



Gastrointestinal Parasites of Savanna Chimpanzees (*Pan troglodytes schweinfurthii*) in Ugalla, Tanzania

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Abstract Understanding variability in patterns of parasite infections requires studies of multiple populations inhabiting a variety of habitats. Gastrointestinal parasites of chimpanzees (*Pan troglodytes*) have been studied extensively at several forested sites, but the parasite fauna of chimpanzees living in dry, open habitats is less well known. We studied the parasites of savanna chimpanzees (*Pan troglodytes schweinfurthii*) living in the Issa Valley, Ugalla (Tanzania). We examined 119 fresh fecal samples using standard coproscopical methods. We detected protozoans including *Blastocystis*

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sp., *Entamoeba coli*, *E. histolytica/dispar*, *Iodamoeba buetschlii*, *Trogloodytella abressarti*, and *Troglocorys cava*, but only two types of spirurid nematodes among the helminths. The parasites of the Ugalla chimpanzees differ from those of forest chimpanzees in the absence of *Strongyloides* sp. and strongylid nematodes and a high prevalence of spirurids. Strongylids and *Strongyloides* sp. have thin-shelled eggs and larvae, which develop in the external environment; thus they may not be able to survive for prolonged periods in the extreme environment of Ugalla. The Ugalla chimpanzees also live at a lower population density and exhibit a larger home range than forest chimpanzees, factors that may lead to lower exposure to infective nematode larvae. Spirurid eggs, however, have thick shells and a life cycle dependent on intermediary hosts, making their survival and transmission in such extreme conditions more feasible. These differences between parasite fauna of closed and open forest chimpanzees contribute to our understanding of the ecology of infectious disease, and have the potential to contribute to conservation policies and practices.

Keywords Hominoid · *Pan troglodytes schweinfurthii* · Gastrointestinal parasites · Savanna · Spirurids · Transmission · Ugalla · Tanzania

Introduction

Parasites play a key role in ecosystems. They affect the ecology and evolution of interspecific interactions, host population growth, regulation, and community biodiversity (Hochachka and Dhondt 2000; Hudson *et al.* 2002). Knowledge of parasite life cycles and transmission modes is essential to understand the impact parasites may have on the host (Nunn and Altizar 2006). Parasites can influence host survival and reproduction both directly through pathological effects and indirectly by reducing the host's physical condition (Boyce 1990; Hudson 1992).

A variety of host traits, together with environmental parameters and parasite transmission mode, determine encounters with and susceptibility to parasites. Primates, like other animals, live in different habitats and experience variations in temperature and rainfall (Nunn and Altizar 2006). Particular parasites are susceptible to variation in temperature and humidity at various stages of their life cycles (Smith 1990). For example, many nematodes require adequate humidity for egg and larvae development (Anderson 2000). Several studies have demonstrated a positive relationship between specific environmental features and levels of parasitic infections in primates (*Pan troglodytes schweinfurthii*: Huffman *et al.* 2009; *Alouatta palliata*: Stoner 1996; *Alouatta* sp.: Stuart *et al.* 1998). For example, the type and prevalence of gastrointestinal parasites in olive baboons (*Papio anubis*) are thought to depend on a combination of weather and habitat; specifically, the prevalence of nematodes with free-living stages exposed to the abiotic environment is higher in forest-dwelling than savanna-dwelling populations, as arid environments are unfavorable to nematode survival (Bezjian *et al.* 2008). The microclimate along forest edges is also expected to be less conducive to transmission for some parasite species infecting primates (*Piliocolobus tephrosceles*, *Procolobus rufomitratu*s, *Colobus guereza*) in comparison to interior forests (Chapman *et al.* 2006; Hodder and Chapman 2012), because forest edges receive increased wind

and increased solar radiation and are drier than interior forest environments (Matlack 1993; Murcia 1995).

