Gastrointestinal Parasites of Vervet Monkeys (*Chlorocebus pygerythrus*) in a High Latitude, Semi-Arid Region of South Africa

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Abstract

Given a changing climate and large-scale human migration, understanding infectious diseases in wildlife and the factors that drive the spread of these diseases is becoming increasingly important. Owing to the close phylogenetic relationship between nonhuman primates and humans, primate parasites are of particular interest due to the potential for zoonotic disease transmission and for the study of social transmission within gregarious social groups. There is a wide range of social and environmental factors that influence the prevalence and transmission of pathogens, and identifying these, and their effects, is crucial to understanding the population-level consequences of climate change for animals that live in obligate social groups. Here we investigated gastrointestinal parasite species richness and used fecal egg counts to estimate worm intensities in 3 vervet monkey troops (*Chlorocebus pygerythrus*) in a high latitude, semi-arid region of South Africa. This region is characterized by unpredictable rainfall and temperature extremes in summer and winter. We identified the gastrointestinal parasites in the population and explored potential demographic predictors, namely sex and troop membership, of parasite species richness and estimated intensity. Additionally, we assessed whether there was short-term intra-individual, inter-sample consistency in egg counts. Six species of gastrointestinal helminths were identified from 3 study troops, with egg counts ranging from 0 eggs/g to 1,100 eggs/g. Neither age nor sex predicted species richness or estimated intensity. This population had the highest prevalence of parasites with an insect vector compared with all other vervet populations studied, and distinctively high prevalences of *Trichostrongylus* sp. (71%) and *Ternidens* sp. (27%). Additionally, we found intra-individual egg count consistency in the short term (mean: 32 days).

Keywords: Vervet; *Chlorocebus pygerythrus*; Helminths; Protozoa; Karoo; Semi-Arid; Prevalence; Richness

A well-documented driver of parasitism and parasite transmission is host environment, whether natural or degraded (Gillespie et al., 2005; Gillespie and Chapman, 2006; Mbora and McPeek, 2009; Schwitzer et al., 2010). Strong evidence suggests that parasite species richness and diversity, as well as disease transmission, are affected by aspects of host environment such as temperature, humidity, and rainfall, all of which may vary along latitudinal gradients (see, for primates, Appleton and Henzi, 1993; Nunn et al., 2005; Altizer et al., 2006). Consequently, documenting a taxon's pathogen diversity and intensity across all the habitats it occupies provides a better understanding of its vulnerability, both locally and globally to shifts in environmental conditions.

Vervet monkeys of the genus *Chlorocebus* are a widely-distributed African cercopithecine (Wolfheim, 1983) and a highly social, group-living taxon that lives in multi-male, female-philopatric groups (Henzi and Lucas, 1980). Although associated primarily with riparian woodland (Isbell et al., 2002) they occupy a range of habitats, from tropical woodland to semi-desert (Pasternak et al., 2013). As such, vervets are exposed to a wide range of predators, resource availability, thermal regimes, and pathogens. Despite their broad distribution, knowledge of their pathogens and parasites is currently restricted to data from 5 tropical sites (McGrew et al., 1989; Muriuki et al., 1998; Gillespie et al., 2004; Legesse and Erko, 2004; Petrášová et al., 2010; Kooriyama et al., 2012; Amenu et al., 2015; Valenta et al., 2017)

and 1 subtropical zone, represented by 4 sites in South Africa (Pitchford et al., 1973; Kaschula et al., 1978; Appleton, 1989; Wren et al., 2015).

