

Differences between chimpanzee and baboon gastrointestinal parasite communities

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SUMMARY

Cross-species infection among humans, chimpanzees (*Pan troglodytes*) and baboons (*Papio* spp.) is potentially a significant public health issue in Africa, and of concern in the conservation of *P. troglodytes*. However, to date, no statistical comparisons have been made between the prevalence, richness and composition of parasite communities in sympatric populations of baboons and *P. troglodytes*. We compared parasite communities in sympatric *P. troglodytes* and *Papio papio* living in a wilderness site, in the Republic of Senegal, West Africa. We asked whether, in the absence of humans, there are significant differences between these hosts in their interactions with gastrointestinal parasites. We tested whether host, location, or time of collection accounted for variation in prevalence, richness and community composition, and compared prevalence across six studies. We concluded that, despite being closely related, there are significant differences between these two hosts with respect to their parasite communities. At our study site, prevalence of *Balantidium*, *Trichuris* and *Watsonius* was higher in *P. papio*. *Papio papio* harboured more parasites per host, and we found evidence of a positive association between *Trichuris* and *Balantidium* in *P. troglodytes* but not *P. papio*.

Key words: *Pan troglodytes*, *Papio papio*, helminths, prevalence, richness, biodiversity, mixed infections, cross infection, community composition.

INTRODUCTION

Cross-species transmission of parasites among humans, chimpanzees (*Pan troglodytes*) and baboons (*Papio* spp.) is a significant public health and conservation concern in Africa (Wolfe *et al.* 1998; Wallis and Lee, 1999; Cooper *et al.* 2012; Gómez *et al.* 2013; Muehlenbein and Wallis, 2014). Pedersen and Davies (2010) refer to central Africa as a ‘hotspot’ of potential cross-species infection among humans and other primates. Most of the population of Africa is at risk of infection by at least one of three common soil transmitted nematodes, *Ascaris lumbricoides*, *Trichuris trichiura* and hookworm (Pullan and Brooker, 2012). All the three have been reported in chimpanzees (e.g. Zommers *et al.* 2013; Drakulovski *et al.* 2014) and baboons (e.g. Ravasi *et al.* 2012; Mafuyai *et al.* 2013). The risk of parasite transmission between humans and primates is also of concern in conservation of endangered primates, including chimpanzees (McGrew *et al.* 1989; Muriuki *et al.* 1998; Wallis and Lee, 1999; Zommers *et al.* 2013; Muehlenbein and Wallis, 2014).

Because of their associations with humans (through crop raiding and use of human refuse as food) and large populations, transmission of parasites from

baboons to humans has long been identified as a particular zoonotic threat (e.g. Miller, 1960; Goldsmid, 1974; Crockett and Dipeolu, 1984; Muriuki *et al.* 1998; Weyher *et al.* 2006; Ravasi *et al.* 2012; Mafuyai *et al.* 2013). Many of the same parasites have been reported in sympatric chimpanzees and baboons (Table 4 and references therein), making baboons a potential risk to chimpanzees as well as to humans (see also Cooper *et al.* 2012; Gómez *et al.* 2013). While the possibility that these two hosts share parasites is well established (all the parasites discussed in this paper have been found in both chimpanzees and baboons), what has not been investigated is whether, in the absence of humans, the parasite communities in these two hosts are similar with respect to prevalence, richness and community composition.

Five parasitological studies of sympatric *P. troglodytes* and *Papio* spp. groups have been conducted. Three occurred in Tanzania, East Africa: two at Gombe National Park, on *Papio anubis* (McGrew *et al.* 1989; Murray *et al.* 2000), and one in Mahale Mountains National Park, on *Papio cynocephalus* (Kooriyama *et al.* 2012). In Tanzania, interactions among chimpanzees, humans and baboons occur daily. The presence of humans adds a third possible host to the dynamics of infection, and human activities have many potential effects on prevalence (Brearley *et al.* 2013). For example, forest fragmentation (Sa *et al.* 2013) and crop-raiding (Weyher *et al.* 2006) alter parasite epidemiology in primates,

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and just the presence of trails used for primate field study can have an impact on prevalence (Zommers *et al.* 2013). Comparing the dynamics of infection between *P. troglodytes* and *Papio* in the absence of the confounding effects of humans and their activities is important to understand the interaction between the three hosts when those complications are present. Two studies of *P. troglodytes* and *Papio papio* occurred in West Africa, in Niokolo-Koba National Park, Senegal (at Mt. Assirik, McGrew *et al.* 1989 and at Fongoli, Howells *et al.* 2011) where interactions with humans are far less likely. This report is on the populations at Mt. Assirik which, at the time of the study, was uninhabited by humans or their domestic plants and animals.

