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RESEARCH ARTICLE

Parasitological Analyses of the Male Chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda

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Numerous intestinal parasites identified in populations of wild nonhuman primates can be pathogenic to humans. Furthermore, nonhuman primates are susceptible to a variety of human pathogens. Because of increasing human encroachment into previously nonimpacted forests, and the potential for disease transmission between human and nonhuman primate populations, further detailed investigations of primate ecological parasitology are warranted. For meaningful comparisons to be made, it is important for methods to be standardized across study sites. One aspect of methodological standardization is providing reliable estimates of parasite prevalence and knowing how many samples are needed to adequately estimate an individual's parasite prevalence. In this study the parasitic fauna of 37 adult, adolescent, and juvenile male chimpanzees from the Ngogo group, Kibale National Park, Uganda, were assessed from 121 fecal samples collected over a 3-month period. Twelve taxa of intestinal species (five helminth and seven protozoan) were recovered from the samples. The four most prevalent species were *Troglodytella abrassarti* (97.3%), *Oesophagostomum* sp. (81.1%), *Strongyloides* sp. (83.8%), and *Entamoeba chattoni* (70.3%). No one species was found in all samples from any one animal, and *Troglodytella abrassarti*, the most common intestinal organism, was found in all of the serial samples of only 69.4% of the chimpanzees. The cumulative species richness for individuals significantly increased for every sequential sample (up to three to four samples) taken per animal during this study. The results indicate that to accurately diagnose total intestinal infection and evaluate group prevalence, three to four sequential samples from each individual must be collected on nonconsecutive days. This conclusion applies only to short study periods in which possible seasonal effects

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are not taken into consideration. Validation of these results at different study sites in different regions with different climatic patterns is needed.
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Key words: intestinal parasites; chimpanzee; parasite richness; ecological parasitology

INTRODUCTION

The interests of primatologists and parasitologists have combined to create a multidisciplinary approach for identifying the ecological, physiological, and behavioral determinants of parasite-induced pathology in natural primate populations [Stuart & Strier, 1995]. The fruits of these combined interests are a number of published field studies of intestinal parasites in natural populations of primates, including free-ranging Cayo Santiago rhesus macaques (*Macaca mulatta*) [Kessler et al., 1984]; Costa Rican squirrel monkeys (*Saimiri oerstedi*) [Appleton & Boinski, 1991]; muriquis (*Brachyteles arachnoides*) and brown howling monkeys (*Alouatta fusca*) in southeastern Brazil [Stuart et al., 1993]; mantled howling monkeys (*Alouatta palliata*) at La Selva Biological Reserve in northeastern Costa Rica [Stoner, 1996]; vervets (*Cercopithecus aethiops*) and sykes (*Cercopithecus mitis*) near Nairobi, Kenya [Munene et al., 1998]; sykes (Samango monkeys) (*Cercopithecus mitis labiatus*) in Natal, South Africa [Appleton et al., 1994]; vervets, sykes, black and white colobus (*Colobus abyssinicus*), Debrazzas monkeys (*Cercopithecus neglectus*) [see also Karere & Munene, 2002], and gray and black mangabeys (*Cercocebus torquatus* and *Cercocebus albigena*) in rural Kenya [Muriuki et al., 1998]; sifaka (*Propithecus verreauxi verreauxi*) at Beza Mahafaly, Madagascar [Muehlenbein et al., 2003]; chacma baboons (*Papio ursinus*) [Goldsmid & Rogers, 1978]; olive baboons (*Papio cynocephalus anubis*) [Muller-Graf et al., 1996; Munene et al., 1998; Muriuki et al., 1998]; bonobos (*Pan paniscus*) in Zaire [Hasegawa et al., 1983]; and gorillas (*Gorilla* sp.) in Gabon and Uganda [Ashford et al., 1990; Landsoud-Soukate et al., 1995; Rothman et al., 2002].

A number of field studies of intestinal parasites in natural populations of chimpanzees (*Pan troglodytes*) in Gombe, Mahale, Kibale (Kanyawara community), Senegal, Gabon, and the Central African Republic [Ashford et al., 2000; File et al., 1976; Goodall, 1968; Huffman et al., 1997; Kawabata & Nishida, 1991; Landsoud-Soukate et al., 1995; Lilly & Doran, 1999; McGrew et al., 1989; Murray et al., 2000] have been published, and it is evident from these studies that chimpanzees harbor numerous different intestinal parasites. However, it is difficult to accurately compare the results of these studies for at least two reasons: 1) the variety of parasitological techniques used (e.g., formalin ethyl-acetate sedimentation, zinc sulfate flotation, volumetric dilution, etc.) [Ashford et al., 2000], and 2) the inability to report true prevalence, which can occur when samples cannot be collected from identified individuals.

