

## SHORT COMMUNICATION

## Comparison of gastrointestinal parasite communities in vervet monkeys

Kim VALENTA,<sup>1</sup> Dennis TWINOMUGISHA,<sup>2</sup> Kathleen GODFREY,<sup>1</sup> Cynthia LIU,<sup>1</sup> Valérie A. M. SCHOOF,<sup>3</sup> Tony L. GOLDBERG<sup>2,4</sup> and Colin A. CHAPMAN<sup>1,2,5</sup>

<sup>1</sup>McGill School of Environment, McGill University, Montreal, Quebec, Canada, <sup>2</sup>Makerere University Biological Field Station, Kampala, Uganda, <sup>3</sup>Bilingual Biology Program, Department of Multidisciplinary Studies, Glendon Campus, York University, Toronto, Ontario, Canada, <sup>4</sup>Department of Pathobiological Sciences, School of Veterinary Medicine, University of Wisconsin-Madison, Madison, Wisconsin, USA and <sup>5</sup>Wildlife Conservation Society, Bronx, New York, USA

### Abstract

Globally, habitat degradation is accelerating, especially in the tropics. Changes to interface habitats can increase environmental overlap among nonhuman primates, people, and domestic animals and change stress levels in wildlife, leading to changes in their risk of parasite infections. However, the direction and consequences of these changes are unclear, since animals may benefit by exploiting human resources (e.g., improving nutritional health by eating nutritious crops) and decreasing susceptibility to infection, or interactions with humans may lead to chronic stress and increased susceptibility to infection. Vervet monkeys are an excellent model to understand parasitic disease transmission because of their tolerance to anthropogenic disturbance. Here we quantify the gastrointestinal parasites of a group of vervet monkeys (*Chlorocebus aethiops*) near Lake Nabugabo, Uganda, that frequently overlaps with people in their use of a highly modified environment. We compare the parasites found in this population to seven other sites where vervet monkey gastrointestinal parasites have been identified. The vervets of Lake Nabugabo have the greatest richness of parasites documented to date. We discuss how this may reflect differences in sampling intensity or differences in the types of habitat where vervet parasites have been sampled.

**Key Words:** anthropogenic disturbance, disease, gastrointestinal parasite, habitat degradation, Nabugabo, vervet, zoonotic disease

### INTRODUCTION

Parasitism is fundamentally linked to the environment and the condition of the host (Holt *et al.* 2003;

Nunn & Altizer 2006). For example, the number of parasite eggs in the environment is lower in hot, dry months compared to wetter months, and increased environmental moisture is positively related to prevalence and intensity of infections (Appleton & Henzi 1993; Appleton & Brain 1995; Larsen & Roepstorff 1999; Chapman *et al.* 2010, 2015). Environmental conditions also affect the host, altering susceptibility to parasite infections. Marginal environmental conditions can cause physiological stress, and chronic stress can suppress the im-

*Correspondence:* Kim Valenta, McGill School of Environment, McGill University, 3534 University St. H3A 2A7 Montreal, Quebec, Canada.  
Email: kim.valenta@McGill.ca

mune system leading to greater risk of infections (Black 1994; Coe & Erickson 1997; Padgett & Glaser 2003). For example, in free-ranging chamois (*Rupicapra rupicapra*), stress hormone levels and gastrointestinal and lung helminth counts were found to co-vary throughout the year (Hoby *et al.* 2006). Similarly, primates experiencing chronically elevated stress and depressed immune function have increased parasite burden and are at a higher risk of acquiring parasites than those that experience less stress (Muehlenbein 2006; Chapman *et al.* 2015). Such host–parasite–environment linkages mean that when people cause environmental change it can have cascading effects on parasitism and the health of nonhuman hosts in those environments.