The five previous studies have other limitations in addressing the issue of whether *P. troglodytes* and *Papio* spp. are comparable hosts. Only one of these studies (Kooriyama *et al.* 2012) presented statistical analysis comparing prevalence in the two hosts; our study makes these statistical comparisons. None of the previous studies conducted statistical comparisons of within-host richness or reported on patterns of parasite co-occurrence in mixed infections; we report on both. All of the previous studies were confined to single surveys of animals in one location, leaving open the possibility that prevalences in *P. troglodytes* may be more closely correlated with variance in time or space than with variance in the prevalences in *Papio* spp. We surveyed animals in two locations over two time periods.

In 2000, we returned to Mt. Assirik to survey the parasite communities of sympatric *P. troglodytes* and *P. papio*. We reported on data from baboons earlier (Ebbert *et al.* 2013). Here we present data on the chimpanzees and use our data and those from other studies to ask if the two hosts harbour similar communities, or if, instead, host is a significant factor in explaining variation in prevalence, within-host richness, and co-occurrence. We tested three hypotheses:

- (1) prevalence, within-host richness and co-occurrence of parasites is the same in *P. troglodytes* and *P. papio* regardless of host location (either of two valleys at Mt. Assirik);
- (2) prevalence is the same in the two hosts regardless of census time (two periods about 20 years apart); and
- (3) prevalence and within-group richness are the same in the two hosts regardless of study (six reports differing in the year conducted, location and methods).

METHODS

We compare the current results with those from *P. papio* collected at the same sites and over the same time period (Ebbert *et al.* 2013). Field, laboratory, identification and statistical methods were identical

to those reported previously and so are briefly summarized here.

Field

WCM and LFM collected fecal specimens of *P. troglodytes* versus at Mt. Assirik, Parc National du Niokolo-Koba, République du Senegal, between 9 March and 6 April 2000. Mt. Assirik (12° 53'N, 12° 46'W) is a low flat hill (elevation 311 m) from which flows only three water courses with year-round running water (McGrew *et al.* 1981). Specimens were collected in two valleys, Lion Valley (LV) and Stella's Valley (SV), which are about 7 km apart (straight-line distance) on opposite sides of Mt. Assirik. At the time of collection no humans lived in this area, nor were there domestic plants or animals. Neither cultigens nor refuse were available to the chimpanzees, who ate only natural foods. We collected fresh specimens ($n = 49$) into 10% neutral-buffered formalin in the morning near sleeping sites, at 1–6 h post-deposition. Feces were deposited upon arising, usually intact on boulders or outcrops, and were undisturbed before collection. Samples were collected anonymously, but we sampled separate sleeping aggregations and so assumed the samples represent distinct individuals.

Field methods and conditions in LV were similar to those of McGrew *et al.* (1989), when 70 samples were collected from *P. troglodytes*. Those samples were collected between March 1976 and June 1978, in both the wet and dry seasons; our current collection was conducted during the dry season.

Laboratory

In 2001, the *P. troglodytes* and *P. papio* samples were provided to MAE as numbered specimens and so were analysed blind. We prepared 7.5 ml of homogenized feces per sample using standard protocols for formalin-ether sedimentation (e.g. Price, 1994). Formalin-ether sedimentation and zinc sulphate flotation was used in our earlier (McGrew *et al.* 1989) study. Four slides were prepared from each sample. We scrutinized each slide under light microscopy at 150X, using a standardized grid to examine all the material under the cover slip (No.1, 22 × 22 mm). We identified helminth eggs and ciliate cysts using published descriptions of primate parasites (e.g. Hasegawa *et al.* 1983; Price, 1994; Petřelková *et al.* 2010; Kooriyama *et al.* 2012). To assist in identification of some parasites, we randomly chose eggs and cysts for measurement using a micrometre at either 300X or 600X.

Statistical analysis

We used JMP statistical software (JMP, Ver. 8.0.2, SAS Institute, Inc., 2008). Throughout, we judged

Table 1. Percent prevalence (binomial error) of parasite taxa in samples from *P. troglodytes* (Pan Pan) and *P. papio* (Papio) collected in two valleys (SV and LV) in 2000