Large home ranges and/or long daily travel distances have been hypothesized to be associated with higher parasite species richness as hosts range in a greater diversity of vegetation types and have increased encounter rates with other host individuals, which can lead to infection by a greater diversity of parasite species (Benavides *et al.* 2012; Freeland 1976; Mohr and Stumpf 1964). However, data from numerous host taxa, including primates, refute this hypothesis, and instead show a negative relationship between directly transmitted parasites (including monoxenous helminths) and home range size (Bordes *et al.* 2009; Lindenfors *et al.* 2007). Larger host home range leads to lower environmental contamination and decreases the risk of infection and rates of reinfection, particularly for soil-transmitted nematodes (Nunn and Dokey 2006; Nunn *et al.* 2011).

The gastrointestinal parasites of wild chimpanzees (*Pan troglodytes*) have been studied extensively at various forested sites across east and west Africa, e.g., Gombe, Tanzania (Bakuza and Nkwengulila 2009; File *et al.* 1976; Murray *et al.* 2000); Rubondo, Tanzania (Petrželková *et al.* 2010); Mahale, Tanzania (Huffman *et al.* 1997; Kawabata and Nishida 1991); Kibale, Uganda (Ashford *et al.* 2000; Krief *et al.* 2005; Muehlenbein 2005); and Lope, Gabon (Landsoud-Soukate *et al.* 1995). However, less is known about parasites from chimpanzees living in dry habitats. Only two studies have been conducted on this topic, both in Senegal, in chimpanzees living <50 km from each other: Mt. Assirik (McGrew *et al.* 1989) and Fongoli (Howells *et al.* 2010). Dry habitat chimpanzees may exhibit specific savanna adaptations in behavior, ranging, and social structure that reflect evolved strategies for coping with such a marginal environment, characterized by low rainfall, high aridity, and high temperatures (Moore 1992). These habitats may represent the ecological edge for chimpanzees, as they support population densities 1/10th of forest-dwelling populations (*ca.* 0.1 individuals/km²; Moyer *et al.* 2006) and savanna communities exhibit larger home ranges than forest chimpanzees, e.g., >85 km² (Fongoli-Skinner and Pruetz 2012); *ca.* 278–333 km² (Mt. Assirik; Baldwin *et al.* 1982); and *ca.* >217 km² (Ugalla, Tanzania; Piel and Stewart *unpubl. data*), likely as a response to sparse and patchily distributed food resources (Moore 1992, 1996). As a result, savanna-dwelling chimpanzees are predicted to differ from forest-dwelling populations in both diet and ranging, and in the pattern, rate, and level of social interactions (Collins and McGrew 1988). An additional consequence of living in a marginal habitat might include changes in the occurrence of parasites and other pathogens and their diversity compared to forest-dwelling populations (Howells *et al.* 2010; McGrew *et al.* 1989).

We report the first full description of gastrointestinal parasite fauna from a chimpanzee community living in the dry, open and seasonal habitat of Issa Valley in Ugalla, Tanzania. If savanna chimpanzees, which are predicted to have atypical sociality because of their low population densities (Moore 1992), experience lower exposure to soil-transmitted parasites, we predict a lower prevalence of directly transmitted parasites, which contain life stages that cannot survive in such extreme conditions, in savanna chimpanzees than in forest-dwelling populations. We also investigate the influence of a seasonal and dry environment by comparing sample parasite prevalence and richness across wet and dry seasons.

Materials and Methods

Study Site

Ugalla is located 80 km east of Lake Tanganyika in western Tanzania. It covers *ca.* 3352 km² with an elevation range of 980–1712 m above sea level. The Ugalla region consists of flat plateaus broken by broad valleys, steep hills, and severe slopes (Kano 1972; Moore 1994). The Malagarasi and Ugalla Rivers form the northern and eastern boundaries of Ugalla, respectively, and support seasonal streams lined with thin riverine forest patches. Ugalla has three main vegetation types: 1) savanna “miombo” woodland, dominated by deciduous trees *Brachystegia* sp. and *Julbernardia* spp., interspersed by 2) small patches of thin riverine forest strips, and 3) swamp and grassland (Hernandez-Aguilar 2009). Average annual rainfall varies from 955 mm (Hernandez-Aguilar 2009) to 1300 mm (Piel and Stewart *unpubl. data*), and the temperature varies between 11 and 35°C (Stewart 2011). The climate of Ugalla includes a prolonged dry season from May to September (monthly mean of rainfall is less than 0.8% of the mean annual total) and rainy seasons from October/November to April/May (Hernandez-Aguilar 2006). The Ugalla region has been described as one of the driest habitats where chimpanzees live (Kano 1972; Kortland 1983; Moore 1992, 1994, 1996; Nishida 1989).