The effects on wild animals living in habitats modified by humans are complex. However, given current trends in forest loss, cropland expansion and human population growth (Foley *et al.* 2011; Balmford *et al.* 2012; Estrada 2013; Hansen *et al.* 2013; Phalan *et al.* 2013), it is reasonable to expect increasing effects of environmental change on wildlife, including changes in the nature of parasite infection. For example, primates that frequent areas heavily used by humans and domesticated animals may be exposed to a higher diversity of parasites than primates in undisturbed habitats. Furthermore, primates in such anthropogenically-disturbed locations may be chronically stressed due to frequent conflict with people and their domesticated animals, thereby increasing their susceptibility to infection (Chapman *et al.* 2006). Alternatively, susceptibility to parasites may decrease as primates gain access to nutritional crops, decreasing nutritional stress (Wallis 2000; Hahn *et al.* 2003). Ekanayake *et al.* (2006) showed higher prevalence of *Cryptosporidium* sp. infections in toque macaques (*Macaca sinica*), gray langurs (*Semnopithecus priam*) and purple-faced langurs (*Trachypithecus vetulus*) in areas used by humans than in areas not used by humans. Furthermore, a greater prevalence of *Enterobius* sp., *Strongyloides* sp., *Trichuris* sp., strongyle-type eggs, *Entamoeba coli* and *E. histolytica/dispar* were found in the macaques that ranged in areas used by humans (Ekanayake *et al.* 2006). Similarly, Chapman *et al.* (2006) found that red colobus (*Procolobus rufomitatus*) in forest fragments who were feeding on crops had higher levels of stress and greater parasite infections than red colobus in continuous old-growth forest.

The objective of the present study was to identify the gastrointestinal parasites in a population of vervet monkeys (*Chlorocebus aethiops*) living in a highly anthro-

pogenically-modified landscape neighboring Lake Nabugabo, Uganda. Vervet monkeys are extremely flexible in terms of diet and habitat use. Vervets are often found living in urban, peri-urban or agricultural environments, sometimes co-existing with humans, as well as in undisturbed savanna, and woodland, riverine systems. Vervet monkeys are considered pests because they frequently crop raid or steal human food (Boulton *et al.* 1996; Saj *et al.* 2001; Gillingham & Lee 2003; Chapman *et al.* 2016). Because of their proximity to (and frequent interaction with) humans and their ability to live in habitats ranging from old-growth forest to cities, vervet monkeys are a good model for understanding parasitic infections in wildlife populations inhabiting highly anthropogenic habitats. Here we present data on the largest sample of vervet gastrointestinal parasites collected to date, and discuss our findings in light of anthropogenic and habitat variables that may influence vervet parasite richness.

## MATERIALS AND METHODS

The study took place on the shores of Lake Nabugabo, Masaka District, Central Uganda (0°22′–12°S, 31°54′E) near McGill's Lake Nabugabo Research Station. Lake Nabugabo is a satellite lake of Lake Victoria and lies at an elevation of 1136 m. The lake is mostly surrounded by wetlands, grasslands and patches of swamp forest; however, a portion to the west side of the lake consists of farmers' fields, degraded forest and a few buildings. The area receives an average of 1348 mm of rain annually, and precipitation is primarily influenced by the north–south migration of the Intertropical Convergence Zone (ITCZ), causing a bimodal rainfall pattern consisting of 2 rainy seasons (March through mid-May and November through early December), separated by 2 dry seasons (late December through February and mid-May through October) (Stampone *et al.* 2011).

We assessed parasite infection non-invasively, by collecting feces from a single habituated group of vervets that has been studied since May 2011. The group contained on average 24 individuals (2 adult males, 5 adult females, 3 subadult males, 3 subadult females, and 11 juveniles and infants), all of which were individually identifiable based on scars, markings and variation in pelage. Two of the juveniles that were sampled died before sex could be determined. Overall, we obtained 403 samples between May 2011–June 2014, and January–February 2015. Fecal samples were labeled with the in-

dividual, date, location and time of collection. At the end of each day, observers weighed 1.0 g of wet fecal matter from each sample and stored it in 2.0 mL of 10% formalin solution for parasite identification.

Samples were examined for helminth eggs, larvae and large protozoan cysts using a modified ethyl acetate sedimentation method, in which 5 slides of the sediment were examined for each sample (Sloss *et al.* 1994; Bowman 1999; Garcia 1999; Greiner & McIntosh 2009). To identify protozoans, we used the hematocrit staining procedure to identify species (Bowman 1999) and examined trichrome-stained slides. We used a Leica

DM2500 light microscope (71 Four Valley Drive, Concord, Ontario, L4K 4V8 Canada) under 10–100× magnification to examine thin preparations of sedimented feces. Parasites were photographed and identified based on morphological traits, including egg size, color, shape and contents. Measurements were made to the nearest 0.1  $\mu\text{m} \pm \text{SD}$  using an ocular micrometer fitted to the compound microscope; parasites were photographed using Infinity camera software for further identification and documentation.