Genus	Pan LV (n = 39)	Papio LV (n = 48)	Pan SV (n = 10)	Papio SV (n = 52)	Effects			Pan Pooled	Papio Pooled
					Host	Valley	H × V		
<i>Ascaris</i>	0	4 (2.9)	10 (9.5)	2 (1.9)	NS	NS	NS	2.0 (2.0)	3.0 (1.7)
<i>Balantidium</i>	10 (4.9)	90 (4.4)	30 (14.5)	60 (6.8)	34.3, ***	NS	8.2, 0.0042	14.3 (5.0)	74.0 (4.4)
<i>Enterobius</i>	10 (4.9)	42 (7.1)	40 (15.5)	36 (6.7)	NS	NS	4.5, 0.0345	16.3 (5.3)	39.0 (4.9)
<i>Protospirura</i>	54 (8.0)	79 (5.8)	60 (15.5)	62 (6.7)	NS	NS	NS	55.1 (7.1)	70.0 (4.6)
<i>Streptophargus</i>	0	6 (3.5)	0	2 (1.9)	NS	NS	NS	0	4.0 (2.0)
<i>Strongyloides</i>	0	2 (2.1)	0	4 (2.6)	NS	NS	NS	0	3.0 (1.7)
<i>Trichuris</i>	21 (6.5)	85 (5.1)	50 (15.8)	92 (3.7)	31.7, ***	4.4, 0.0365	NS	26.5 (6.3)	89.0 (3.1)
<i>Troglodytella</i>	3 (2.5)	0	10 (9.5)	0	5.1, 0.0233	NS	NS	4.1 (2.8)	0
<i>Watsonius</i>	13 (5.4)	54 (7.2)	30 (14.5)	35 (6.6)	6.6, 0.0102	NS	NS	16.3 (5.3)	44.0 (5.0)
Other taxa									
cf <i>Enterobius</i>	8 (4.3)	0	0	0	NS	NS	NS	6.1 (3.4)	0
cf <i>Trichuris</i>	5 (3.5)	10 (4.4)	40 (1.5)	4 (2.6)	NS	NS	8.4, 0.0038	12.2 (4.7)	7.0 (2.5)
Strongylid	3 (2.5)	4 (2.9)	0	6 (3.2)				2.0 (2.0)	5.9 (2.4)
Spirurid	0	4 (2.9)	10 (9.5)	0				2.0 (2.0)	2.0 (1.4)

Results are for logistic models (G, P) testing whether host, valley and their interaction effect prevalence. *P* values ≥ 0.05 are indicated by NS, those < 0.0001 by asterisks; other values are specified. Data for *P. papio* previously reported (Ebbert *et al.* 2013).

results as significant if these analyses indicated a < 0.05 (two-tailed) probability of obtaining results at random. We present means as $x \pm$ s.d. and percentages as $p \pm$ binomial error.

We compared the length and width of eggs between valleys and hosts using MANOVA and Wilk's lambda approximation of the *F*-distribution. We use logistic models and the significance of likelihood ratios (G) to test effects of host and valley (Mt. Assirik data), host and year (Mt. Assirik data from LV) and host and study (data across six studies) on prevalence (number of specimens infected with a particular parasitic taxon, divided by the number of specimens examined). *Within-host richness* (number of parasitic taxa in a specimen) and *within-group richness* (number of parasitic taxa across specimens within a group) had skewed distributions; we therefore used a non-parametric assessment (Wilcoxon rank test) to test for differences in richness across valleys and hosts, and across studies and hosts. We used Fisher's exact tests and data from the most common genera ($n \geq 10$) to test whether genera co-occurred within a host more often than expected from the group prevalence.

RESULTS

Parasite identification

Among our *P. troglodytes* samples we identified seven parasites to genus and four other taxa (Table 1). As detailed below, parasite morphology was similar to that seen in *P. papio* (Ebbert *et al.* 2013), which supports our assumption that the two hosts were exposed to similar species within the genera.

Watsonius watsoni (Paramphistomata: Echinostomida) was a new record for *P. troglodytes*. There was no effect of host, location or their interaction on egg size (MANOVA of length and width, D.F. = 6, $F = 1.5$, $P = 0.19$ for full model). Pooling across valleys ($n = 47$), the *P. troglodytes* eggs averaged 116 ± 8.0 by $69 \pm 2.6 \mu\text{m}$. In the original description of *Watsonius watsoni* (Stiles and Goldberger, 1910) eggs ranged from 122 to 130 μm in length and from 75 to 80 μm in width. Little is known about this parasite (Toft and Eberhard, 1998) and we know of no other reports of *Watsonius* in wild African primates other than a report of infection in a mandrill (Pick, 1951) which did not include a description of the eggs.

Both *Trichuris* and the *Trichuris*-like morph (referred to here as cf. *Trichuris*) we reported in *P. papio* were present in *P. troglodytes*. There was no effect of host, location or their interaction in the egg size of cf. *Trichuris* (MANOVA, D.F. = 6, $F = 1.0$, $P = 0.47$). Pooling across valleys ($n = 6$) cf. *Trichuris* averaged 37 ± 3.8 by $16 \pm 1.9 \mu\text{m}$ in *P. troglodytes*. Because we randomly selected samples for parasite measurement, *Trichuris* was measured only in *Papio*. It averaged 55 ± 2.8 by $25 \pm 1.6 \mu\text{m}$, ($n = 10$), a size similar to that seen previously in *P. troglodytes* (e.g. Petrželková *et al.* 2010; Kooriyama *et al.* 2012).