The Ugalla region remains an intact ecosystem, but in recent years, the area has been under increasing pressure from humans. The greatest threats to the region include agricultural expansion, cattle herding, annual grass fires, logging, and poaching. The nearest Tanzanian village is Uvinza, 70 km north of the study area, which is <10 km from the border of the Mishamo Refugee Settlement, an area where >50,000 Burundian refugees have lived since 1972 and are known to enter the ecosystem frequently.

The study area includes several other primate species in addition to chimpanzees: yellow baboons (*Papio cynocephalus*), redbelt (*Cercopithecus ascanius*), vervets (*Chlorocebus pygerythrus*), and red colobus monkeys (*Piliocolobus tephrosceles*), as well as nocturnal bushbabies (*Otolemur crassicaudatus*; *Galago senegalensis*). The population density of Ugalla chimpanzees (*Pan troglodytes schweinfurthii*) is estimated to be between 0.08 and 0.14 individuals/km² based on nest censuses (Hernandez-Aguilar 2006; Moyer *et al.* 2006; Ogawa *et al.* 2007), which is one of the lowest known densities across Africa. However, chimpanzee density is slightly higher in the Issa study area, in the center of Ugalla, at 0.28 individuals/km² (Piel and Stewart *unpubl. data*), likely representing a core area of these wide-ranging chimpanzees.

Sample Collection and Examination

We collected fresh (<12 h old) samples from chimpanzees over an 85 km² study area of the Issa Valley from September 2008 to August 2009. All samples are likely to have originated from a single community, for which genotyping ($N = >350$ samples) indicated a minimum community size of >67 individuals (Rudicell *et al.* 2011). We collected most of the fecal samples underneath fresh nests (85), and some from chimpanzee trails (34). The chimpanzees are unhabituated and therefore we could not attribute the fecal samples to specific individuals. We attempted to collect samples from all fresh nests built on the same night, as these samples are likely to have originated

from different individuals. Samples from chimpanzee trails could have been from the same individual, however. It is also possible that fecal samples collected on the trails were from the individuals already sampled during the collection from the nests. We attempted to collect similar numbers of samples each month for seasonal comparisons. In total we collected 119 chimpanzee fecal samples, 68 samples in the dry and 51 samples in the wet season. The median was 10 (range 5–15) samples per month in the wet season and 12 samples (range 6–14) per month in the dry season.

We collected 2 g of feces and placed it in 10 ml of 4% formaldehyde. We collected samples using sterile spatulas and took fecal material only from the center of the feces that had not touched the ground. We stored the samples at room temperature and shipped them to the Department of Pathology and Parasitology, University of Veterinary and Pharmaceutical Sciences, Brno.