Ashford et al. [2000] provided a detailed analysis of the Kanyawara community in Kibale National Park, Uganda, as well as a comparison of many of the previous parasitological surveys of wild chimpanzees. However, their comparison reported true prevalences for some studies [File et al., 1976; Landsoud-Soukate et al., 1995; Murray, 1990; Murray et al., 2000] and percent of samples found positive for others [Ashford et al., 2000; Kawabata & Nishida, 1991; McGrew et al., 1989], although all surveys are reported as ''samples found positive (%) for'' in Ashford et al.'s [2000, p. 175] comparison. Huffman et al.

[1997] demonstrated that significant reporting bias is created when one uses the number of samples instead of the number of individuals to calculate the prevalence of parasitic infection in a population. Methodological standardization is necessary for future parasitological analyses of wild primate populations.

Many of the intestinal parasites identified in populations of wild nonhuman primates can be pathogenic to humans, and nonhuman primates are susceptible to a variety of human pathogens. Increasing human encroachment into previously nonimpacted forests increases the potential for disease transmission between human and nonhuman primate populations [Brack, 1987; Lilly, 2003; Wolfe et al., 1998]. This poses a great concern in terms of public health and nonhuman primate conservation. Detailed investigations of primate ecological parasitology are therefore warranted, especially at sites for which we currently have no information regarding parasite presence and prevalence.

Although the Ngogo community is the largest known habituated population of chimpanzees in the wild, there is as yet no detailed parasitological data for this group. Therefore, in this study a detailed analysis of parasite fauna in the chimpanzees at Ngogo was undertaken. The present study addresses methodological standardization for future parasitological comparisons of wild primate populations, and emphasizes the importance of sequential sampling of individuals.

MATERIALS AND METHODS

Study Site

Ngogo is in the Kibale National Park in western Uganda, and is maintained by the Makerere University Biological Field Station. The park is located between 0°41′N, 30°19′E and 0°13′N, 30°32′E, with a total area of approximately 750 km^2. The Ngogo study area is approximately 25 km^2 and contains mature, regenerating, and swamp forest, *Acanthus* scrub, and other types of vegetation [Ghigliere, 1984; Struhsaker, 1997]. The field site is devoid of domestic herbivores and pets. Human contact with the chimpanzees is minimal and is restricted to park caretakers and researchers. Latrines and garbage pits are used for disposal of human waste and refuse at the research camp. The chimpanzees do not enter the camp, nor do they enter fields outside of the park boundaries. This limits potential contact between the chimpanzees and human or domestic animal feces.

Subjects

The Ngogo chimpanzee community was originally studied by Ghiglieri in the late 1970s and early 1980s [Ghigliere, 1984]. Research and habituation efforts resumed at Ngogo in 1991, and have been continuous since 1995. All adult and adolescent males are well habituated and are observable within 5–10 m on the ground. At the time of this study, the Ngogo community had about 150 members, including 24 adult males and 14 adolescent males. Ngogo males are more gregarious and more habituated than the females, and thus the males were the subject group of this study. Because of this sampling protocol, sex differences could not be evaluated in the present study. Nonetheless, sex differences are important for a complete evaluation of presence and prevalence in any parasitological investigation, when individual host identification is possible.

Although the exact ages of the males at Ngogo are unknown, the adult animals were assigned to the following age categories based on physical characteristics and history of observations: 1 = old, 2 = old prime, 3 = prime,

4 = young prime, and 5 = young. Likewise, the age classes of adolescent males were also based on physical characteristics and history of observations, but were scaled differently compared to the adults: 1 = adolescents closest to young adulthood (oldest adolescents), and 6 = adolescents close to juvenile stage (youngest adolescents). The methods behind this age categorization are detailed elsewhere [Muehlenbein et al., 2004].

Sample Collection

A total of 121 fecal samples were collected opportunistically from 22 adults, 14 adolescents, and one juvenile male chimpanzee at Ngogo between July and September 2002. Of the 22 adults sampled, one was sampled once, two were sampled twice, six were sampled three times, 12 were sampled four times, and one was sampled five times. Of the 14 adolescents, one was sampled once, three were sampled twice, five were sampled three times, five were sampled four times, and none were sampled five times. One juvenile was sampled two times. On average, 3.24 samples were collected from each animal.

Samples were obtained immediately following defecation to ensure a positive match of the individual with the fecal sample collected. Care was taken to avoid collecting portions of samples that may have been contaminated by soil or pooled water. No blood or mucus was observed in any fecal mass collected, nor did color or consistency differ significantly between masses. Diarrhea was observed on very few occasions, and this was almost always prior to or during a boundary patrol or hunt. Such samples were never collected.

Following defecation, the samples were immediately preserved in Para-Pak plastic transport vials (Meridian Diagnostics, Cincinnati, OH) prealiquoted with 10% neutral buffered formalin. All tubes were labeled with the name of the animal and the date. For each individual animal, samples were collected on nonconsecutive days.

Parasitological Analyses

Each specimen was directly examined by means of the formalin-ethyl acetate sedimentation technique [Ash & Orihel, 1991]. Stool samples were emulsified and filtered through two layers of wet gauze into a plastic cup. The stool was washed with saline solution, placed into a 15-ml conical-bottom centrifuge tube, and centrifuged at 500 rpm $\times$ gm for 3 min. The supernatant was discarded, and the sediment was resuspended in 10 ml of 10% formalin. Then 3 ml of ethyl acetate was added to separate the fat in the sample, and the suspension was shaken vigorously for 30 sec. The specimen was recentrifuged, the fat/debris plug was removed with an applicator stick, and the supernatant was discarded. The remaining pellet was resuspended with a drop of Lugol's iodine solution.