There were two *Enterobius* morphs present in *P. troglodytes*. The more numerous had the same length and width as those seen in *P. papio*: there was no effect of host, valley or their interaction on egg size (MANOVA, D.F. = 6, $F = 2.0$, $P = 0.06$ for model). This morph is referred to here as *Enterobius*. Pooling over locations ($n = 21$) it measured 37 ± 3.3 by $33 \pm 2.1 \mu\text{m}$ in *P. troglodytes*. The second morph (cf. *Enterobius*), which was

confined to LV and to *P. troglodytes*, measured an average of 56 ± 2.4 by $27 \pm 1.7 \mu\text{m}$ ($n = 10$). It was consistent with *Enterobius anthropopithecii* from *P. troglodytes* samples in Tanzania (Petrželková *et al.* 2010; average 55 by $27 \mu\text{m}$) and oxyurid eggs from *Pan paniscus* samples in Democratic Republic of Congo (DRC) (Hasegawa *et al.* 1983; 49–53 by $23\text{--}25 \mu\text{m}$).

Protospirura egg size did not differ between hosts or locations (MANOVA, D.F. = 4, $F = 1.2$, $P = 0.34$ for model; data did not allow a host by location comparison). Eggs ($n = 9$) measured 54 ± 4.2 by $44 \pm 2.8 \mu\text{m}$ in *P. troglodytes*. These eggs have a thick shell covered with a hyaline coat; the coat often appeared rough. They were consistent with photos of *Protospirura muricola* in *P. troglodytes* (52 by $39 \mu\text{m}$, Petrželková *et al.* 2010) and ‘cf *Protospirura muricola*’ ($51 \times 38.5 \mu\text{m}$) described by Petrášová *et al.* 2010 from the same population of *P. troglodytes*. We chose to identify the spirurid eggs in our samples as *Protospirura* because they were so similar to those described in Petrželková *et al.* 2010, an identification that was confirmed with adult worms. However, we note that the eggs in our samples also closely resemble those found in *P. troglodytes* from Gombe National Park in Tanzania (pictured, but no average measurements presented, in Gillespie *et al.* 2010, Fig. 2) and identified as *Abbreviata caucasica*. An apparently identical micrograph in Howells *et al.* (2011, Fig. 2) was labeled as *Physaloptera* sp. in a *P. troglodytes* sample collected in Fongoli, Senegal. Goldsmid and Rogers (1978) pictured an egg with the same thick shell and hyaline coat from *Papio ursinus* in South Africa (average $57 \times 25.6 \mu\text{m}$) and identified it as ‘*Abbreviata* (= *Physaloptera*) *caucasica*’.

We noted a second spirurid in our samples, which we did not identify further. The one egg in *P. troglodytes* was similar to two eggs seen in *P. papio*, with an undifferentiated embryo and without the hyaline coat. In *P. troglodytes* it measured 43 by $29 \mu\text{m}$.

As in *P. papio*, two sizes of strongylid eggs were noted. The first was larger, averaging 68 ± 3.5 by $38 \mu\text{m}$ ($n = 2$); one egg had about 32 cells and the other about 64. These are similar to unidentified strongylids noted in Petrželková *et al.* 2010 (74 by $42 \mu\text{m}$) and to *Oesophagostomum* eggs reported by File *et al.* 1976 (85 by $50 \mu\text{m}$), Kooriyama *et al.* 2012 (57–93 by $37\text{--}60 \mu\text{m}$) and Hasegawa *et al.* 1983 (75–80 by $43\text{--}48 \mu\text{m}$). The second ($n = 1$) had only about 16 cells, and measured $52 \times 30 \mu\text{m}$. It was similar to unidentified strongylids noted in Petrželková *et al.* 2010 (62 by $33 \mu\text{m}$), unidentified hookworm eggs (Hasegawa *et al.* 1983; 75–80 by $43\text{--}48 \mu\text{m}$) and to *Necator* eggs reported by File *et al.* 1976 (64 by $40 \mu\text{m}$).

Although other humans were rarely seen at our field sites, the identification of a few *Ascaris* eggs, a parasite of humans and pigs (Roberts and Janovy, 2005), raises the possibility of *P. papio* and *P.*

troglodytes contact with human feces. These infections could also stem from chance encounters with red river hog (*Potamochoerus porcus*) or warthog (*Phacochoerus aethiopicus*) feces (McGrew *et al.* 2014).

Within-host richness

We found 15 morphologically distinct taxa in *P. papio* and 11 in *P. troglodytes*. Two taxa (cf. *Enterobius* and *Troglodytella*) were present in *P. troglodytes* but not in *P. papio*. Neither G tests (Table 1) nor Fisher exact tests (not shown) could distinguish between low prevalences in *P. papio* and absence in *P. troglodytes* of seven taxa (*Streptophargus*, *Strongyloides*; data not shown for flukes ‘A’ and ‘B’ or for nematodes ‘A’, ‘B’ and ‘C’, each identified in $1.0 \pm 1.0\%$ of *P. papio* samples, Ebbert *et al.* 2013).