We plotted the frequency of eggs or larvae at different size classes (0.1 mm bins) to examine variation in

**Table 1** Parasites identified in different wild vervet populations

		This study	Mahale	Rubondo	Rural Kenya	Sodore	Wondo	Loskop	Hawassa
Cestodes	<i>Cestode</i> (unidentified)	X							X
Nematode	<i>Anatrichosoma</i>			X					
	<i>Ascaris</i> spp.	X							X
	<i>Hyostromylyus</i> spp.	X							
	<i>Mammonogamus</i> spp.								X
	<i>Metastrongylus</i>	X							
	<i>Necator</i> (hookworm, likely this genus)							X	X
	<i>Oesophogostomum</i>	X	X					X	
	Spirurid			X				X	
	<i>Streptophargus</i>		X						
	Strongylida	X		X	X				
	<i>Strongyloides</i> (possibly <i>fuelleborni</i> )	X	X	X	X	X		X	X
	<i>Subulura</i>		X	X					
	<i>Toxocara</i>	X							
<i>Trichuris</i>	X	X	X	X	X	X	X	X	
Trematode	<i>Trematode</i> (unidentified)	X							
	<i>Fasciola</i>	X							
	<i>Dicrocoeliida</i>		X						
	<i>Schistosoma mansoni</i>				X				
Protist	<i>Balantidium coli</i>				X				X
	<i>Blastocystis hominis</i>			X		X			
	Coccidia								X
	<i>Cryptosporidium</i>					X	X		
	<i>Cyclospora</i>					X	X		
	<i>Entamoeba coli</i>		X	X		X	X	X	X
	<i>Entamoeba histolytica/dispar</i>		X		X	X	X		
	<i>Giardia</i> spp.			X					X
	<i>Iodamoeba</i> spp.			X					X
Sample number		403	72	111	123	25	16	272	140
Richness	Excluding Protozoans	11	6	6	3	2	1	6	6

X indicates that parasites are present.

egg size, but no evidence was found for any subdivision of a taxonomic group that we considered for any type of parasite. Parasites were identified to the genus level wherever possible, but for some parasites identification at a higher taxonomic level was necessary (Greiner & McIntosh 2009; Ghai *et al.* 2014a,b). An individual was considered infected if at least one helminth egg or larva was identified. We aggregated data to calculate parasite richness (the number of parasite species or types found in the population). When interpreting results based on richness, it should be cautioned that if host communities have a high species richness index, this does not necessarily imply that the animals in the community are less healthy, as the parasite species are not all equivalent and different parasite infections have different effects.

To determine whether there were age class or sex differences in parasite occurrence, we compared the number of fecal samples positive for parasites divided by the total number of fecal samples collected for each group for all juveniles and subadults ( $N = 10$ ), to all adults ( $N = 14$ ), and all males ( $N = 9$ ) to all females ( $N = 13$ ) using a  $\chi^2$ -test (IBM SPSS Statistics, V 23). To determine parasite prevalence in the community, we calculated the number of hosts infected with each parasite, then divided this number by the total number of vervets sampled ( $N = 24$ ) (Margolis *et al.* 1982).

We compared our results with published results of parasite richness in other vervet monkey populations (Table 1). These included the Mahale Mountains National Park, Tanzania (Kooriyama *et al.* 2012); Rubondo Island, Tanzania (Petrasova *et al.* 2010); rural Kenya (Muriuki *et al.* 1998); Sodore, Ethiopia, a recreational area where vervets roam on hotel premises; Wondo Grenet, Ethiopia, where vervets are found on the Wabe Shebele Hotel premises (Legesse & Erko 2004); Lake Hawassa in southern Ethiopia (Amenu *et al.* 2015); and the protected area of Loskop Dam Nature Reserve, South Africa (Wren *et al.* 2015).