Intestinal fauna prevalence and richness are both reported here. Prevalence is defined as the ''number of individuals of a host species infected with a particular intestinal species $\div$ number of hosts examined'' [Margolis et al., 1982, p. 131]. Richness is defined as the number of unique intestinal species recovered from the host's fecal samples.

Statistical Analyses

The data were entered into an Access database that was then imported into SAS for analysis with SAS/STAT software [SAS Institute Inc., 2001]. Frequencies were determined via the PROC FREQ command, and Pearson correlations were

determined with the PROC CORR command. The frequencies of intestinal species were compared between adults and adolescents by means of Fisher's exact test. Differences in intestinal species richness between adults and adolescents were assessed via unpaired t-tests. Differences in cumulative intestinal species richness between sample days 1–4 were assessed via paired t-tests.

Power analyses were calculated for all tests that revealed nonsignificant results (P-value > 0.05) to assess the likelihood of false negatives. Power analyses were performed with the program G-Power [Faul & Erdfelder, 1992]. Power of less than 80% should suggest to the reader that the data (with the present sample size) are not strong enough to disprove the null hypothesis (of a significant difference in intestinal species prevalence or richness between adults and adolescents, or between animals of different age classes).

RESULTS

Species Prevalence and Richness

Twelve taxa of intestinal fauna (five species of helminths and seven species of protozoa) were recovered from the samples. Some of these organisms are not named at the species level because of doubt about the accuracy of identification, especially with strongyles in the absence of coproculture. Table I presents the prevalences for each of the intestinal taxa recovered in the present study, as well as those obtained in Ashford et al.'s [2000] study of the Kanyawara chimpanzee

TABLE I. Prevalences for Intestinal Fauna at Ngogo [Present Study] and Kanyawara [Ashford et al., 2000]*

Species	NGOGO Prevalence (%)		KANYAWARA Prevalence (%)	
	n = 37 individuals	n = 121 samples	n = 45 individuals	n = 123 samples
Troglodytella abrassarti	97.3	84	98	91
Oesophagostomum sp.	81.1	49	NF	NF
Strongyloides sp.	83.8	52	UR	4.9
Entamoeba coli	2.7	1	UR	1.6
Entamoeba hartmanni	16.2	7	13 ?	13
Entamoeba chattoni	70.3	33	40 ?	40
Endolimax sp.	5.4	2	NF	NF
Iodamoeba sp.	29.7	13	47 ?	47
Blastocystis sp.	2.7	1	27 ?	27
Physaloptera caucasica	29.7	11	NF	NF
Probstmayria gombensis	16.2	6	UR	7.3
Hymenolepis sp.	32.4	10	NF	NF
''Flagellates''	NF	NF	UR	9.8
''Strongyles''	NF	NF	UR	31
''Small Ciliate''	NF	NF	98	81.3
Bertiella	NF	NF	UR	1.6
Trichuris	NF	NF	UR	0.8
Giardia	NF	NF	UR	4.9
Enterobius	NF	NF	UR	0.8

*Prevalence is defined as the ''number of individuals of a host species infected with a particular parasite species ÷ number of hosts examined'' [Margolis et al., 1982, p.131].
NF, not found; UR, unreported; ?, reported as ''observed prevalence'' as well as ''samples found positive (%) for'' in Ashford et al. [2000].

community. In the present study, the four most prevalent species were *Troglodytella abrassarti* (97.3%), *Oesophagostomum* sp. (81.1%), *Strongyloides* sp. (83.8%), and *Entamoeba chattoni* (70.3%). The frequency of samples positive for each intestinal taxa (number of positive samples divided by 121 samples total) ranged from 1% to 84%. Only 2% of the samples had no parasites.

The mean total richness values (both helminths and protozoa) were 4.75 for the total sample, 4.77 for the adults, and 4.71 for the adolescents. The mean numbers of unique helminth and protozoan species recovered were 2.43 and 1.27, respectively, for the total sample.

In the total sample of adult and adolescent animals (n = 36 chimpanzees, 119 samples), *Troglodytella abrassarti* was found in all of the serial samples of 69.4% of the animals, *Oesophagostomum* sp. was found in 22.2%, *Strongyloides* sp. was found in 13.9%, and *Entamoeba chattoni* was found in only 2.8%. Table II illustrates the sampling variation for each intestinal taxa. In this table, ''variation'' is the mean percentage of an individual's samples in which a taxa occurred (for all animals in which that was found; n = 36 chimpanzees, 119 samples). No intestinal organism was present in all samples from any one animal. Even with the four most prevalent taxa (*Troglodytella abrassarti*, *Oesophagostomum* sp., *Strongyloides* sp., and *Entamoeba chattoni*), of the animals in which these species were found, they were found in 88.4%, 59%, 59.1%, and 45.8%, of their samples, respectively.