The *P. troglodytes* samples were less likely to be infected than the *P. papio* samples. All of the *P. papio* samples were infected with at least one parasite taxon and averaged 3.6 taxa each (Ebbert *et al.* 2013); we identified three or four taxa in most hosts. In contrast, only $65.3 \pm 6.8\%$ (32 of 49) of the *P. troglodytes* samples were infected; samples with no patent infections were more common than any other class. Among infected samples, those with a single parasite type were most common (12 of 32, $37.5 \pm 8.6\%$). The mean number of taxa per *P. troglodytes* sample was 1.6 ± 1.7 . In *P. papio* the average was more than twice that, 3.6 ± 1.3 taxa per sample, a significant difference (Wilcoxon rank test, $P < 0.0001$). Richness did not vary between locations in *P. troglodytes* (Wilcoxon rank test, $P = 0.3$) or *P. papio* (Ebbert *et al.* 2013).

Prevalence and community composition

Prevalences differed between host species in four cases (Table 1). *Balantidium* and *Trichuris* prevalences were higher in *P. papio*, *Watsonius* prevalence was higher in *P. troglodytes* and *Troglodytella* was absent in *P. papio*. *Streptophargus* and *Strongyloides* were absent in *P. troglodytes* and at very low prevalence in *P. papio*; in these cases, G tests could not distinguish between the two hosts.

Location had an effect on prevalence in only a few cases. Prevalence in *Enterobius* and cf. *Trichuris* showed host by location interactions without corresponding host effects. Prevalence of *Enterobius* in *P. troglodytes* samples collected from LV was about one-fourth of that seen in SV and in *P. papio* from both valleys. Prevalence of cf. *Trichuris* was 4–10X higher in *P. troglodytes* samples from SV than that seen in LV and *P. papio* samples from both valleys.

In *P. papio*, a trio of species (*Trichuris*, *Balantidium* and *Protospirura*) was present in most of the samples, each with a prevalence of 70% or more (Ebbert *et al.* 2013). In *P. troglodytes*,

Table 2. Percent prevalence (binomial error) of parasite genera in samples of *P. troglodytes* and *P. papio* in LV from 1976 to 1979 (McGrew *et al.* 1989, $n = 70$ for *P. troglodytes*, $n = 39$ for *Papio*)

Genus	Pan %	Papio %	Effects		
			Host	Time	H × T
<i>Balantidium</i>	0	72 (7.2)	140, ***	13, 0.0004	NS
<i>Enterobius</i>	13 (4.0)	0	NS	12, 0.0005	18, ***
<i>Physaloptera</i>	31 (5.5)	31 (7.4)	NS	44, ***	NS
<i>Protopharynx</i>	0	0	NS	122, ***	NS
<i>Streptophargus</i>	0	23 (6.7)	16, ***	NS	NS
<i>Strongyloides</i>	21 (4.9)	26 (7.0)	NS	27, ***	NS
<i>Trichuris</i>	0	28 (7.2)	58, ***	41, ***	NS
<i>Troglodytella</i>	77 (5.0)	0	12, 0.0005	NS	NS
<i>Watsonius</i>	0	0	NS	37, ***	NS

Results are from logistic models (G, P) testing whether host, time (compared with 2000 collections, Table 1) or their interaction effect prevalence. P values ≥ 0.05 are indicated by NS, those < 0.0001 by asterisks; other values are specified.

Protopharynx was the most common infection (found in $55 \pm 7.1\%$ of samples), but the second most common infection (*Trichuris*) was only about half of this value ($26 \pm 6.3\%$). None of the other taxa was found in more than 16% of *P. troglodytes* samples (Table 1).

Similar to *P. papio* (Ebbert *et al.* 2013), community composition in *P. troglodytes* shifted over the 22 years between sampling dates at LV (Table 2). Three genera seen in the present study were absent from the previous collection, despite the earlier study's larger ($n = 70$) sample size. *Watsonius* was absent from both hosts in the first study; *Trichuris* and *Balantidium* were previously present in *P. papio*, but not *P. troglodytes*. For reasons outlined above, we cannot be sure that the *Physaloptera* identified in the first study was different than the *Protopharynx* identified in the present study, and so draw no conclusions about the influence of time on their prevalences.

Correlations among taxa

Contingency table analysis of taxa with sample sizes of 10 or more pointed to associations among a triad of genera, *Trichuris*, *Watsonius* and *Enterobius* in both *P. troglodytes* and *P. papio* (Table 3). In each case, there were significantly more samples in which either both were present or both were absent when compared with the counts expected from the group prevalence. In *P. troglodytes*, *Trichuris* and *Balantidium* were positively associated, with more cases of co-occurrence (6) than expected (2), and a deficit of observations with only one parasite present.

Comparison across studies

We compared the prevalence of 10 parasite types in sympatric *P. troglodytes* and *Papio* spp. using data from this and five other studies (Table 4).