## RESULTS

In total, 65% of fecal samples were positive for at least one parasite (262/403), and no differences were detected between parasite infections by age or sex classes (Table 2); 68% of subadult and juvenile fecal samples, and 64% of adult fecal samples had at least 1 parasite species present, and the difference was not significant ( $\chi^2 = 0.38$ ,  $P = 0.54$ ). Sex also did not have an effect on parasite presence in the vervets studied here: 64% of female fecal samples had at least 1 parasite spe-

**Table 2** Fecal sample numbers, positive samples and parasites per fecal sample for 24 monkeys, by age and sex class

Age/Sex Class	Number of individuals	Number of positive samples	Sample number	Percent of positive samples	Mean parasites per sample	Number of samples with >1 parasite species present	Percent of samples with >1 parasite species present
Subadults and juveniles	10	57	84	68%	1.26	12	21%
Adults	14	205	319	64%	1.29	43	21%
All males	9	84	125	67%	1.34	21	25%
All females	13	170	267	64%	1.26	34	20%
All individuals	24	262	403	65%	1.29	55	21%

Note: Sex is unknown for 2 juveniles. They are included in the adult versus subadult/juvenile analysis ( $N = 24$  monkeys), and excluded from the male/female analysis ( $N = 22$  monkeys).

**Table 3** Percent of individual monkeys found to have parasite species or types.  $N = 24$  monkeys

Ascaris	Cestode	Fasciola	Hyostrongylus	Metastrongylus	Unknown Protozoan	Unknown Oesophogostomum	Strongyle	Strongyloides	Toxocara	Trematode	Trichuris	Unknown spp.
33%	38%	38%	4%	4%	17%	4%	8%	29%	25%	17%	13%	75%

cies present and 65% of male fecal samples had at least 1 parasite species present, and the difference was not significant ( $\chi^2 = 0.47$ ,  $P = 0.50$ ).

Trematodes were the most prevalent, occurring in 92% of individuals at least once, followed by *Fasciola* spp. (38%), cestodes (38%), *Ascaris* spp. (33%) and *Strongyloides* spp. (29%). All other parasites were found in less than 25% of the individuals (Table 3). Many fecal samples (21%) had only 1 parasite present (55/403), and, overall, fecal samples had a mean of 1.29 parasite species per sample.

In total, 11 identifiable parasite taxa were found in the Lake Nabugabo vervet population (Table 1). Of these, 3 have not been found in other vervet populations sampled: *Metastrongylus*, *Toxocara* and *Fasciola*. Of these 3, 1 is associated with the ingestion of intermediate hosts (e.g. earthworms, *Metastrongylus*), 1 is directly ingested in contaminated soil or vegetation (*Fasciola*), and 1 can be ingested directly or through an intermediate host (*Toxocara*, Cheng 1973).

When compared to the results of 7 other studies, non-protozoan vervet parasite species richness at Lake Nabugabo ( $N = 11$ ) was almost double that of the next highest studies ( $N = 6$ , Mahale, Rubondo, and Hawassa). Some component of this difference in parasite species richness between studies likely results from variation in sampling intensity, which ranged from a low of 16 fecal samples at Wondo Genet, Ethiopia, to 403 fecal samples (this study). Across all studies, a mean of 4.8% of samples were positive for non-protozoan parasites (SD = 2.8%, range = 1.9–8.3%).

## DISCUSSION

Compared to 7 other sites where vervet monkey gastrointestinal parasites have been described, the vervets of Lake Nabugabo have the greatest parasite richness. This finding is likely the result of a number of factors. To some degree, the increased parasite richness observed in this study may be due to our larger sample size. It is also possible that the higher parasite richness observed in the Lake Nabugabo population results from the highly anthropogenically disturbed nature of the study group's habitat: vervets at Lake Nabugabo have frequent interactions with humans, dogs and livestock (Chapman *et al.* 2016). However, living in a highly disturbed habitat does not alone explain the higher parasite species richness observed in this study, as 4 of the 7 other vervet populations sampled also live in highly disturbed habitats (Table 4). Of the 7 extant studies

of vervet parasites, 3 were conducted in holiday resorts in Ethiopia, where tourists are known to interact closely with vervets (Sodore, Wondo Genet, and Lake Hawassa [Legesse & Erko 2004; Amenu *et al.* 2015]), and in one, vervet samples were collected from village sites in Kenya, where interactions with humans are likely to have occurred (Muriuki *et al.* 1998). Of the 3 studies that took place in protected habitats, all 3, nonetheless, had long-term researcher presence, one had long-term research presence and tourism (Mahale Mountains, Tanzania [McGrew *et al.* 1996]), and one was notable for the release of many captive-bred primates into the ecosystem (Lake Hawassa, Ethiopia [Amenu *et al.* 2015]). The number of individual variables contributing to anthropogenic disturbance at these sites highlights the difficulty of establishing anthropogenic drivers behind differences among populations in parasite infections.