Before parasitological analyses, we homogenized each fecal sample and strained it through a sieve into conical tubes (50 ml). We diluted each sample with phosphate buffer solution up to 50 ml volume and centrifuged it for 5 min at 2000 rpm. We then re-fixed the sediment in 10 ml of 4% formaldehyde. For initial coprological examination we used Sheather's flotation with modified sugar solution (specific gravity 1.33; Sheather 1923). We mixed 2 ml of resuspended fecal sediment with distilled water in a flotation tube and centrifuged it for 3 min at 2000 rpm. We then removed the supernatant and mixed the sediment with sugar solution and centrifuged it for 3 min at 2000 rpm. We transferred the surface film from the top onto a microscopic slide with a horizontal loop, added a cover slip, and examined each sample initially using a light microscope under $\times 200$ magnifications. To examine the sample by merthiolate-iodine-formaldehyde concentration (MIFC; Blagg *et al.* 1955) we took 2 ml of fecal suspension and mixed it with 6 ml of MIFC solution, 1 ml of Lugol's iodine, and 5 ml of ether in a 15-ml tube and centrifuged it for 2 min at 1500 rpm. We poured the supernatant off and transferred the remaining sediment with a Pasteur pipette onto a microscopic slide, added a cover slip, and examined it again using a light microscope under $\times 400$ and $\times 1000$ magnification. We identified parasite taxa on the basis of identified characteristics of known stages, such as shape, size, and external and internal structures of eggs, cysts, or trophozoites (Ash and Orihel 2007; Jessee *et al.* 1970).

Statistical Analyses

We report sample parasite prevalence (percent of samples with a given parasite taxa) and richness (the number of unique parasite taxa recovered from the sample). We conducted comparisons of parasite prevalence of each parasite taxa between dry and wet seasons using Fisher exact tests. We made sequential Bonferroni adjustments of *P*-values for these tests (Rice 1989) and performed Mann-Whitney *U* tests to compare parasite richness between wet and dry seasons. We analyzed all data using STATISTICA, version 8.0 (StatSoft Inc., Tulsa, OK) and SISA (<http://www.quantitativeskills.com/sisa/>).

Ethical Note

We collected the fecal samples from chimpanzees noninvasively and did not cause any observable distress to the subjects.

Results

We examined 119 fecal samples in which we detected six protozoan taxa: *Blastocystis* sp.; entodiniomorphid ciliates *Troglodytella abrossarti* and *Troglocorys cava*; and amoebae *Entamoeba coli*, *E. histolytica/dispar*, and *Iodamoeba butschlii* (Table 1). Cysts of *Blastocystis* sp. (Heterokontophyta: Blastocystida) were spherical to subspherical, ranging between 6 and 40 μm in size ($N = 30$). The thin-walled cysts contain a large central body and peripheral rim containing four nuclei and inclusion bodies. Cysts of *Entamoeba coli* (Amoebozoa: Entamoebida) were most often spherical but also oval-shaped and thick-walled, and the number of nuclei ranged between two and eight. Cyst size was 15–30 μm ($N = 30$). Thick-walled cysts of *Entamoeba histolytica/dispar* (Amoebozoa: Entamoebida) were spherical and contained one to four nuclei. Cyst size ranged between 10 and 20 μm ($N = 30$). Thick-walled cysts of *Iodamoeba butschlii* (Amoebozoa: Entamoebida) were spherical to ellipsoidal and contained a single nucleus and single vacuole with compact glycogen, appearing yellow in Lugol's iodine stained samples. Cyst size ranged between 5 and 20 μm ($N = 30$). Trophozoites of *Troglodytella abrossarti* (Ciliophora: Entodiniomorphida) typically pointed toward the caudal end and measured 100–180 μm ($N = 30$). Cilia were organized into four bands partially surrounding the body and one band of adoral cilia around the cytostome. However, in most cases the cilia were decomposed. The L-shaped macronucleus was sometimes visible. Trophozoites of *Troglocorys cava* (Ciliophora: Entodiniomorphida) were ovoid with a large cytostome and varied between 30 and 50 μm in size ($N = 30$). The ciliary bands were situated around the caudal end of the body and on the upper side of the cytostome.

We found two types of spirurid nematode eggs (Nematoda: Spirurida), which differed in size (Fig. 1). The eggs were colorless, ellipsoidal with hyaline substance around the egg, and contained first-stage larva. The size of eggs ranged between 55 and 65 μm ($N = 30$) for the larger type and between 20 and 30 μm ($N = 5$) for the small type. We did not observe the eggs or larvae of other helminths.