Here we provide new data from a study population close to its latitudinal limits in the semi-arid, temperate Karoo biome of South Africa. This is a region under escalating risk from climate change (Jury, 2013) and is distinctive in its low annual rainfall, very high summer temperatures, and very cold winters (Pasternak et al., 2013; McFarland et al., 2015). Our aim was to describe the primary gastrointestinal parasites recorded from this population and to provide a preliminary assessment of whether prevalence and intensity are linked to sex and social group membership. Comparing across previous vervet monkey studies, we also assessed parasite species richness across a latitudinal gradient. Additionally, where fecal egg counts vary stochastically across samples from individual animals in the short term, they may be considered an unreliable index of adult worm burden (Coadwell and Ward, 1982; Stear et al., 1995; Roepstorff et al., 1996; Vidya and Sukumar, 2002; Gillespie, 2006). We therefore also determined, where possible, whether consecutive fecal egg counts from individuals were positively correlated.

Materials and Methods

Data were collected during the austral winter (May–July 2016) from 3 fully habituated groups (Picnic Troop [PT], River Bend Mob [RBM], Riverside Troop [RST]) of wild vervet monkeys that have been the subject of intensive data collection since 2009 at Samara Private Game Reserve, South Africa (32°22′S, 24°52′E). All group members are individually identified based on natural markings. The study area is semi-arid riverine woodland (Pasternak et al., 2013), with a declining annual average rainfall of 386 mm, and average minimum and maximum temperatures of 6.1 C and 21.2 C, respectively.

Fecal sampling and analysis

As part of a comprehensive research program, 4 to 5 observers, spread over the 3 troops, were responsible for all fecal sample collection during each of 55 study days, each lasting 10 hr. Fecal samples were collected noninvasively from all 56 individually-identifiable adults across the 3 troops: RBM (M = 4, F = 11), PT (M = 6, F = 8), and RST (M = 11, F = 16). Total group sizes, including juveniles and infants, were 34 for RBM, 33 for PT, and 37 for RST. For each sample, approximately 1 g of fresh feces was weighed in the field immediately after defecation and directly placed into 10% neutral, buffered formalin and stored in a field lab, after which samples were transported to the University of Lethbridge, Canada, where fecal flotation and sedimentation techniques were used to identify parasites.

A modified zinc sulfate flotation was used to isolate helminth eggs, whereby an additional washing step was included in the fecal flotation to avoid egg damage, which had been evident in the initial samples that were analyzed (Moodley et al., 2008). Briefly, fecal samples suspended in formalin were placed in 15 ml Falcon tubes and centrifuged at 1,389 *g* for 6 min, and the supernatant was discarded. The test tube was filled with water, mixed with the fecal material, centrifuged at 1,389 *g* for 6 min, and the supernatant was discarded. The deposit was resuspended in $ZnSO_4$ (specific gravity 1.3), vortexed to mix, and centrifuged at 617 *g* for 8 min. The supernatant was pipetted into 4×15 ml tubes that were filled with water. The pellet that remained after flotation was kept aside for sedimentation (see following paragraph). This step reduced the specific gravity (sp.gr.) of the $ZnSO_4$ after flotation, thus preventing egg damage and allowing the eggs to deposit upon sedimentation. These supernatant-water tubes were centrifuged at 964 *g* for 6 min. The supernatant was discarded, and the deposits were combined into 1 test tube, which was filled with water and centrifuged at 964 *g* for 6 min. The supernatant was discarded, and the entire pellet was examined under the microscope. Parasites were identified to genus-level based on egg shape, size, color, and contents, and all eggs were counted (Gillespie, 2006). Representative eggs were photographed.

Ethyl-acetate sedimentation was used to isolate potential trematodes that were too heavy to float during $ZnSO_4$ flotation. Here, the deposit from the flotation was suspended in water, vortexed, and centrifuged at 964 *g* for 6 min. The supernatant was discarded, and the sample was rewashed. Water was added to the pellet to the 7 ml mark of the centrifuge tube and vortexed. Then, 3 ml of ethyl-acetate was added to the tube, mixed thoroughly, and centrifuged at 1,389 *g* for 6 min, and the supernatant was then discarded. The entire pellet was examined under the microscope. As with the zinc-sulfate flotation, parasites were identified to genus-level based on egg shape, size, color, and contents, and all eggs were counted (Gillespie, 2006). Representative eggs were photographed.

