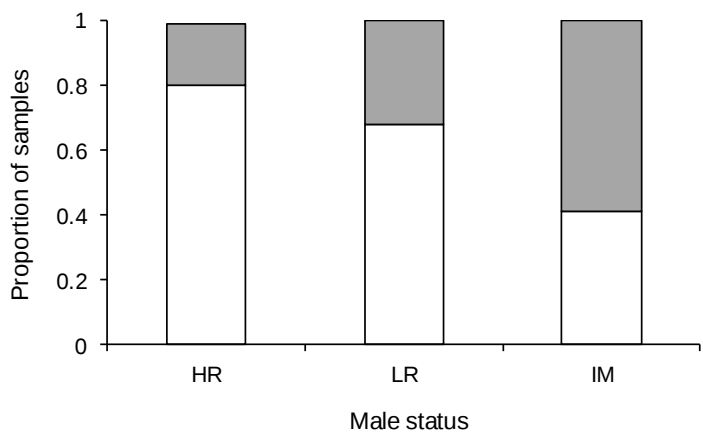


Fig.1 Nematode incidence (proportion of samples with parasites) in male gray-cheeked mangabeys relative to male status (HR/LR/M) in Kibale National Park, Uganda, 2006-2007. Shaded proportions are those with parasites; white proportions are those without parasites. HR = high-ranking males, LR = low-ranking males, IM = immigrant males.

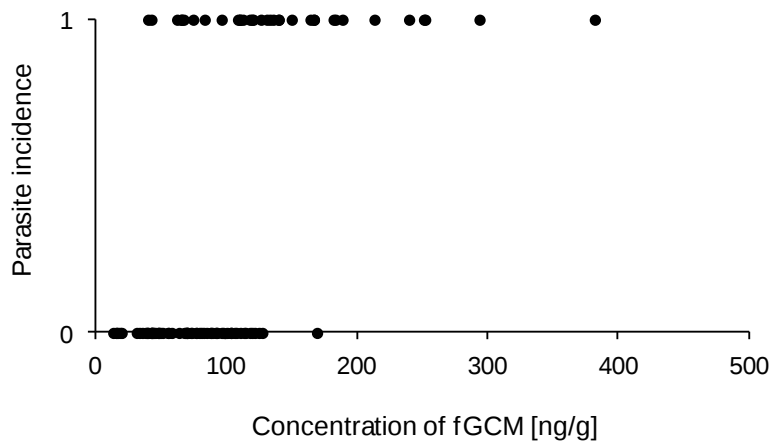


Fig. 2 Samples with and without parasites in male gray-cheeked mangabeys relative to concentrations of fecal glucocorticoid metabolite in Kibale National Park, Uganda, 2006-2007

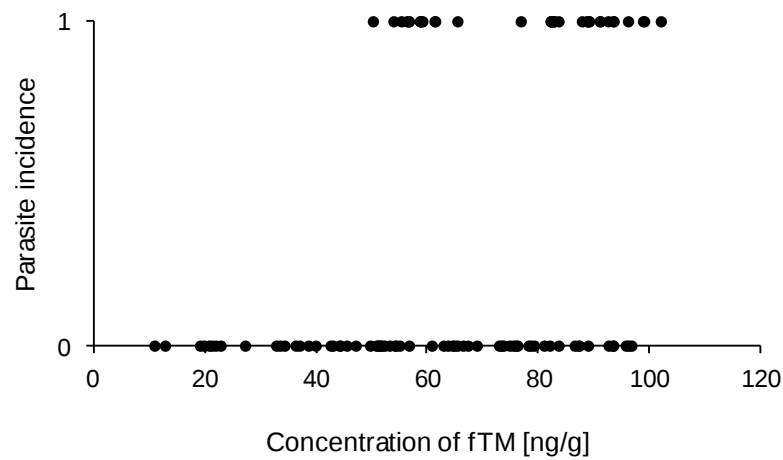


Fig. 3 Samples with and without parasites in male gray-cheeked mangabeys relative to concentrations of fecal testosterone metabolite in Kibale National Park, Uganda, 2006-2007

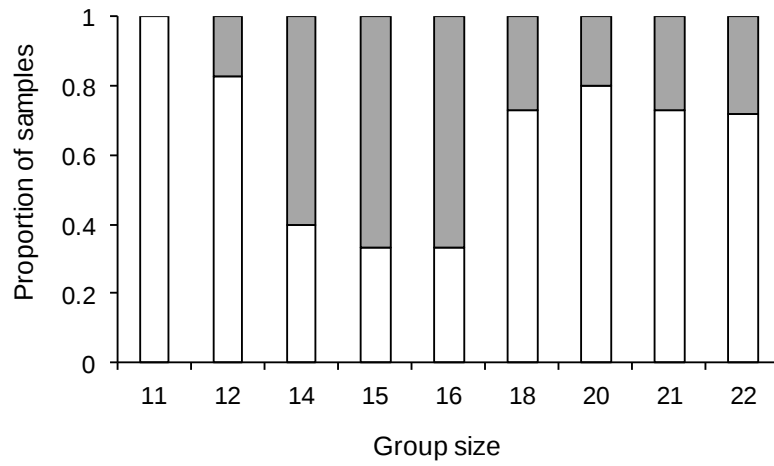


Fig.4 Nematode incidence (proportion of samples with parasites) in male gray-cheeked mangabeys relative to group size in Kibale National Park, Uganda, 2006-2007. Shaded proportions are those with parasites; white proportions are those without parasites