While continental-wide comparisons of vervet parasite species contribute to a broader picture of vervet-parasite interactions, caution should be used in interpreting comparisons between populations for at least 4 reasons: (i) the methods and ability to identify parasites vary among studies which produces variance for which we cannot determine the magnitude; (ii) the sample size is not the same at each site and species richness may at least partly result from the number of samples assessed; (iii) it is difficult to control for habitat-specific factors that could influence the parasites that infect host populations (e.g. soil moisture, frequency of intra-group interactions); and (iv) it is difficult to assess the regional pool of parasites in a rigorous quantitative manner. The regional parasite pool will be a function of vervet monkey population size and composition and for parasite species that are host generalists, the community of host species present in the region and their respective abundance.

Without genetic analysis of parasites, it is not possible to ascertain if human to nonhuman primate parasite transmission is occurring (de Grijter *et al.* 2005; Ghai *et al.* 2014a,b). Genetic analysis of transmission is valuable. For example, research based only on coproscopic analysis concluded that nodular worms (*Oesophagostomum* spp.) could be transmitted from nonhuman primates to people and thus primates posed a health risk to humans (Polderman & Blotkamp 1995). However, additional genetic analyses determined that the nodular worms found in human and nonhuman primates were in fact genetically distinct (Gasser *et al.* 2006). Similarly, researchers identified 3 genetically distinct groups of whipworms that could not be distinguished by mi-

**Table 4** Descriptions of vervet parasite sampling locations: Habitat type, degree of disturbance and observed direct human interactions

Location	Habitat type	Degree of anthropogenic habitat disturbance	Direct human interactions observed	Source
Lake Nabugabo, Uganda	Anthropogenic landscape, adjacent to large lake. Mixed use recreational areas, hotel compounds, small-scale subsistence agricultural plots, village, small patches of secondary forest.	High	Yes	Personal observations
Mahale Mountains National Park, Tanzania	Tropical semi-evergreen forest, adjacent to large lake.	Low. Protected as a national park. Ecotourism and permanent researcher presence. Nearest village is 20 km away from research site.	No	McGrew <i>et al.</i> (1996)
Rubondo Island National Park, Tanzania	Mixed evergreen forest, semi-deciduous forest, grassland. Protected as game reserve since 1928. Island within a large lake (Lake Victoria).	Low. Protected as a game reserve since 1928, and later as a national park. Researcher presence, and captive-bred primates released onto island.	No	Petrasova <i>et al.</i> (2010)
Various locations throughout Kenya	Villages	Presumed high	No	Muriuki <i>et al.</i> (1998)
Sodere Resort, Ethiopia	Anthropogenic – a resort.	High	Yes. Frequent interactions with tourists reported.	Legesse and Erko (2004)
Wondo-Genet Resort, Ethiopia	Anthropogenic – a resort.	High	Yes	Legesse and Erko (2004)
Lake Hawassa, Ethiopia	Anthropogenic – various resorts and recreation areas, including hotels.	High	Yes. Frequent interactions with tourists reported.	Amenu <i>et al.</i> (2015)
Loskop Dam Nature Reserve, South Africa	Mixed bushveld and woodland. Protected reserve, but with tourist resorts and facilities.	Moderate	No, though sometimes followed by researchers.	Wren <i>et al.</i> (2015, 2016) and B. Wren (personal communication)

croscopic examination of their eggs (Ghai *et al.* 2014b). One of these genetically unique groups was found in all 9 species of primates examined, including humans, but the other 2 *Trichuris* groups were not. Some parasites are transmissible between humans and nonhuman primates, while others are not, which emphasizes the need for genetic studies when examining inter-species transmission.

Previous studies have found that variations in parasite infection among individuals, age/sex categories, and populations are linked to the environment and the condition of the host (Holt *et al.* 2003; Padgett & Glaser 2003; Ekanayake *et al.* 2006; Nunn & Altizer 2006).

In this study, we observed no significant differences in parasite species richness between age and sex classes. As well, when compared to other studies of vervet parasites from areas ranging from highly anthropogenically disturbed to relatively pristine, differences in sample size do not allow us to draw conclusions about the role of environmental factors in the likelihood of parasite transmission. With respect to the condition of the host, while stress is known to be a factor influencing parasitic infection (Chapman *et al.* 2006), host condition is difficult to quantify and compare. Our study group was likely chronically stressed by frequent interactions with humans - who are known to chase and kill group mem-

bers—and dogs, which are a known predator of vervets in this population (Chapman *et al.* 2016). However, this stress may have been mitigated by the year-round availability of food sources, namely crops planted by humans. Determining how physiological stress and diet interact to influence parasite infection in this population could contribute to a growing body of literature about the complex effects of environmental variation on parasite infection in primates (Gulland 1992; Pride 2005; Snaith *et al.* 2008).