Statistical analysis

All statistical testing was carried out using R version 3.5.1 (R Core Team, 2015). Individual parasite intensity was estimated by combining the egg counts of all species in each fecal sample and expressed as total eggs per fecal sample (EPS) while controlling for fecal weight during statistical analysis. Initial data exploration and visualization were conducted according to the methods outlined in Zuur et al. (2007).

To assess whether sex and study group size influenced individual parasite intensity, we used the "DHARMa" package (Hartig, 2018) to run a generalized linear mixed model (GLMM). A Poisson regression was run on total EPS, with sex and group size as fixed effects, and log fecal weight for each sample as an offset variable to account for sample differences. Additionally, individual identification was included as a random factor to account for repeated sampling on the same individuals, and an observation-level random effect (sample number) was included to address the over-dispersion of zeros (Harrison, 2014).

Species richness was defined as the total number of parasite species per sample. We used the "DHARMa" package (Hartig, 2018) to assess whether sex and group membership influenced species richness. GLMMs were fitted with a Poisson link function. Sex and group size were specified as fixed effects, and individual identity as a random factor. As with parasite intensity, log fecal weight was included as an offset variable and sample number as an observation-level random effect to account for over-dispersion.

For both sets of analyses, we used the "MuMIn" package (Barton and Barton, 2015) to generate marginal r^2 values for the fixed effects and conditional r^2 values for the model as a whole (Nakagawa and Schielzeth, 2012). The models we present are those that best met the assumptions of normal error structure. Following Colquhoun (2014), we consider $P \sim 0.05$, 0.01, and