Table 1 Prevalence of gastrointestinal parasites of Ugalla chimpanzees

	Prevalence (%)			<i>P</i> -values
	Total (<i>N</i> = 119)	Dry season (<i>N</i> = 68)	Rainy season (<i>N</i> = 51)	
<i>Blastocystis</i> sp.	51.3	57.3	43.1	0.017
<i>Entamoeba</i> spp. ^a	6.7	2.9	11.5	0.281
<i>Iodamoeba butschlii</i>	13.5	13.2	15.7	1.000
<i>Troglocorys cava</i>	19.3	22.1	15.7	0.187
<i>Troglodytella abrossarti</i>	62.2	55.9	82.4	0.681
Spirurida fam.gen. ^b	40.3	63.2	9.8	<<0.001

^a Include *Entamoeba histolytica/dispar*, *Entamoeba coli*.

^b Include *Protospiruramuricola* and one unidentified species.

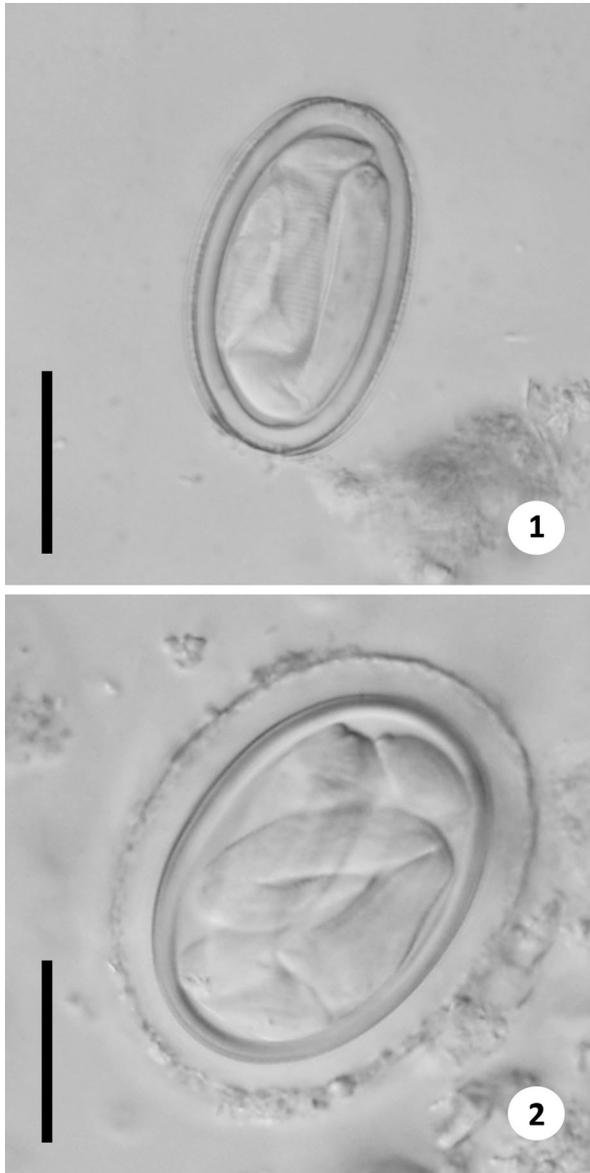


Fig. 1 Two types of eggs of spirurid nematodes found in chimpanzee feces at Ugalla, Tanzania (September 2008–August 2009). Scale bar = 20 μ m.

We found no difference in prevalence between dry and wet seasons for any parasite taxa (Table I), with the exception of spirurid nematodes, the prevalence of which was higher in the dry season (Table I). The median parasite richness was one parasite taxa per sample and the mean was two parasite taxa per sample (range 0–5). There was no difference in parasite richness between the seasons (Mann-Whitney U test, $Z = -0.53$, $P = 0.61$).