Figure 1 illustrates the mean species richness (the number of unique intestinal species recovered from the hosts' fecal samples) by the number of sequential samples taken per animal. The mean richness increased when more than one sample was collected from each animal. However, there appeared to be little difference in mean richness in animals from which two, three, or four samples were taken. Figure 2 illustrates the mean cumulative richness by the cumulative number of samples taken per animal. For example, the mean cumulative richness for the first sample was calculated from the sum of the number of unique intestinal species found in the first sample of each animal, whereas the mean cumulative richness for the fourth sample was calculated from the sum of the number of unique intestinal species found in the first through fourth samples of each animal from which four samples were collected. The mean richness was 2.7 (SD = 1.4) for one sample (n = 37 animals), 4.0 (SD = 1.7) for

TABLE II. Sampling Variations

Species	Mean (%)[a]	n[b]
Troglodytella abrassarti	88.4 ± 0.201	36
Oesophagostomum sp.	59 ± 0.300	30
Strongyloides sp.	59.1 ± 0.228	31
Entamoeba coli	25	1
Entamoeba hartmanni	37.5 ± 0.209	6
Entamoeba chattoni	45.8 ± 0.196	26
Endolimax sp.	25	2
Iodamoeba sp.	43.2 ± 0.244	11
Blastocystis sp.	50	1
Physaloptera caucasica	36.4 ± 0.114	11
Probstmayria gombensis	38.9 ± 0.125	6
Hymenolepis sp.	31.9 ± 0.093	12

[a]Of the animals in which this parasite was found, it was found in X% of their samples ±SD.
[b]Number of animals (of 37 total) from which this intestinal species was recovered.

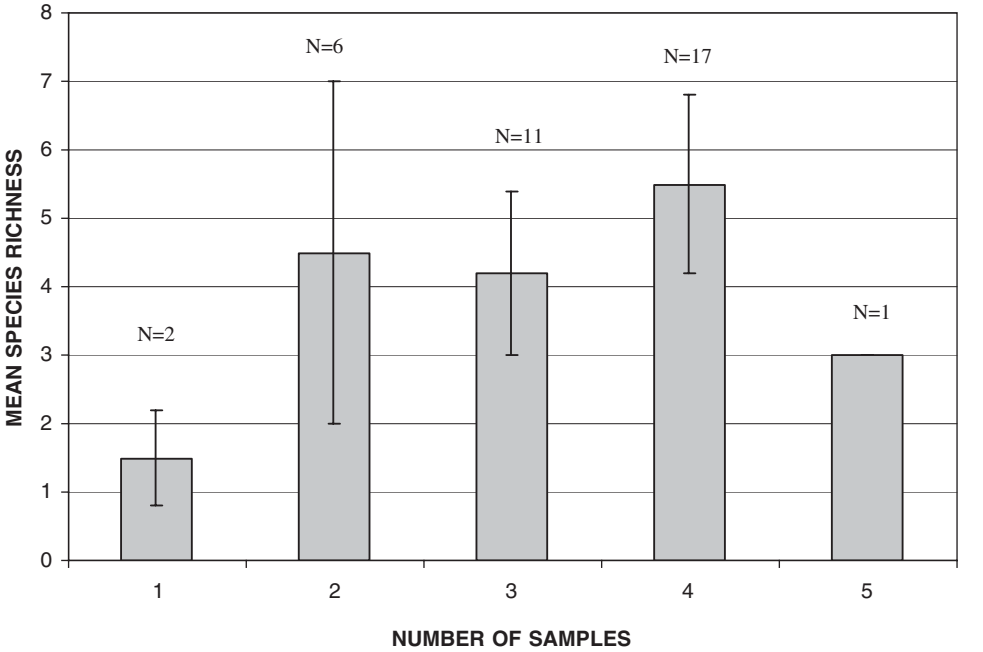

Fig. 1. Mean parasite richness (±SD) by number of sequential samples taken per animal. The mean richness (number of unique parasitic species recovered from hosts' fecal samples) increased when more than one sample was collected from each animal. However, there appeared to be little difference in mean richness in animals from which two, three, or four samples were taken. The n's refer to the number of animals in each group (for example, in the second group, two sequential samples were collected from each of six animals).

two samples (n = 35 animals), 4.6 (SD = 1.5) for three samples (n = 29 animals), and 5.4 (SD = 1.4) for four samples (n = 18 animals). The mean cumulative richness appeared to increase with the number of sequential samples taken from each animal. Paired comparisons between the mean cumulative richness of sampling days 1–4 revealed that species richness significantly increased for every sequential sample taken per animal (Table III). Paired comparisons were made only between groups that contained the same animals (i.e., the comparison between days 1 and 4 included only those 18 individuals that were sampled on four different time points; if an animal was sampled only three times, his values were not included in that comparison).