Because of the lack of detailed data on environmental variables, host condition, and vervet stress in multiple sites, it is impossible at present to robustly delineate the role of these factors in parasite infection. However, our study did uncover 3 parasite genera previously undocumented in vervets – *Metastrongylus*, *Toxocara* and *Fasciola*. The presence of these parasites in our study population may reflect the increased sampling effort in this study, or their presence may reflect the proximity of the vervets in this population to villages, small-scale farms (*Metastrongylus*, *Toxocara*), and a lakeshore (*Fasciola*) – features not present in other studies of vervet parasites (Table 4). *Metastrongylus* spp. is a lung worm that frequently infects domestic pigs. *Metastrongylus* spp. reproduces when eggs are passed in the feces of a mammalian (often pig) host, swallowed by earth worms, after which the earth worms are ingested (Cheng 1973). In 46 months of behavioral observations at Nabugabo, vervets were never seen to ingest earthworms, though vervets in this population frequently crop-raided farms that include pigs (Chapman 2016, unpubl. data). While other vervet parasite studies have taken place in disturbed habitats, or areas with high monkey–human interactions, they tended to also be areas without small-scale farming (Table 4). Similarly, while diverse in its life cycle based on species, *Toxocara* spp. often develop to second-stage larvae in intermediate hosts including cockroaches, chickens, mice, dogs, and cats, all of which are common in the villages occurring within the home range of the Lake Nabugabo vervet monkeys (Cheng 1973). *Fasciola* spp., the liver flukes discovered for the first time in this population of vervets, may reflect their foraging along the lake shore, particularly on vegetation overhanging water, where vervets are safe from predatory dogs (see also James *et al.* 1983). *Fasciola* spp. reach their infective larval stage on aquatic plants, on which vervets in our study population frequently forage (Chapman, pers. obs.). In contrast, other vervet populations may not have associated as closely with water and aquatic vegetation.

In the future, studies would benefit from a controlled

comparative perspective—quantifying both habitat disturbance, and levels of human and domestic animal interaction by vervet monkeys. As well, consistent sampling intensity and lab methods for parasite detection should be employed across studies. Given the abundance of vervet monkeys in many human modified habitats, they are a useful species for such investigations. Furthermore, anthropogenically-disturbed habitats are ubiquitous, thus it is vital that we understand animal behavioral and ecological responses to these environments to better understand and predict future changes in wildlife populations, and for the construction of informed conservation plans. Vervet monkeys are an excellent model for understanding the role of anthropogenic habitat change on behavioral and ecological responses, and on parasite transmission to wildlife.

## REFERENCES

- Amenu K, Tesaye D, Tilahun G, Mekibib B (2015). Gastrointestinal parasites of vervet monkeys around Lake Hawassa recreational sites, southern Ethiopia. *Comparative Clinical Pathology* **24**, 1491–6.
- Appleton CC, Brain C (1995). Gastrointestinal parasites of *Papio cynocephalus ursinus* living in the Central Namib Desert, Namibia. *African Journal of Ecology* **33**, 257–68.
- Appleton CC, Henzi SP (1993). Environmental correlates of gastrointestinal parasitism in montane and lowland baboons in Natal, South Africa. *International Journal of Primatology* **14**, 623–35.
- Balmford A, Green RE, Phalan B (2012). What conservationists need to know about farming. *Proceedings of the Royal Society of London B* **279**, 2714–24.
- Black PH (1994). Central nervous system-immune system interactions – Psychoneuroendocrinology of stress and its immune consequences. *Antimicrobial Agents and Chemotherapy* **38**, 1–6.
- Boulton AM, Horrocks JA, Baulu J (1996). The Barbados vervet monkey (*Cercopithecus aethiops sabaens*): Changes in population size and crop damage, 1980–1994. *International Journal of Primatology* **17**, 831–44.
- Bowman DD (1999). *Georgis' Parasitology for Veterinarians*, 7th edn. Elsevier, St Louis.
- Chapman CA, Wasserman MD, Gillespie T *et al.* (2006). Do nutrition, parasitism, and stress have synergistic effects on red colobus populations living in forest fragments? *American Journal of Physical Anthropology* **131**, 525–34.