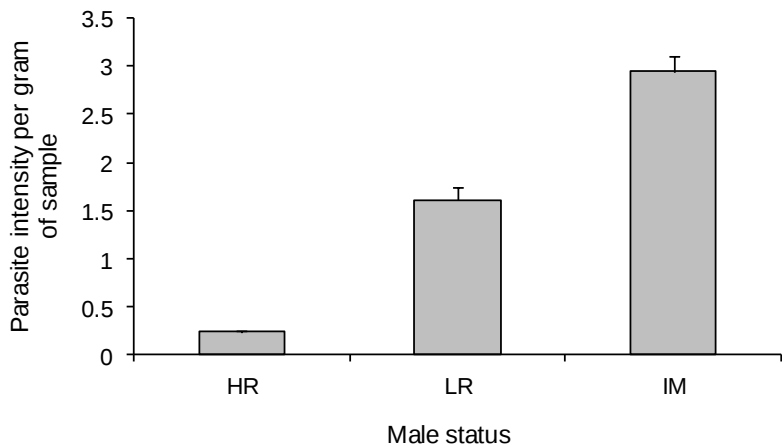


Fig. 5 Nematode intensity (abundance of parasites per gram fecal sample) in male gray-cheeked mangabeys relative to male status in Kibale National Park, Uganda, 2006-2007. HR = high-ranking males, LR = low-ranking males, IM = immigrant males

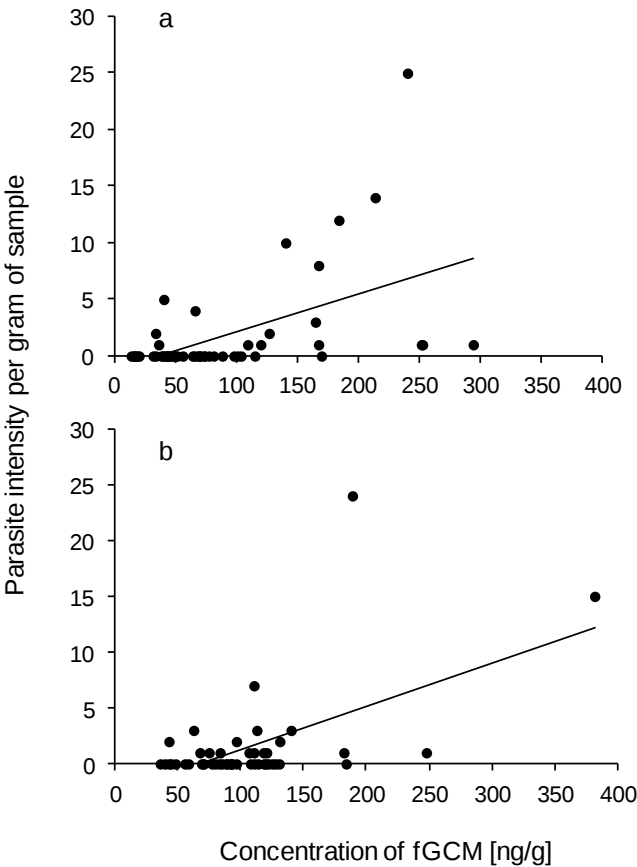


Fig. 6 Nematode intensity (abundance of parasites per gram fecal sample) in male gray-cheeked mangabeys relative to fecal glucocorticoid metabolites: a) when fTM was below the mean of 62.3 ng/g and b) when fTM was above the mean of 62.3 ng/g

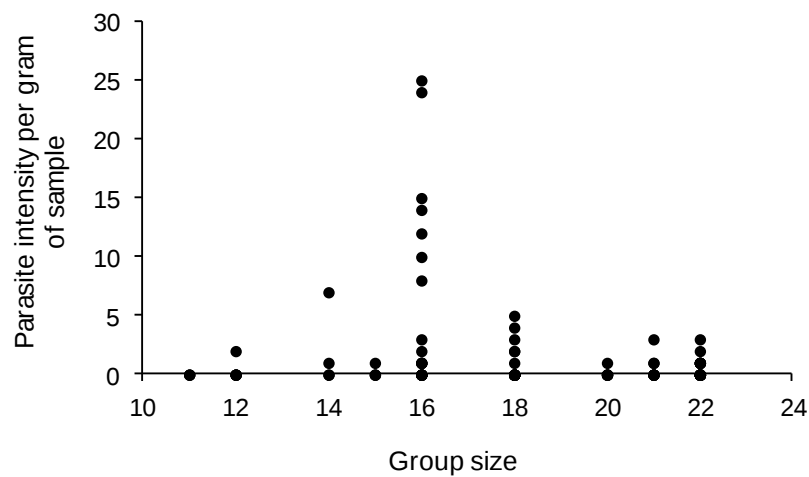


Fig. 7 Nematode intensity (abundance of parasites per gram fecal sample) in adult male gray-cheeked mangabeys relative to group size in Kibale National Park, Uganda, 2006-2007

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

Male	Status	Group	Group size	Incidence (mean±SD)	<i>Physaloptera</i> sp.	<i>Trichuris</i> sp.	<i>Strongyloidea</i> sp.	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

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

	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

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

	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
fGCM x fTM	-0.003	<0.001	<0.001