The average time between consecutive samples collected was 7.74 days (SD = 6.07; range = 1–24 days). It is important to emphasize that this study took place over the course of only 3 months, which precludes analyses of seasonal variation in parasite presence and prevalence. The results described above might have been quite different if the samples had been collected throughout an entire year or more. Thus, these results are only a relative measurement for this specific study period, and possible seasonal effects were not taken into consideration. Further validation of these results at different study sites in different regions with different climatic patterns is needed.

Correlations With Host Age and Life Stage

No correlation (Pearson r = 0.21, P = 0.22, n = 37, power = 27%) was found between the total number of protozoan species (excluding *Troglodytella*

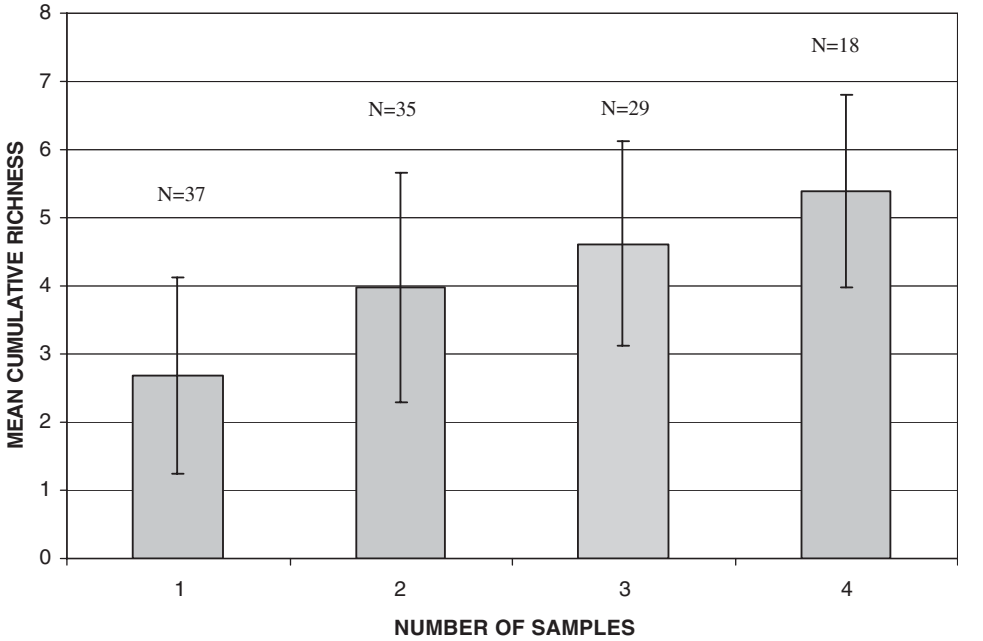

Fig. 2. Mean cumulative richness (±SD) by cumulative number of samples. The mean cumulative richness for the first sample was calculated from the sum of the number of unique parasite species found in the first sample from each animal, whereas the mean cumulative richness for the fourth sample was calculated from the sum of the number of unique parasite species found in the first through fourth samples of each animal from which four samples were collected. The n's refer to the number of animals in each group. The mean richness was 2.7 (SD = 1.4) for one sample (n = 37 animals), 4.0 (SD = 1.7) for two samples (n = 35 animals), 4.6 (SD = 1.5) for three samples (n = 29 animals), and 5.4 (SD = 1.4) for four samples (n = 18 animals). The mean cumulative richness apparently increased with the number of sequential samples taken from each animal.

abrassarti, a symbiont) and the total number of helminth species found. In a comparison of adults vs. adolescents, there was no significant difference in the mean total number of different intestinal species recovered (measured as the 12 possible parasites × the number of samples per animal that were positive for each parasite) between the two life stages (1 = adult, 2 = adolescent; t = 1.44, P = 0.16, power = 32%).

Within each life stage, there were no significant correlations between adult or adolescent age and species richness (adult animals —all intestinal species: r = −0.13, P = 0.56, helminths: r = −0.05, P = 0.82, protozoa: r = −0.11, P = 0.63; adolescent animals —all intestinal species: r = −0.24, P = 0.41, helminths: r = −0.15, P = 0.62, protozoa: r = 0.22, P = 0.44). However, the power was <80% for all of these analyses, and thus the reader should not be convinced that adults and adolescents, or animals of different age classes, do not differ in richness of intestinal infections.

DISCUSSION

Because of increasing human encroachment into previously nonimpacted forests and the potential for disease transmission between human and nonhuman primate populations, further detailed investigations of primate ecological parasitology are warranted, especially at sites for which we currently have no

TABLE III. Paired Comparisons between Mean Cumulative Richness of Animals Sampled Days One Through Four*

	Day 2: 3.97 (1.7)	Day 3: 4.62 (1.5)	Day 4: 5.39 (1.4)	Day 3: 4.62 (1.5)	Day 4: 5.39 (1.4)	Day 4: 5.39 (1.4)
Day 1: 2.74 (1.4)	t = 6.4, $P<0.001$, n = 35					
Day 1: 2.79 (1.3)		t = 7.4, $P<0.001$, n = 29				
Day 1: 2.94 (1.4)			t = 10.5, $P<0.001$, n = 18			
Day 2: 3.86 (1.5)				t = 3.6, $P<0.001$, n = 29		
Day 2: 4.22 (1.7)					t = 5.4, $P<0.001$, n = 18	
Day 3: 4.89 (1.6)						t = 3.4, $P<0.01$, n = 18

