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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. We aimed 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 from 18 adult males over 19 mo 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-

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ranking males compared to high-ranking males. Fecal samples with more parasites had higher concentrations of fecal glucocorticoid and testosterone metabolites than those 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.

Keywords Fecal glucocorticoids · Fecal testosterone · Helminths · Immigrants · Male rank · Nematodes

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's 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), and 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 (McEwen 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, although 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 (Arlet *et al.* 2009a; Barrett *et al.* 2002; Bercovitch 1993; Cavigelli and Pereira 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 complicate matters further, 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 among 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, b; Nunn *et al.* 2000; Semple *et al.* 2002; Snaith *et al.* 2008; Vitone *et al.* 2004, *cf.* Rifkin *et al.* 2012). A study of red colobus monkeys (*Procolobus rufomitratus*) 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 howlers (*Alouatta palliata*: Stuart *et al.* 1990), and black howlers (*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 (fGCMs) 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 mo were similar to those of resident males (Arlet *et al.* 2009a).

We aimed to identify the social, physiological, and environmental factors that positively correlate 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 km^2) 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 individuals 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 nonstudy groups. Nevertheless, we knew that all four collared males were ≥20 yr 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 that won 20 % more fights than other males and low rank to four males that 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, labeling males more precisely than high- or low-rank seems unwarranted.

Immigrant Males

Four males that 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 and the sample was collected within minutes of defecation, placed in a sterile scintillation vial, and stored on ice (for hormone analysis). Approximately 5 g 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.* 1998).

We collected one sample per male per particular day, with time intervals of at least 1 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 I), 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 analyzed 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

Table I 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)	*Physaloptera* sp.	*Trichuris* sp.	*Strongyloidea* 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	6
LM	HR	BT1	18	0.4 ± 0.55	0	3	0	1	4	71.1 ± 16.1	5
PL	LR	BT1	18	1.0 ± 0.0	3	1	3	0	7	36.5 ± 4.7	2
BG2	LR	BT1	18	0.43 ± 0.53	7	0	0	0	7	53.8 ± 9.79	7
KR	HR	CC	15	0.33 ± 0.58	0	0	0	1	1	67.8 ± 25.3	3
MF	HR	CC	18	0.25 ± 0.5	2	0	0	0	2	82.8 ± 13.5	4
KJ	LR	CC	16	0.6 ± 0.55	25	0	0	1	26	68.7 ± 69.4	5
KK	M	CC	16	0.7 ± 0.48	51	0	12	3	66	137.4 ± 57.2	10
MF	M	CC	16	0.7 ± 0.5	18	0	8	0	18	220.5 ± 107.6	4
MG	HR	LC1	22	0.0 ± 0.0	0	0	0	0	0	110.1 ± 15.9	7
R	HR	LC1	21	0.0 ± 0.0	0	0	0	0	0	132.6 ± 29.7	5
YM	HR	LC1	21	0.5 ± 0.6	0	0	2	0	2	115.3 ± 47.8	4
MR	LR	LC1	22	0.0 ± 0.0	0	0	0	0	0	28.7 ± 15.2	6
NK	LR	LC1	22	0.4 ± 0.55	1	0	3	0	4	70.2 ± 37.7	5
BW	M	LC1	22	0.4 ± 0.52	2	1	4	0	7	98.6 ± 29.3	8
HL	M	LC1	21	0.6 ± 0.52	2	0	2	0	4	183.1 ± 29.3	7
IB	HR	LC2	12	0.2 ± 0.45	1	1	0	0	2	41.8 ± 4.66	5
NY	LR	LC2	12	0.0 ± 0.0	0	0	0	0	0	33.7 ± 13.1	4
KY	HR	MK	15	0.33 ± 0.58	0	0	1	0	1	71.0 ± 3.05	3
KC	LR	MK	14	0.5 ± 0.7	5	0	2	0	7	82.8 ± 38.7	2

involved examining the total sediment (Sloss *et al.* 1994; C. A. Chapman *et al. unpubl. 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 μm ± 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 (Stear *et al.* 1995), limiting the conclusions we can draw using this method. However, it is frequently used to describe infections (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 authors of 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 fecal testosterone metabolite (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 the 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 h. After mixing, samples were spun in a centrifuge for 30 min at 3200 rpm 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 of methanol. This methanol was dried, resuspended in 1 ml of ethanol, and 50 μl was taken for the enzyme immunoassay.

The WNPRC lab used the antibody R4866 for cortisol analysis which was developed by Munro and Stabenfeldt (1984) and is well characterized. The antibody cross-reacts 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 cross-reacts 92.4 % with dihydrotestosterone, 11.2 % with 4-androsten-3β, 17β-diol, 5.4 % with dehydroandrosterone, 3.4 % with androstenediol, 2.1 % with androstenedione, and <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 interassay coefficients of variation were 13.6 and 12.8 for the low and high pools, respectively, and the intraassay 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 interassay coefficients of variation were 10.6 and 11.7 for the low and high pools, respectively, and the intraassay 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 one 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 (GLMMs), 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), fGCM concentration, fTM concentration, 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 gram of fecal sample) using the same predictor variables with centered values for fGCMs and fTMs. 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 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 II).