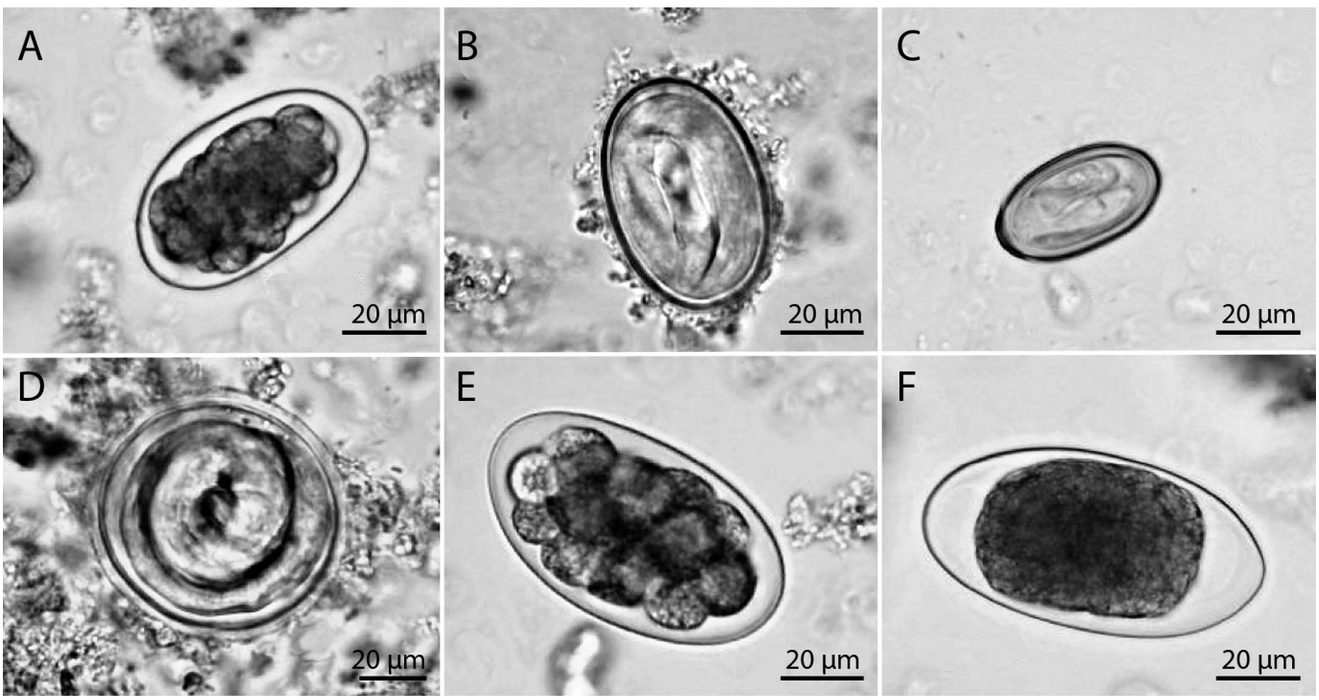

Figure 1. Helminth eggs from vervet monkey feces in the karoo, South Africa. (**A**) *Oesophagostomum* sp. (**B**) Spirurid 1 (considered to be *Protospirura* sp.). (**C**) Spirurid 2 (likely *Streptopharagus pigmentatus*). (**D**) S*ubulura* sp. (**E**) *Ternidens* sp. (**F**) *Trichostrongylus* sp.

0.001 to constitute weak, moderate, and strong evidence for an effect, respectively.

To assess whether there was similarity between samples from the same individual, estimated parasite intensity was expressed as total eggs per gram (EPG) of feces. Here, we used Pearson product-moment (r) partial correlation to compare the EPG across 2 samples from the same individual while considering the number of days between the 2 samples. This was done for combined total EPG as well as individual species EPG for taxa with sufficient data.

Results

One hundred and sixteen fecal samples were collected from 56 known adult vervet monkeys across the 3 troops. Four samples were subsequently excluded from analysis due to egg damage. A resultant mean of 1.92 (± 0.53 SD) samples/adult were analyzed.

Eggs of 6 helminth taxa, namely, *Trichostrongylus* sp., *Ternidens* sp., *Oesophagastomum* sp., *Subulura* sp., and 2 spirurids, were recovered from fecal samples (Fig. 1) and 5 were identified to genus-level based on size, shape, and color of eggs (Table 1). Spirurid 1 could not be identified to species- or genus-level based only on microscopy. Given the morphological characteristics, we consider it to be *Protospirura* sp. (hereafter referred to as *?Protospirura*), although molecular analysis is still being conducted to confirm this. No protozoa were recovered from fecal samples.

Fifty-five of the 56 subjects were infected with 1 or more parasite(s) (Table 1). *Protospirura* was the most prevalent species found in all positive individuals. *Subulura* sp. and spirurid 2 (likely *Streptopharagus pigmentatus*) were the least prevalent and found

Table 1. Percentage of individuals infected, percentage host group prevalence (HGP: number of hosts infected/number of hosts examined) and percentage sample prevalence (SP: number of positive samples/number of samples analyzed) for each parasite genus identified across 3 troops of wild vervet monkeys (PT, Picnic Troop; RBM, River Bend Mob; RST, Riverside Troop) at Samara Private Game Reserve, South Africa.

	PT		RBM		RST		Total	
Species/genus	Males (n = 6)	Females (n = 8)	Males (n = 4)	Females (n = 11)	Males (n = 11)	Females (n = 16)	HGP	SP
Spirurid 1 (*?Protospirura* sp.)	100.0	100.0	100.0	100.0	100.0	93.8	98.2	96.3
Trichostrongylus spp.	83.3	75.0	75.0	63.6	63.6	75.0	71.4	63.0
Ternidens spp.	33.3	25.0	0.0	27.3	45.5	25.0	26.8	20.4
Oesophagostomum spp.	0.0	12.5	0.0	18.2	9.1	31.3	16.1	10.2
Subulura spp.	0.0	0.0	0.0	0.0	9.1	12.5	5.4	2.8
Spirurid 2 (likely *Streptopharagus pigmentatus*)	0.0	0.0	0.0	0.0	9.1	0.0	1.8	0.9