In every case, host was a significant factor in explaining prevalence and in seven cases the direction

of the effect was clear. These seven included three cases where a parasite found in one host was not found in the other: *Probstmayria* was absent from *Papio* spp. and *Streptophargus* and *Schistosoma* were absent from *P. troglodytes*. In two cases, infection was common in one host and found only once in the other: *Balantidium* was recorded only once in *P. troglodytes*, and *Troglodytella* only once in *Papio* spp. *Oesophagostomum* was always at a higher prevalence in *P. troglodytes*, while *Trichuris* was always at a higher prevalence in *Papio* spp. In the remaining three cases, host as a main factor was either not significant (*Necator*, *Strongyloides*, the interaction term was significant for these analyses) or weakly significant (0.04, *Physaloptera*, the interaction term was not significant in this case).

Within-group richness was estimated by counting all the parasitic animal taxa identified in the study and pooling across strongylids, as not all studies distinguished among the strongylid genera. Within-group richness averaged 6.3 (± 2.7) in *P. troglodytes* and 8.2 (± 3.5) in *Papio*, a non-significant difference (Wilcoxon rank test, $P = 0.26$).

Studies varied in their isolation method which could affect within group-richness, however, within-group richness did not differ among studies (Wilcoxon rank test, $P = 0.35$). Murray *et al.* (2000) was the only study to use a direct smear technique, and the only study not to use formalin-ether concentration. Three studies used flotation methods (McGrew *et al.* 1989; Murray *et al.* 2000; Howells *et al.* 2011). Two studies used only one method (formalin-ether concentration; Kooriyama *et al.* 2012; Ebbert *et al.* 2013), however, richness in these two studies did not differ from that found in the studies using two methods (Wilcoxon rank test, $P = 0.12$).

DISCUSSION

Our analysis contradicted each of our hypotheses, showing clear differences between *P. troglodytes*

Table 3. Observed *vs* expected occurrences of parasites in *P. troglodytes* (A) and *P. papio* (B) samples collected at Mt. Assirik

Genus A	Genus B	Comparison	Observed	Expected	<i>P</i>
A. Comparisons among <i>P. troglodytes</i> samples (<i>N</i> = 70)					
<i>Enterobius</i>	<i>Trichuris</i>	Both present	7	2	0.0001
		Both absent	35	30	
		Genus A only	1	6	
		Genus B only	6	11	
<i>Enterobius</i>	<i>Watsonius</i>	Both present	5	1	0.0014
		Both absent	38	34	
		Genus A only	3	7	
		Genus B only	3	7	
<i>Trichuris</i>	<i>Watsonius</i>	Both present	7	2	0.0001
		Both absent	35	30	
		Genus A only	6	11	
		Genus B only	1	6	
<i>Trichuris</i>	<i>Balantidium</i>	Both present	6	2	0.0007
		Both absent	35	31	
		Genus A only	7	11	
		Genus B only	1	5	
B. Comparisons among <i>Papio</i> samples (<i>N</i> = 49)					
<i>Enterobius</i>	<i>Trichuris</i>	Both present	38	35	0.03
		Both absent	10	7	
		Genus A only	1	4	
		Genus B only	51	54	
<i>Enterobius</i>	<i>Watsonius</i>	Both present	22	17	0.04
		Both absent	39	34	
		Genus A only	17	22	
		Genus B only	22	27	
<i>Trichuris</i>	<i>Watsonius</i>	Both present	43	36	0.01
		Both absent	10	6	
		Genus A only	46	50	
		Genus B only	1	5	

P values are from comparisons of observed *vs* expected using Fisher's exact test.

and *P. papio* as parasite hosts. At Mt. Assirik, within-host richness in *P. troglodytes* was lower than in *P. papio*, and more *P. troglodytes* samples were free of detectable parasites. Regardless of whether we compared across valleys (Table 1), years (Table 2) or studies (Table 4), host was a main effect in explaining prevalence in *Balantidium* and *Trichuris*: the prevalence of both was much lower in *P. troglodytes* than in *Papio* spp. Of the five common (>10% prevalence in at least one host and location) genera at our site, three (*Balantidium*, *Trichuris* and *Watsonius*) were more prevalent in *P. papio* when compared across hosts and valleys. We did not observe *Oesophagostomum* at Mt. Assirik; in the comparison among studies, its prevalence was consistently and significantly higher in *P. troglodytes* than in *Papio* spp. *Streptophargus* and *Schistosoma* were not found in *P. troglodytes* in any study, and *Probstmayria* was not found in *Papio* spp. The positive association of *Trichuris* and *Balantidium* we detected in *P. troglodytes* did not occur in *P. papio*.

We found some similarities between the hosts. At Mt. Assirik, egg morphology was consistent between hosts: this supports our assumption that we were detecting the same parasites in both hosts. Genera that were positively associated in *P. troglodytes*

(*Trichuris*, *Watsonius* and *Enterobius*) also co-occurred more than expected in *P. papio*. Our data and the comparison among studies suggested that host was not an important factor in explaining the prevalence of *Necator*, *Physaloptera*, *Protospirura* and *Strongyloides*. Within-group richness did not differ between the hosts when compared across studies.