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, $P < 0.001$; Fig. 1). Samples with parasites had higher fGCM and fTM levels than those without parasites (Table II, Figs. 2 and 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; Fig. 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 III).

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

Table II 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	–5.3	2.2	0.02
Status	4.75	3.09	0.002
fGCM	0.03	0.009	0.001
fTM	0.09	0.03	0.001
Group size	–0.43	0.12	0.001
Rainfall	0.08	0.09	0.35

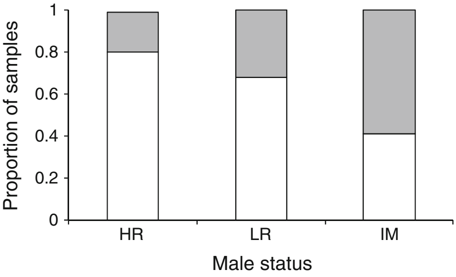

Fig. 1 Nematode incidence (proportion of samples with parasites) in male gray-cheeked mangabeys relative to male status (HR/LR/M) in Kibale National Park, Uganda, 2006–2007. Shaded proportions are those with parasites; white proportions are those without parasites. HR = high-ranking males; LR = low-ranking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

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, $P = 0.05$; Fig. 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 III): 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 (Fig. 6). Further, nematode intensity was greatest at intermediate group sizes of 14–18 individuals within the group (Table III, Fig. 7). Finally, samples collected during rainy season months had greater nematode intensities than those from dry season months (Table III, Fig. 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

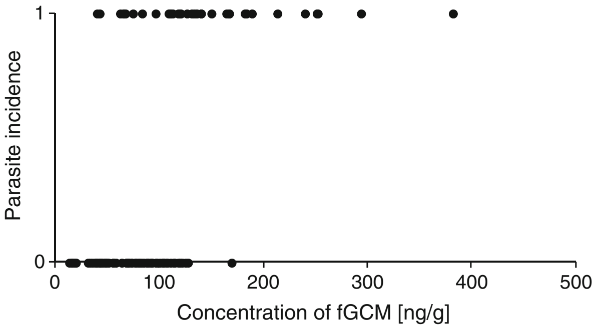

Fig. 2 Samples with and without parasites in male gray-cheeked mangabeys relative to concentrations of fGCM in Kibale National Park, Uganda, 2006–2007.

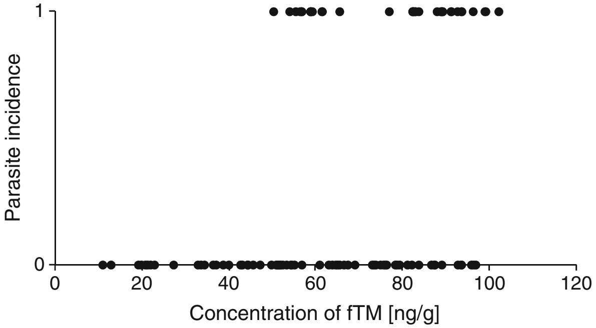

Fig. 3 Samples with and without parasites in male gray-cheeked mangabeys relative to concentrations of fecal testosterone metabolite in Kibale National Park, Uganda, 2006–2007.

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 that 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). Although 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 6 mo after males have transferred into a new group (Arlet

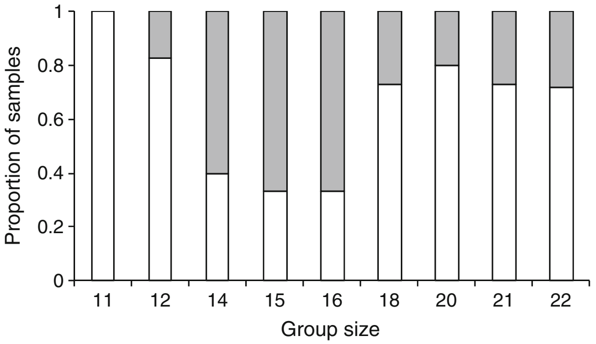

Fig. 4 Nematode incidence (proportion of samples with parasites) in male gray-cheeked mangabeys relative to group size in Kibale National Park, Uganda, 2006–2007. Shaded proportions are those with parasites; white proportions are those without parasites.