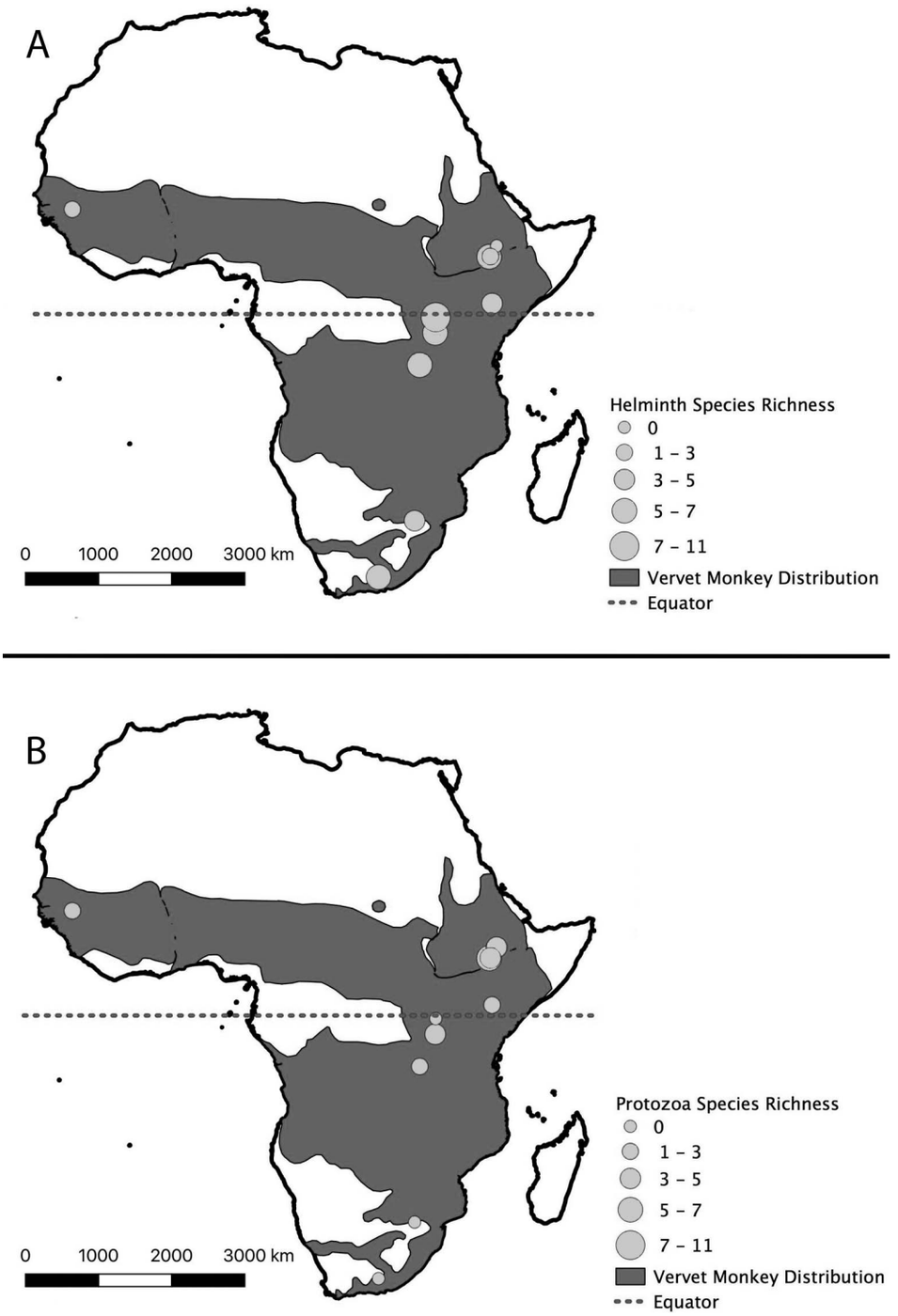

Figure 2. Parasitic taxon richness in wild vervet monkey populations in Africa. (**A**) Helminths. (**B**) Protozoa. (Data from: Pitchford et al., 1973; Appleton, 1989; McGrew et al., 1989; Muriuki et al., 1998; Gillespie et al., 2004; Legesse and Erko, 2004; Petrášová et al., 2010; Kooriyama et al., 2012; Amenu et al., 2015; Wren et al., 2015; Valenta et al., 2017; and this study.)

only in members of 1 troop (RST). While we predict the spirurid 2 to be *S. pigmentatus*, the very low host group prevalence means we were unable to examine and measure enough representative eggs to conclusively identify this parasite. Group parasite prevalence is best described in terms of host group prevalence from known individuals (proportion or percentage of hosts infected out of total number of hosts examined; Bush et al., 1997) rather than sample prevalence (proportion or percentage of positive samples out of total number of samples analyzed). However, we present both of these measures for the purpose of comparison with other studies.

Overall, we found that helminth diversity did not change across a latitudinal gradient (Fig. 2A). However, in studies that

Table 2. Generalized linear mixed model results to assess fixed effects of sex and troop on parasite intensity. n = 112. SE: Standard Error. CI: Confidence interval.

Parameter	β	SE	z	*P*	95% CI	
Group size	−0.016	0.024	−0.666	0.506	−0.064	0.031
Sex (ref: female)	−0.532	0.365	−1.458	0.145	−1.261	0.198
Intercept	6.043	1.120	5.395	<0.001	3.816	8.294

Table 3. Generalized linear mixed model results to assess fixed effects of sex and troop on parasite diversity. n = 112. SE: Standard Error. CI: Confidence interval.

Parameter	β	SE	z	*P*	95% CI
Group size	−0.001	0.009	−0.069	0.945	−0.019, 0.018