The positive relationships we found among *Trichuris*, *Watsonius* and *Enterobius* in both hosts, and between *Trichuris* and *Balantidium* in *P. troglodytes* raise the intriguing possibility these co-infections can improve host habitat, perhaps through immunosuppression, excluding a common competitor, or altering the microbial community (reviews in Graham *et al.* 2007; Pedersen and Fenton, 2007; Eswarappa *et al.* 2012; Leggett *et al.* 2014).

Although we cannot be sure that the *Protospirura* we identified in this study differ from the *Physaloptera* identified earlier, we argue that the other three new genera detected in the present study represent a shift in parasite community composition. The alternative explanations, that the changes are due to the difference in the methods between the two studies, or to issues of identification, seem unlikely. The possibility that *Watsonius*, *Trichuris* and *Balantidium* were present

Table 4. Percent prevalence (binomial error) in sympatric *P. troglodytes* and *Papio* spp. populations

	Site	Mt. Assirik ^a	Mt. Assirik ^b	Fongoli ^c	Gombe ^d	Gombe ^e	Mahale ^f			
	Year	1976–79	2000	2005	1973	1989	2007			
	<i>Pan</i> n	70	49	132	32	22	300			
	<i>Papio</i> n	39	100	17	52	35	125			
	<i>Pan</i> R	3	11	7	6	6	5			
	<i>Papio</i> R	7	15	5	6	8	8			
Genus	Host	%	%	%	%	%	%	Effect test		
								Host ^g	Study ^h	H × S
<i>Balantidium</i>	<i>Pan</i>	0	14 (5·0)	0	0	0	0	69, ***	70, ***	13, 0·01
	<i>Papio</i>	72 (7·2)	74 (4·4)	12 (7·9)	42 (6·9)	0	10 (2·7)			
<i>Necator</i>	<i>Pan</i>	0	(s) ^j	0	41 (8·7) ⁱ	9 (6·1)	0	NS	11, 0·01	83, ***
	<i>Papio</i>	38 (7·8) ⁱ	(s) ^j	29 (11·0)	0	43 (8·4)	0			
<i>Oesophagostomum</i>	<i>Pan</i>	0	(s) ^j	0	91 (6·8)	73 (9·5)	63 (2·8)	78, ***	26, ***	NS
	<i>Papio</i>	0	(s) ^j	0	42 (6·8)	17 (6·3)	14 (3·1)			
<i>Physaloptera</i>	<i>Pan</i>	31 (5·5)	0	13 (3·0)	66 (8·4)	18 (8·2)	0	4, 0·04	46, ***	NS
	<i>Papio</i>	31 (7·4)	0	0	44 (6·9)	23 (7·1)	0			
<i>Probstmayria</i>	<i>Pan</i>	0	0	0	59 (8·7)	23 (9·0)	17 (2·2)	65, ***	NS	NS
	<i>Papio</i>	0	0	0	0	0	0			
<i>Schistosoma</i>	<i>Pan</i>	0	0	0	0	0	0	16, ***	NS	NS
	<i>Papio</i>	23 (6·7)	0	26 (10·6)	0	3 (2·9)	0			
<i>Streptophargus</i>	<i>Pan</i>	0	0	0	0	0	0	64, ***	NS	NS
	<i>Papio</i>	23 (6·7)	4 (2·0)	0	35 (6·6)	49 (8·4)	5 (1·3)			
<i>Strongyloides</i>	<i>Pan</i>	21 (4·9)	0	20 (3·5)	87 (5·9)	59 (10·5)	52 (2·9)	NS	206, ***	16, 0·007
	<i>Papio</i>	26 (7·0)	3 (1·7)	41 (11·9)	58 (6·8)	29 (7·7)	54 (4·5)			
<i>Trichuris</i>	<i>Pan</i>	0	27 (6·3)	1 (0·9)	9 (5·1)	5 (4·6)	4 (1·1)	153, ***	82, ***	NS
	<i>Papio</i>	28 (7·2)	89 (3·1)	35 (11·6)	42 (6·8)	66 (8·0)	68 (4·2)			
<i>Troglodytella</i> ^k	<i>Pan</i>	77 (5·0)	4 (2·8)	65 (4·2)	75 (7·7)	14 (7·4)	44 (2·9)	80, ***	NS	NS
	<i>Papio</i>	0	0	6 (5·8)	0	0	0			

Parasitic taxa are those found in at least one host in at least three studies. Effect tests are results (χ^2 , P) of logistic models. P values $\geq 0\cdot05$ are indicated by NS, those $< 0\cdot0001$ by asterisks; other values are specified. Within-group richness (R) includes all parasitic animals identified in the study and pooling across strongylids.