Discussion

The prevalence of *Trogloodytella abressarti* in Ugalla chimpanzees is comparable to that in savanna chimpanzees at Mt. Assirik (McGrew *et al.* 1989) and Fongoli (Howells *et al.* 2010) as well as in some forest-dwelling communities, e.g., Kibale, Uganda (Ashford *et al.* 2000; Krief *et al.* 2005) and Gombe, Tanzania (File *et al.* 1976). Commensal ciliates *Trogloodytella abressarti* and *Troglocorys cava* are ubiquitous inhabitants of the chimpanzee colonic ecosystem (Pomajbíková *et al.* 2010, 2012; Tokiwa *et al.* 2010). Variation in their prevalence between studies and study sites is most likely to be attributable to the sensitivity of detection methods and fluctuation of ciliate populations below the detection threshold, rather than to ecological or behavioral differences. Repeated individual sampling and presenting cumulative prevalence are needed to reveal the real prevalence of these ciliates (Kaur *et al.*, 2010; Muehlenbein 2005). Long-term persistence of ciliate-negative animals in positive groups is unlikely (Modrý *et al.* 2009).

Our findings concerning the prevalence of other protists, *Blastocystis* sp. and amoebae, are also comparable to those from other chimpanzee populations (Ashford *et al.* 2000; Muehlenbein 2005; Petrášová *et al.* 2010). Based on cyst morphology, we found three amoebae species—*Entamoeba coli*, *E. histolytica/dispar*, and *Iodamoeba buetschlii*—in Ugalla chimpanzees. However, a polymerase chain reaction (PCR) approach is needed to detect and identify these protists reliably, and prevalence data based on microscopic examination should be treated with extreme caution (Diamond and Clark 1993; Petrášová *et al.* 2010; Tachibana *et al.* 2000; Verweij *et al.* 2001). Reports of different species of *Entamoeba* from wild chimpanzees are common (Ashford *et al.* 2000; Huffman *et al.* 2009), but differences in the prevalence of individual taxa most likely reflect differences in the coproscopical methods used (see Bakuza and Nkwengulila 2009 for a comparison of parasitological examinations of Gombe National Park chimpanzees, Tanzania) and the inability to discriminate species that are morphologically identical.

Our results from Ugalla, together with results of McGrew *et al.* (1989) and Howells *et al.* (2010), reveal that the most striking difference between savanna and forest chimpanzee populations is the absence or low prevalence of directly transmitted soil nematodes in open habitat populations. This is also characteristic of baboons (*Papio* spp.) living in savanna (Appleton and Brain 1995; Bezjian *et al.* 2008; Ghandour *et al.* 1995; McGrew *et al.* 1989). Both Ugalla and Mt. Assirik chimpanzees lack strongylids, and their prevalence was also low in Fongoli chimpanzees (16%; Howells *et al.* 2010). We suspect that larvae of strongylids have a low probability of prolonged survival in extremely dry and hot savanna habitats. Similarly, we did not find *Strongyloides* nematodes, the larvae of which need a moist external environment to develop, in Ugalla and their prevalence at Mt. Assirik chimpanzees and at Fongoli (Howells *et al.* 2010; McGrew *et al.* 1989) was lower than in forest-dwelling populations. It seems likely that an extremely dry and hot environment, combined with living at low population densities in a large home range, in comparison with forest-dwelling populations, has a substantial impact on parasites that have free-living stages in their life cycle.

The high prevalence of spirurid nematodes at Ugalla in comparison to forested populations also supports the results of McGrew *et al.* (1989) and Howells *et al.* (2010). The prevalence of spirurids in chimpanzees is low at most forested sites, e.g., 1.5% at Lope, Gabon (Landsoud-Soukate *et al.* 1995) and 5.4% at Rubondo, Tanzania (Petrželková *et al.* 2006), whereas chimpanzee spirurids are recorded in high