*Paired t-tests between the mean cumulative richness (SD in parentheses) of animals sampled on different days. Sample sizes reflect number of individual animals, not samples, within each paired comparison (e.g., comparison between days one and four include only those 18 individuals that were sampled on four different time points). Days represent the nth sample taken per animal, not one through four consecutive days.

information regarding parasite presence and prevalence. The findings presented here provide an initial assessment of the intestinal fauna of the Ngogo chimpanzees. In addition, the present study addresses the importance of methodological standardization for parasitological comparisons of wild primate populations by illustrating the necessity of performing sequential sampling to obtain reliable estimates of parasite prevalence.

Comparisons Between Studies

The results of the current study have both similarities and differences in comparison with previous works regarding the intestinal parasites of wild chimpanzee communities. Parasitic taxa that were present in the previous surveys but absent in the current one include *Strongyloides fuelleborni*, *Necator* sp., *Enterobius* sp., *Ascaris lumbricoides*, *Trichuris* sp., *Prosthenorchis* sp., *Bertiella* sp., *Chilomastix mesnili*, *Dicrocoelium* sp., *Gongylonema* sp., *Giardia* sp., and unidentified strongyles, nematodes, ciliates, and flagellates. *Hymenolepis* sp. was the only parasite that was identified in the current study but was absent in all previous ones; however, the diagnosis of this parasite in the current study is not absolutely certain, due to the absence of ''hooks'' within the oncosphere of the eggs.

The Kanyawara chimpanzee community [Ashford et al., 2000] is a smaller group of animals that are part of the same chimpanzee population (*Pan troglodytes schweinfurthii*) in Kibale National Park that includes the Ngogo community. These two groups differ in terms of the relative amounts of potential

contact that animals have with human waste. The Kanyawara community has much greater potential contact with human waste because more researchers and assistants use the Kanyawara study area, and because the chimpanzees at Kanyawara enter fields to raid crops, which is not the case at Ngogo. Therefore, parasitological comparisons of the less-impacted Ngogo community with the Kanyawara community may permit an assessment of the impact of human encroachment on disease transmission potential in wild chimpanzee communities. Unfortunately, it is not presently possible to accurately compare these two populations because of differences in the diagnostic techniques used (formalin-ethyl acetate sedimentation in the present study, and volumetric dilution in the Kanyawara study [Ashford et al., 2000]). Nonetheless, the two communities appear to be similar in terms of the prevalence of *Troglodytella abrassarti* and the percentage of samples positive for *Entamoeba coli* and *Probstmayria gombensis* (Table I). The Kanyawara group had a higher percentage of total samples positive for *Entamoeba hartmanni*, *Entamoeba chattoni*, *Iodamoeba* sp., and *Blastocystis* sp., whereas the Ngogo group had a higher percentage of total samples positive for *Strongyloides* sp. A number of parasitic species were present in the Kanyawara group but not the Ngogo group, and vice versa. At least one parasite was found in each sample analyzed from the Kanyawara group, whereas two Ngogo samples contained no intestinal parasites.

A small number of parasitological studies of wild nonhuman primates have assessed differences in parasite prevalence between animals of different age groups. In the present sample, the adult and adolescent animals did not differ significantly in parasite prevalence or richness, and within each of the male groups (adults or adolescents), parasite richness was not significantly correlated with age. This is similar to previous findings by File et al. [1976] in Gombe chimpanzees, which indicated that prevalence was not related to animal age. However, Muller-Graf et al. [1996] found that *Strongyloides* sp. was significantly more prevalent in younger olive baboons than in older individuals. Further studies are clearly warranted, especially long-term field projects in which the approximate ages of the animals are known.

Pathogenity

Though the majority of the intestinal fauna found in this and all other studies of wild chimpanzees can be pathogenic to humans [Orihel, 1970], the effects of these intestinal parasites on the survival and reproduction of wild chimpanzees are difficult to determine. According to Ashford et al. [2000], there is little reason to believe that parasites can significantly alter the fitness of wildlife. Similarly, Huffman et al. [1997, p. 122] stated that ''parasites alone can not be responsible for serious disease'' in wild chimpanzees. Within the Ngogo sample, intestinal infections seemed to be well tolerated, based on the lack of clinical signs (i.e., loose or bloody stool). The level of infection intensity, along with the lack of clinical signs, within this population may reflect well-maintained infections rather than incidental ones [Ghandour et al., 1995]. This is especially true for *Troglodytella abrassarti*, an entodiniomorph ciliate that is widely considered to be a symbiont involved in cellulose digestion [Collet et al., 1984; Goussard et al., 1983; Landsoud-Soukate et al., 1995]. These ciliates are almost universally present, in high numbers, in all African wild apes studied, suggesting a symbiotic relationship. They are also morphologically similar to ciliates that are known to be symbionts of ruminants [Landsoud-Soukate et al., 1995].