Sex (ref: female)	0.023	0.143	0.164	0.870	−0.261, 0.301
Intercept	0.735	0.443	1.659	0.097	−0.151, 1.588

examined protozoa, protozoan species diversity was found to be higher closer to the equator (Fig. 2B).

There was no evidence to suggest that either group size or sex influenced individual parasite intensity (Table 2) with a r^2_{marginal} of 0.141 and $r^2_{\text{conditional}}$ of 0.95. Similarly, neither group nor sex predicted parasite richness (Table 3) where both the r^2_{marginal} and $r^2_{\text{conditional}}$ values were 0.007.

After partitioning out the number of intervening days (mean: 32.8 days), there was strong evidence to indicate that the total egg counts from consecutive samples were positively correlated ($r = 0.80$; n = 46; $P < 0.001$). This general finding held for the most prevalent parasites in the population, namely, *?Protospirura* ($r = 0.67$, n = 46, $P < 0.001$), *Ternidens* sp. ($r = 0.47$, n = 46, $P = 0.001$), and *Trichostrongylus* sp. ($r = 0.82$, n = 46, $P < 0.001$).

Discussion

To the best of our knowledge, this is the first report on the gastrointestinal parasites of vervet monkeys living in a semi-arid, temperate region. Several parasites reported here have been previously recorded from other vervet monkey populations (Appleton, 1989; McGrew et al., 1989; Gillespie et al., 2004; Wren et al., 2015), although estimates of prevalence differ markedly. Comparison of prevalence across populations is problematic due to varying methods of estimation. While we expressed group prevalence as the number of infected individuals out of all individuals studied, as recommended by Bush et al. (1997), we also considered sample prevalence, expressed as positive samples out of all samples, to aid in comparison.