^a McGrew *et al.* 1989, *Papio papio*.

^b This study, Ebbert *et al.* 2013, *Papio papio*.

^c Howells *et al.* 2011, *Papio papio*.

^d McGrew *et al.* 1989, *Papio anubis*.

^e Murray *et al.* 2000, *Papio anubis*.

^f Kooriyama *et al.* 2012, *Papio cynocephalus*.

^g D.F. = 1.

^h D.F. = number of studies in which genus is present, minus 1.

ⁱ Data for 'hookworm'.

^j Strongylids not identified to genus.

^k Data for *Troglodytella abressarti*.

in *P. troglodytes* but not correctly identified in the earlier studies seems remote: the eggs of *Watsonius* and *Trichuris* are large and distinctive, as are *Balantidium* cysts, and the latter two genera were identified in *P. papio*. There were two differences in methods between our studies, and both would be likely to increase the number of genera in the first study over the second. The first sampling effort was conducted over a much longer time span, 28 months, during wet and dry seasons; the present study occurred during the dry season over a period of 1 month. In the earlier study (McGrew *et al.* 1989) we used two methods of preparing samples for examination. Both a longer sampling period and a second method of preparing each sample should yield more, not less, variation in the parasite community. Our first study included collections during the wet season; how this difference would affect the results is not clear. For example, we observed a decline in *Strongyloides* prevalence between our studies. Previous studies of *P. troglodytes* in Tanzania have shown both a decrease in *Strongyloides* during the dry season (Gillespie *et al.* 2010) and no effect of season on *Strongyloides* prevalence (Huffman *et al.* 1997; Bakuza and Nkwengulila 2009). Huffman *et al.* (1997) also found no effect of season on *Trichuris* prevalence.

We identified parasites by morphology, as is standard in the current primate literature. The lack of molecular tools for confirmation of these identifications is a serious problem, as highlighted by the issues with distinguishing among the genera *Protospirura*, *Physaloptera* and *Abbreviata* already mentioned. If *P. troglodytes*, humans and *Papio* spp. harbour morphologically indistinct species specialized to each primate host, then the concerns about cross-species transmission become much less pressing, although not moot. Recent studies on genetic variation in *Balantidium coli* (Pomajbíková *et al.* 2013), *Oesophagostomum* (Ghai *et al.* 2014a) and *Trichuris* (Ravasi *et al.* 2012; Ghai *et al.* 2014b) have shown both specialist and generalist clades. For example, isolates of *Trichuris* from South Africa showed two clades shared by humans and *P. ursinus* (Ravasi *et al.* 2012). Isolates of *Trichuris* from Uganda revealed a different pattern, clustering in three clades, one specific to humans, one specific to red colobus and black-and-white colobus, and one found in every primate tested, which included humans, *P. anubis* and *P. troglodytes* (Ghai *et al.* 2014b).

Understanding the mechanisms for the patterns we observed, and their relevance to either conservation of *P. troglodytes* or human health will require further study. Surveys tracking prevalence, community composition and within-host richness over extended time periods would be of particular value in determining whether our observations can be replicated. We speculate that, in those parasites that are spread via fecal contamination of food or water,

host physiology is more likely to explain differences between the hosts than differences in contact rates. There are no obvious gross behavioural or environmental differences between these two primates that might make one more likely to contact a fecal-borne parasite than the other. In the open, dry and hot habitat of Mt. Assirik, both species spend most of their days on the ground, and all of their nights in the trees (Sharman 1981; Baldwin *et al.* 1982), and their ranges overlap (LFM, WCM personal observation). In contrast to the fecal-borne parasites, contact with infective stages of parasites with intermediate hosts depends on more specific behaviours that could differ between hosts. These behaviours might include, among the parasites we identified at Mt. Assirik, differential rates of consuming particular arthropod intermediates of *Streptophargus* or encountering infective metacercaria of *Watsonius* encysted on plants.

We have shown that two closely related primates, *P. troglodytes* and *P. papio*, are significantly different as hosts of gastrointestinal parasites when compared across locations, times and studies. Of the five common genera at our site, three (*Balantidium*, *Trichuris* and *Watsonius*) were more prevalent in *P. papio* when compared across hosts and locations. This result was echoed in our comparison across studies, and suggests that baboons may be of particular public health concern in the epidemiology of *Trichuris*, a major human parasite found across Africa (Pullan and Brooker, 2012). Our results provide a baseline for comparison in studies of the interactions among humans, baboons and chimpanzees as hosts of gut parasites. For example, we showed that individual *P. troglodytes* were much more likely to be free of parasites than baboons, and those that were infected carried less than half as many types of parasites as *P. papio*. If, contrary to our results, chimpanzees showed a higher within-host richness than baboons in an area impacted by humans, this could suggest that factors associated with human activity (e.g. fragmentation, crowding and altered diet) disproportionately impact chimpanzees.

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