prevalence at all savanna sites: 40% at Ugalla (this study); 31% at Mt Assirik, Senegal (McGrew *et al.* 1989); and 13.3% at Fongoli, Senegal (Howells *et al.* 2010). Although several species of spirurids have been identified in chimpanzees (File *et al.* 1976; Landsoud-Soukate *et al.* 1995; McGrew *et al.* 1989; Muehlenbein 2005, Murray *et al.* 2000; Myers *et al.* 1973; Petrželková *et al.* 2006, 2010), identification based on egg morphology is unreliable. We detected two types of spirurid eggs in Ugalla. Based on morphology and size we tentatively identified the larger one as *Protospirura muricola*, while the smaller one resembled *Streptopharagus pigmentatus* (Hasegawa *pers. comm.*). In contrast to strongylid and rhabditid nematodes, the life cycle of spirurids is typically dixenous, requiring the ingestion of an intermediate insect host (Anderson 2000). Ugalla chimpanzees consume termites, ants, and coleopteran larvae (Piel *et al.* 2013; Piel and Stewart *unpubl. data*). Owing to seasonal ripe fruit scarcity in these drier habitats (Bogart and Pruetz 2011), savanna chimpanzees may eat invertebrates more often than forest chimpanzees (McGrew 1979; Stewart and Piel 2013; Uehara 1986), which may explain the higher prevalence of spirurids. We recorded a significantly higher prevalence of spirurid parasites in the dry season, similar to that in Mt Assirik chimpanzees (McGrew *et al.* 1989), which may be due to seasonal availability of insect intermediate hosts preyed on by chimpanzees.

Given the high diversity in both chimpanzee behavior (Boesch *et al.* 2002) and ecology (Caldecott and Miles 2005), it is difficult to know whether one or both better explain variation in population differences in parasite richness and diversity. An extremely low prevalence of strongylid nematodes (1.1%) and *Strongyloides* sp. (6.9%) was also recorded in chimpanzees introduced into humid forest ecosystem on isolated Rubondo Island, Tanzania, resulting in low parasite richness (Petrášová *et al.* 2010; Petrželková *et al.* 2010). The original 17 chimpanzees were from several African countries, had spent between 3.5 mo and 9 yr in captivity, and were released onto the island between 1966 and 1969. Their individual health conditions varied greatly, with some receiving antimalaria treatment before their release (Huffman *et al.* 2008). Like savanna populations, Rubondo chimpanzees have much larger home ranges (Baldwin *et al.* 1982; Kano 1972; Moscovice *et al.* 2007) than those in other sites (Yamagiwa 2004). This interesting parallel suggests that home range, daily path length, and/or population density influence the abundance of strongylids and other directly transmitted soil nematodes, e.g., *Strongyloides*, in primate populations.

Although it has been suggested that the last common ancestor of humans and chimpanzees might have hosted parasite fauna more similar to that of baboons than to modern chimpanzees (Ashford *et al.* 2000; Glenn and Brooks 1986) due to a similar diet, we suggest that savanna chimpanzees may also serve as a good model for human ancestor parasite infections, due to their similar diet. The gastrointestinal parasite fauna of chimpanzees living in seasonal, dry habitats may resemble those of early Plio-Pleistocene hominids, given the similar habitats in which these hominids lived (Cerling *et al.* 2011). Contemporary assemblages of parasites of humans probably differ from those from of early hominids. A major shift in infectious disease followed the rise of agriculture, animal domestication, environmental modifications, and greater population densities as permanent settlements formed (Nunn and Altizar 2006). Comparison of data obtained from savanna and Rubondo chimpanzees living in different ecological conditions further supports the role of sedentary life and home range on prevalence of so-called heirloom parasites. These parasites refer to species that we inherited from our

ancestor insofar as they continued to infect them as they evolved into modern humans (Brooks and Ferrao 2005).

Not only do studies of savanna chimpanzee parasite fauna potentially inform us about the hominoid evolutionary past, but they also have critical implications for the hominoid future. Parasite infections and their subsequent consequences for primate fitness present an increasingly important issue for conservation biologists (Gillespie *et al.* 2008). More specifically, studying parasite ecology in the same species across different habitats can inform us about the roles of both the host environment and host behavior in parasite infection, as we have tried to argue here between closed and open forest chimpanzees. In summary, then, understanding the ecology of infectious disease has the potential to contribute to policies and practices that can enhance protection for otherwise threatened or endangered species and/or even whole ecosystems.

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