We found 3 parasites that have an insect intermediate host, namely, *?Protospirura*, spirurid 2 (likely *S. pigmentatus*), and *Subulura* sp. Of the 56 individuals, 98.21% were positive for *?Protospirura*, which differs strongly from the spirurid prevalence reported in another vervet monkey population. In South Africa (Wren et al., 2015), the highest reported infection proportion was a combined *Physaloptera* sp. and *S. pigmentatus* host group prevalence of 68%. Arthropods and reptiles serve as the intermediate host for spirurid transmission, and research has shown that primates increase their insect intake under dry conditions (Garber, 1987; Chapman, 1988). Given the semi-arid conditions at this study site, increased dietary intake of intermediate hosts could be responsible for the unusually high prevalence of *?Protospirura* in our population. Our host group prevalence of 4% for *S. pigmentatus*, found in 3 other vervet monkey studies (Appleton, 1989; Gillespie et al., 2004; Kooriyama et al., 2012), was most comparable to the Tanzanian population (Kooriyama et al., 2012). *Subulura* sp. has only been found in 1 other vervet population (Petrášová et al., 2010), although *Primasubulura* sp. was reported in vervet monkeys (Kooriyama et al., 2012), while *Subulura distans* has been reported in other *Cercopithecus* species (Cameron, 1930; Yamashita, 1963). To better understand the high diversity and prevalence of insect transmitted parasites in our study population, we will need to know which insects serve as the vectors and how environmental conditions affect their prevalence. This is something we intend to investigate in the future.

Of the 3 environmentally acquired parasites, the prevalence of *Trichostrongylus* sp. was markedly higher than that reported from the other 2 study populations where it has been found (Appleton, 1989; Chapman et al., 2016). *Trichostrongylus* is a genus primarily known to affect ruminants (Acha and Szyfres, 2003) and, since our population spends a large amount of time foraging on the ground in areas with many different ruminants, infection with *Trichostrongylus* sp. is likely to be due to their exposure to infective larvae in ruminant species' feces. *Ternidens* sp. was the second most prevalent helminth in our study population. Vervet monkeys are frequently cited as a common host of *Ternidens deminutus* (Kouassi et al., 2015), although it has only been reported in 1 study, where Blackie (1932) found that 3 of the 5 vervet monkeys examined were positive for *T. deminutus*. It has been found in sympatric baboons (Obanda, 2015) and other cercopithecids (Kouassi et al., 2015). Finally, the prevalence of *Oesophagostomum* sp. in our population was lower than recorded from another South African vervet population, where Wren et al. (2015) reported a host group prevalence of 84%. *Oesophagostomum* sp. thrives in warm and humid tropical and subtropical regions (Rose and Small, 1980), and the semi-arid conditions of the study site may be responsible for this lower prevalence. *Oesophagostomum* sp. prevalence has also been found to be higher in primates that travel large distances in smaller groups (Ghai et al., 2014). Given the larger than average group sizes in our study population and their relatively short travel distances (Pasternak et al., 2013), this may combine with the drier climate to reduce susceptibility to *Oesophagostomum* sp. infection.

Notably absent from our study population was *Trichuris*, which has been recorded from vervets elsewhere, with only McGrew et al. (1989), in Senegal, also finding no evidence of *Trichuris* infection, although he did find *Trichuris* in sympatric patas monkeys (*Erythrocebus patas*). Prevalence of *Trichuris* in vervet populations varies widely, with host group prevalence of as high as 92% in South African vervets (Wren et al., 2015). The absence of *Trichuris* is also likely to be due to the semi-arid conditions of our study site, where ground cover can be limited, since *Trichuris* egg development in the environment is sensitive to direct sunlight and relative humidity (Nolf, 1932).