Oesophagostomum sp. is also a parasite commonly found in wild chimpanzee populations [Ashford et al., 2000], and although the deleterious effects of this nematode have been questioned by some [Smith & Jones, 1961], *Oesophagostomum* infection can increase morbidity and mortality [Brack, 1987; Huffman et al., 1997]. Although parasites are a part of the natural fauna of wild nonhuman primates, it is still important to conduct ecological parasitology studies of wild primates.

Methodological Considerations

Future investigations of primate parasitology are warranted because of the potential for disease transmission between human and nonhuman primate populations. This is especially important as human populations encroach into previously nonimpacted forests. However, accurate comparisons across populations depend on methodological standardization. Serial samples should be collected on multiple, nonconsecutive days for proper diagnoses to be made. In the present study, no one intestinal organism was found in all of the samples from any one animal, and *Troglodytella abrassarti*, the most common organism, was found in all of the serial samples of only 69.4% of the chimpanzees. The mean species richness (the number of unique intestinal species recovered from the host's fecal samples) also increased when more than one sample was collected from each animal (Fig. 1). However, over the 3-month period of this study there appeared to be little difference in mean richness in animals from which two, three, or four samples were taken. This suggests that in short-term studies two or three samples per animal (rather than four or more samples per animal) may be adequate to assess parasite prevalence or richness in such a population.

When the mean cumulative species richness was plotted against the cumulative number of samples collected, richness appeared to increase with the number of sequential samples taken from each animal (Fig. 2). Paired comparisons between sampling days revealed that species richness significantly increased for every sequential sample taken per animal (Table III). Likewise, Huffman et al. [1997] concluded that the accuracy of assessing parasite prevalence of a group will increase with a greater number of samples obtained per individual. Furthermore, protozoan cyst output can be highly variable, making detection difficult [Ash & Orihel, 1991], and the seasonality of some infections may compound the difficulty of detecting certain parasites, such as *Oesophagostomum* [Huffman et al., 1997].

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REFERENCES

Appleton CC, Boinski S. 1991. A preliminary parasitological analysis of fecal samples from a wild population of Costa Rican squirrel monkeys (*Saimiri oerstedi*). J Med Primatol 20:402–403.

Appleton CC, Krecek RC, Verster A, Bruorton MR, Lawes MJ. 1994. Gastro-intestinal parasites of the Samango monkey, *Cercopithecus mitis*, in Natal, South Africa. J Med Primatol 23:52–55.

Ash LR, Orihel TC. 1991. Parasites: a guide to laboratory procedures and identification. Chicago: American Society of Clinical Pathologists 328p.

Ashford RW, Reid GDF, Butynski TM. 1990. The intestinal faunas of man and mountain gorillas in a shared habitat. Ann Trop Med Parasitol 84:337–340.

Ashford RW, Reid GDF, Wrangham RW. 2000. Intestinal parasites of the chimpanzee *Pan troglodytes* in Kibale Forest, Uganda. Ann Trop Med Parasitol 94:173–179.

Boesch C, Boesch-Achermann H. 2000. The chimpanzees of the Tai Forest. Oxford: Oxford University Press.

Brack M. 1987. Agents transmissible from simians to man. Berlin: Springer-Verlag.

Collet JY, Bourreau E, Cooper RW, Tutin CEG, Fernandez M. 1984. Experimental demonstration of cellulose digestion by *Troglodytella gorillae*, an intestinal ciliate of lowland gorillas (*Gorilla g. gorilla*). Int J Primatol 5:328.

Faul F, Erdfelder E. 1992. GPower: a priori, post-hoc, and compromise power analyses for MS-DOS. Department of Psychology, Bonn University, Bonn, FRG.

File SK, McGrew WC, Tutin CEG. 1976. The intestinal parasites of a community of feral chimpanzees, *Pan troglodytes scheinfurthii*. J Parasitol 62:259–261.

Ghandour AM, Zahid NZ, Banaja AA, Kamal KB, Bouq AI. 1995. Zoonotic intestinal parasites of hamadryas baboons *Papio hamadryas* in the western and northern regions of Saudi Arabia. J Trop Med Hyg 98:431–439.

Ghigliere MP. 1984. The chimpanzees of Kibale Forest: a field study of ecology and social structure. New York: Columbia University Press.

Goldsmid JM, Rogers S. 1978. A parasitological study on the chacma baboon (*Papio ursinus*) from the northern Transvaal. J S Afr Vet Assoc 49:109–111.

Goodall J. 1968. The behaviour of free living chimpanzees in the Gombe Stream Reserve. Anim Behav Monogr 1:161–311.

Goussard B, Collet J-Y, Garin Y, Tutin CEG, Fernandez M. 1983. The intestinal entodiniomorph ciliates of wild lowland gorillas (*Gorilla gorilla gorilla*) in Gabon, West Africa. J Med Primatol 12:239–249.