Table III 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	1.08	0.72	0.14
Status	3.94	3.97	<0.001
fGCM	0.01	0.001	<0.001
fTM	0.06	0.009	<0.001
Group size	–0.28	0.04	0.01
Rainfall	0.13	0.03	0.003
fGCM × fTM	–0.003	<0.001	<0.001

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) and 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

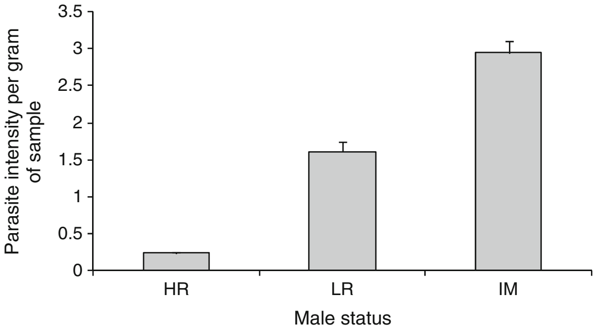

Fig. 5 Nematode intensity (abundance of parasites per gram of fecal sample) in male gray-cheeked mangabeys relative to male status in Kibale National Park, Uganda, 2006–2007. HR = high-ranking males; LR = low-ranking males; IM = immigrant males.

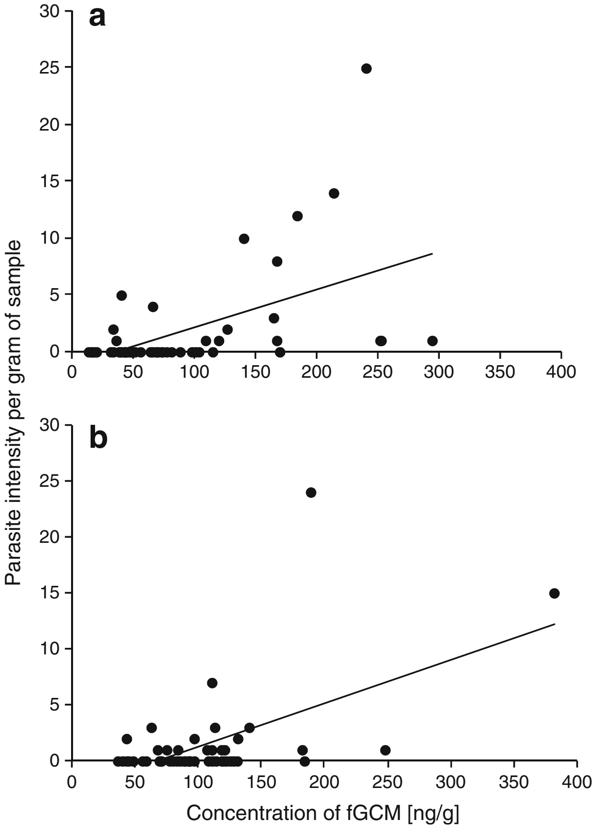

Fig. 6 Nematode intensity (abundance of parasites per gram fecal sample) in male gray-cheeked mangabeys relative to fGCMs. **(a)** When fTM was below the mean of 62.3 ng/g and **(b)** when fTM was above the mean of 62.3 ng/g.

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 I) than low-ranking males (testosterone: 46.6; nematode intensity: 7.3; Table I). The trend is similar if outlier immigrant male KK, with the highest nematode load, is removed.

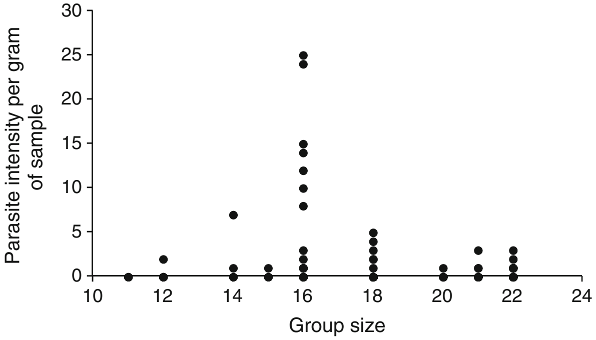

Fig. 7 Nematode intensity (abundance of parasites per gram of fecal sample) in adult male gray-cheeked mangabeys relative to group size in Kibale National Park, Uganda, 2006–2007.

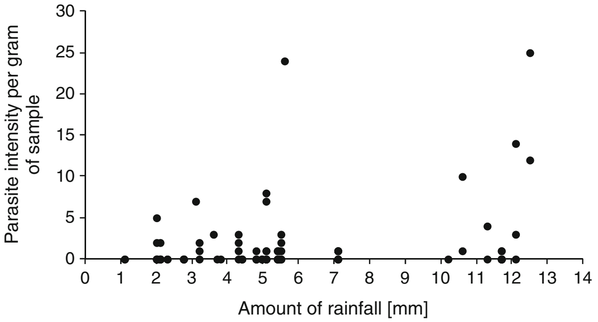

Fig. 8 Nematode intensity (abundance of parasites per gram of fecal sample) in adult male gray-cheeked mangabeys relative to monthly rainfall (mm) in Kibale National Park, Uganda, 2006–2007. Each point represents one fecal sample (*N* = 102).

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 the 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 acquired from their former groups.

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