We did not detect any protozoan species in our study population. While highly diverse in some vervet studies across Africa (see Legesse and Erko, 2004; Amenu et al., 2015), identifiable protozoans were not recorded in some other studies (Valenta et al., 2017) or were not considered (Appleton, 1989;

Gillespie et al., 2004). In South Africa, Wren (2013) reported finding only *Entamoeba coli*. Our findings that helminth species richness does not vary across a latitudinal gradient while protozoan species richness is higher closer to the equator are in line with those described in a comparative study on primate parasite species richness (Nunn et al., 2005).

Our findings of no sex differences for both parasite intensity and parasite species richness was consistent with 2 other studies of vervet monkeys that also considered this (Wren et al., 2015; Valenta et al., 2017), where individual differences explained much of the variance. As with our population, Wren et al. (2015) found that group membership did not predict infection status for any of the parasites. Group size is thought to impact prevalence and intensity, although this relates strongly to the mode of transmission of the specific parasite (Snaith et al., 2008). In gastrointestinal helminths, intrinsic disease risk and infection rates should increase with group size due to increased proximity and contact rates among individuals and to contaminated substrates (Freeland, 1976; May and Anderson, 1979; Arneberg et al., 1998; Brown et al., 2001; Arneberg, 2002; Altizer et al., 2003); however, findings related to this vary widely (see, Freeland, 1976; McGrew et al., 1989; Snaith et al., 2008; Griffin and Nunn, 2012). While we may expect infection rates to be higher in larger troops, the vervet monkeys in our study population have an unusually high range overlap (Pasternak et al., 2013). As such, troops would have similar exposure to helminths, and this may account for the lack of variation.

Although often used in parasite studies, there is significant controversy regarding whether fecal egg counts can serve as a measure of parasite intensity or load (Gillespie, 2006). In livestock studies, differences in parasite size, age, fecundity, and sex ratio affect worm ovulation (Coadwell and Ward, 1982; Stear et al., 1995; Roepstorff et al., 1996) as do host immunity, density-dependent factors, and environmental cues (Christensen et al., 1995; Stear et al., 1995; Roepstorff et al., 1996). At the same time, as for Asian elephants, there may be large variation of parasite load within a day, which points to periodicity in egg release from adult worms (Vidya and Sukumar, 2002). It is also argued that fecal sample condition, such as moisture content and consistency, prevents inter-sample comparisons (Anderson and Schad, 1985; Eberhard et al., 2001). However, our results show that, over a relatively short period of time, intra-individual egg counts were consistent and may thus indicate intensity of infection reliably. Evidence has been presented in horses that there is intra-individual consistency in strongyle egg shedding (Nielsen et al., 2006; Becher et al., 2010). Our results suggest that the number of eggs shed in vervet monkey feces points to an underlying infection rather than a stochastic event and may therefore serve as a reliable indicator of individual levels of infection that can be tracked over time. It may then be possible to consider parasite intensity from egg counts using within-subject models, which warrants further investigation.

Our study highlights some limitations of parasite identification via microscopy only. In many cases parasite identification can only be made to genus-level at best, owing to the similarities in egg morphology across species. Additional methods, such as PCR, are recommended to overcome this limitation. We have initiated molecular work to identify our *?Protospirura* and, where possible, to improve identification of the other genera to species-level. While this study provides an initial comprehensive report on the gastrointestinal parasites of this vervet population, the results are generalized, and there may be seasonal variation in parasite species intensity and richness, and a longitudinal study is required for a better understanding of host-parasite dynamics in this environment. Additionally, this work would benefit from a larger sample size. Moreover, given the importance of understanding insect vectors in host-parasite interactions, we have also started work on identifying the insect vector in our population.

In summary, it is clear that there is large variation in parasite prevalence across vervet monkey populations. The unique presence of *Ternidens* sp. in our study population and the relative rarity of *Trichostrongylus* in vervet monkeys, as well as the absence of *Trichuris*, points to the need for further research. At the same time, the higher prevalence and diversity of parasites that have intermediate insect vectors indicates a strong environmental driver of parasitism in an omnivore occupying a low rainfall area.

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