- Chapman CA, Speirs ML, Hodder SAM, Rothman JM (2010). Colobus monkey parasite infections in wet and dry habitats: Implications for climate change. *African Journal of Ecology* **48**, 555–8.
- Chapman CA, Bonnell TR, Gogarten JF, Schoof VAM, Calme S (2015). Competing pressures on populations: Long-term dynamics of food availability, food quality, disease, stress, and animal abundance *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* **370**, 20140112.
- Chapman CA, Friant S, Godfrey K *et al.* (2016). Social behaviours and networks of vervet monkeys are influenced by gastrointestinal parasites. *PLoS ONE* **11**, e0161113.
- Cheng TC (1973). *General Parasitology*. Academic Press, New York.
- Coe CL, Erickson CM (1997). Stress decreases lymphocyte cytolytic activity in the young monkey even after blockade of steroid and opiate hormone receptors. *Developmental Psychobiology* **30**, 1–10.
- de Gruijter JM, Gasser RB, Polderman AM, Asigiri V, Dijkshoorn L (2005). High resolution DNA fingerprinting by AFLP to study the genetic variation among *Oesophagostomum bifurcum* (Nematoda) from human and non-human primates from Ghana. *Parasitology* **130**, 229–37.
- Ekanayake DK, Arulkanthan A, Horadagoda NU *et al.* (2006). Prevalence of *Cryptosporidium* and other enteric parasites among wild non-human primates in Polonnaruwa, Sri Lanka. *American Journal of Tropical Medicine and Hygiene* **74**, 322–9.
- Estrada A (2013). Socioeconomic context of primate conservation: Population, poverty, global economic demands, and sustainable land use. *American Journal of Primatology* **75**, 30–45.
- Foley JA, Ramankutty N, Brauman KA *et al.* (2011). Solutions for a cultivated planet. *Nature* **478**, 337–42.
- Garcia LS (1999). *Practical Guide to Diagnostic Parasitology*. ASM Press, Washington, DC.
- Gasser RB, de Gruijter JM, Polderman AM (2006). Insights into the epidemiology and genetic make-up of *Oesophagostomum bifurcum* from human and non-human primates using molecular tools. *Parasitology* **132**, 453–60.
- Ghai RR, Chapman CA, Omeja PA, Davies TJ, Goldberg TL (2014a). Nodule worm infection in humans and wild primates in Uganda: Cryptic species in a newly identified region of human transmission. *PLoS Neglected Tropical Diseases* **8**, e2641.
- Ghai RR, Simons ND, Chapman CA *et al.* (2014b). Hidden population structure and cross-species transmission of whipworms (*Trichuris* sp.) in humans and non-human primates in Uganda. *PLoS Neglected Tropical Diseases* **8**, e3256.
- Gillingham S, Lee PC (2003). People and protected areas: A study of local perceptions of wildlife crop-damage conflict in an area bordering the Selous Game Reserve, Tanzania. *Oryx* **37**, 316–25.
- Greiner EC, McIntosh A (2009). Collection methods and diagnostic procedures for primate parasitology. In: Huffman MA, Chapman CA, eds. *Primate Parasite Ecology: The Dynamics and Study of Host–Parasite Relationships*. Cambridge University Press, Cambridge, pp. 3–28.
- Gulland FMD (1992). The role of nematode parasites in Soay sheep (*Ovis aries* L.) mortality during a population crash. *Parasitology Research* **105**, 493–503.
- Hahn NE, Proulx D, Muruthi PM, Alberts S, Altmann J (2003). Gastrointestinal parasites in free-ranging Kenyan baboons (*Papio cynocephalus* and *P. anubis*). *International Journal of Primatology* **24**, 271–9.
- Hansen MC, Potapov PV, Moore R *et al.* (2013). High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–3.
- Hoby S, Schwarzenberger F, Doherr MG, Roberta N, Walzer C (2006). Steroid hormone related male biased parasitism in chamois, *Rupicapra rupicapra*. *Veterinary Parasitology* **138**, 337–48.
- Holt RD, Dobson AP, Begon M, Bowers RG, Schaub EM (2003). Parasite establishment in host communities. *Ecology Letters* **6**, 837–42.
- James C, Adobison AR, Harrison RA, Nelson GS (1983). Long-term infection of *Schistosoma mansoni* in a vervet monkey (*Cercopithecus aethiops*). *Transactions of the Royal Society of Tropical Medicine and Hygiene* **77**, 51–2.
- Kooriyama T, Hasegawa H, Shimozuru M, Tsubota T, Nishida T, Iwaki T (2012). Parasitology of five primates in Mahale Mountains National Park, Tanzania. *Primates* **53**, 365–75.
- Larsen MN, Roepstorff A (1999). Seasonal variation in development and survival of *Ascaris suum* and *Trichuris suis* eggs on pastures. *Parasitology* **1999**, 209–20.
- Legesse M, Erko B (2004). Zoonotic intestinal parasites in *Papio anubis* (baboon) and *Cercopithecus aethiops* (vervet) from four localities in Ethiopia. *Acta Tropica* **90**, 231–6.