Hasegawa H, Kano T, Mulavwa M. 1983. A parasitological survey on the feces of pygmy chimpanzees, *Pan paniscus*, at Wamba, Zaire. Primates 24:287–297.

Huffman MA, Gotoh S, Turner LA, Hamai M, Yoshida K. 1997. Seasonal trends in intestinal nematode infection and medicinal plant use among chimpanzees in the Mahale Mountains, Tanzania. Primates 38: 111–125.

Karere GM, Munene E. 2002. Some gastrointestinal tract parasites in wild DeBrazza's monkeys (*Cercopithecis neglectus*) in Kenya. Vet Parasitol 110:153–157.

Kawabata M, Nishida T. 1991. A preliminary note on the intestinal parasites of wild chimpanzees in the Mahale Mountains, Tanzania. Primates 32:275–278.

Kessler ML, Yarbrough B, Rawlins RG, Berard J. 1984. Intestinal parasites of the free-ranging Cayo Santiago rhesus monkeys (*Macaca mulatta*). J Med Primatol 13:57–66.

Landsoud-Soukate J, Tutin CEG, Fernandez M. 1995. Intestinal parasites of sympatric gorillas and chimpanzees in the Lope Reserve, Gabon. Ann Trop Med Parasitol 89:73–79.

Lilly A, Doran D. 1999. Intestinal parasite loads in western lowland gorillas (*Gorilla gorilla gorilla*), chimpanzees (*Pan troglodytes*) and researchers in Dzanga-Ndoki National Park, Central African Republic. Am J Primatol 49:73–74.

Lilly A. 2003. Human social issues, disease, and sympatric apes in the Central African Republic. Am J Phys Anthropol 36:140.

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). J Parasitol 68:131–133.

McGrew WC, Tutin CEG, Collins DA, File SK. 1989. Intestinal parasites of sympatric *Pan troglodytes* and *Papio* Spp. at two sites: Gombe (Tanzania) and Mt. Assirik (Senegal). Am J Parasitol 17:147–155.

Muehlenbein MP, Schwartz M, Richard A. 2003. Parasitologic analyses of the sifaka (*Propithecus verreauxi verreauxi*) at Beza Mahafaly, Madagascar. J Zoo Wild Med 34:274–277.

Muehlenbein MP, Watts DP, Whitten P. 2004. Dominance rank and fecal testosterone levels in adult male chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda. Am J Primatol 64:71–82.

Muller-Graf CDM, Collins DA, Woolhouse MEJ. 1996. Intestinal parasite burden in

five troops of olive baboons (*Papio cynocephalus anubis*) in Gombe Stream National Park, Tanzania. Parasitology 112:489–497.

Munene E, Otsyula A, Mbaabu DAN, Mutahi WT, Muriuki SMK, Muchemi GM. 1998. Helminth and protozoan gastrointestinal tract parasites in captive and wild-trapped African nonhuman primates. Vet Parasitol 78:195–201.

Muriuki SMK, Murugu RK, Munene E, Karere GM, Chai DC. 1998. Some gastrointestinal parasites of zoonotic (public health) importance commonly observed in Old World nonhuman primates in Kenya. Acta Tropica 71:73–82.

Murray S. 1990. Intestinal parasites of baboons and chimpanzees in Gombe National Park. Senior thesis, School of Veterinary Medicine, Tufts University, North Grafton, MA.

Murray S, Stem C, Boudreau B, Goodall J. 2000. Intestinal parasites of baboons (*Papio cynocephalus anubis*) and chimpanzees (*Pan troglodytes*) in Gombe National Park. J Zoo Wild Med 31:176–178.

Orihel TC. 1970. The helminth parasites of nonhuman primates and man. Lab Anim Care 20:395–401.

Rothman JM, Bowman DD, Eberhard ML, Pell AN. 2002. Intestinal parasites found in the research group of mountain gorillas in Bwindi Impenetrable National Park, Uganda. Ann N Y Acad Sci 969:346–349.

Smith HA, Jones TC. 1961. Veterinary pathology. 2nd ed. Philadelphia: Lea and Febiger.

Stoner KE. 1996. Prevalence and intensity of intestinal parasites in mantled howling monkeys (*Alouatta palliata*) in northeastern Costa Rica: implication for conservation biology. Conserv Biol 10:539–546.

Struhsaker TT. 1997. Ecology of an African rain forest: logging in Kibale and the conflict between conservation and exploitation. Gainesville: University Press of Florida.

Stuart MD, Strier KB, Pierberg SM. 1993. A coprological survey of parasites of wild muriquis, *Brachyteles arachoides*, and brown howling monkeys, *Alouatta fusca*. J Helminth Soc Was 60:111–115.

Stuart MD, Strier KB. 1995. Primates and parasites: a case for a multidisciplinary approach. Int J Primatol 16:577–593.

Wolfe ND, Escalante AA, Karesh WB, Kilbourn A, Spielman A, Lal AA. 1998. Wild primate populations in emerging infectious disease research: the missing link? Emerg Infect Dis 4:149–158.