- Margolis L, Esch GW, Holmes JC, Kuris AM, Schad GA (1982). The use of ecological terms in parasitology (report of an ad hoc committee of the American Society of Parasitologists). *Journal of Parasitology* **68**, 131–3.
- McGrew WC, Marchant LF, Nishida T (1996). Appendix: Great ape study sites. In: McGrew WC, Marchant LF, Nishida T). *Great Ape Societies* Cambridge University Press, Cambridge, pp. 309–19.
- Muehlenbein MP (2006). Intestinal parasite infections and fecal steroid levels in wild chimpanzees. *American Journal of Physical Anthropology* **130**, 546–50.
- Muriuki SMK, Murugu RK, Munene E, Karere GM, Chai DC (1998). Some gastro-intestinal parasites of zoonotic (public health) importance commonly observed in old world non-human primates in Kenya. *Acta Tropica* **71**, 73–82.
- Nunn CL, Altizer S (2006). *Infectious Diseases in Primates: Behavior, Ecology and Evolution*. Oxford University Press, Oxford.
- Padgett DA, Glaser R (2003). How stress influences the immune response. *Trends in Immunology* **24**, 444–8.
- Petrasova J, Modry D, Huffman MA *et al.* (2010). Gastrointestinal parasites of indigenous and introduced primate species of Rubondo Island National Park, Tanzania. *International Journal of Primatology* **31**, 920–36.
- Phalan B, Bertzky M, Butchart SHM *et al.* (2013). Crop expansion and conservation priorities in tropical countries. *PLoS ONE* **8**, e51759.
- Pride RE (2005). High faecal glucocorticoid levels predict mortality in ring-tailed lemurs (*Lemur catta*). *Biology Letters* **1**, 60–3.
- Saj TL, Sicotte P, Paterson JD (2001). The conflict between vervet monkeys and farmers at the forest edge in Entebbe, Uganda. *African Journal of Ecology* **39**, 195–9.
- Sloss MW, Kemp RL, Zajac AM (1994). *Veterinary Clinical Parasitology*, 6th edn. Iowa State University Press, Iowa, Ames.
- Snaith TV, Chapman CA, Rothman JM, Wasserman MD (2008). Bigger groups have fewer parasites and similar cortisol levels: A multi-group analysis in red colobus monkeys. *American Journal of Primatology* **70**, 1–9.
- Stampone M, Hartter J, Chapman CA, Ryan SJ (2011). Trends and variability in localized precipitation around Kibale National Park, Western Uganda, Africa. *Research Journal of Environmental and Earth Sciences* **3**, 14–23.
- Wallis J (2000). Prevention of disease transmission in primate conservation. *Annals of the New York Academy of Sciences* **916**, 691–3.
- Wren BT, Gillespie TR, Camp JW, Remis MJ (2015). Helminths of vervets monkeys, *Chlorocebus aethiops*, from Loskop Dam Nature Reserve, South Africa. *Comparative Parasitology* **82**, 101–8.
- Wren BT, Remis MJ, Camp JW, Gillespie TR (2016). Number of grooming partners is associated with hookworm infection in wild vervet monkeys (*Chlorocebus aethiops*). *Folia Primatologica* **87**, 168–79.

**Cite this article as:**

Valenta K, Twinomugisha D, Godfrey K *et al.* (2017). Comparison of gastrointestinal parasite communities in vervet monkeys. *Integrative Zoology* **12**, 512–20.