Published in final edited form as:

J Parasitol. 2012 February ; 98(1): 205–208. doi:10.1645/GE-2493.1.

***Trichuris* sp. and *Strongyloides* sp. Infections in a Free-Ranging Baboon Colony**

J. Anderson[†], R. Upadhyay, D. Sudimack, S. Nair, M. Leland[‡], J. T. Williams, and T. J. C. Anderson^{*}

[†]Perry R. Bass Marine Fisheries Research Station, Coastal Fisheries Division, Texas Parks and Wildlife Department, Palacios, Texas 77465, USA

[‡]University of Texas Health Science Center at San Antonio, Lab Animal Resources, Texas Biomedical Research Institute (TBRI), San Antonio, Texas, USA

Abstract

We conducted cross-sectional surveys of parasites infecting a large free-living colony of baboons at the Southwest National Primate Research Center in San Antonio in October 2003 and April 2004, immediately before and 6 mo after treatment with ivermectin. *Trichuris* sp. was the predominant species present infecting 79 and 69% of individual animals in the 2 surveys, with fecal egg counts (FEC) of up to 60,200 eggs per g (epg) (mean = 1,235 in Oct 2003 and 1,256 in Apr 2004). Prevalence remained fairly stable across age groups, while intensity was highest in animals <1- or >15-yr-old, in contrast to patterns observed in humans where school age children show the heaviest infections. *Strongyloides* sp. was also identified, but the species remains uncertain. Small subunit ribosomal DNA sequences differed from published sequences of *S. fuelleborni* at multiple sites but resided in a monophyletic group with other *Strongyloides* species with 92% bootstrap support. This may reflect a recent acquisition from a local host, or that the published sequence of *S. fuelleborni* is incorrect. Widespread infections with 2 nematode genera in a free-ranging baboon colony that are an important source of morbidity in human populations provides a useful model system for work on the epidemiology, control, pathology, and genetics of these parasites in a host species that is physiologically, immunologically and genetically similar to humans.

In 2003-2004, there were approximately 3,800 baboons housed in the Southwest National Primate Research Center (SNPRC) colonies at the Texas Biomedical Research Institute. Of these, ~1,200 free-range animals were maintained in 2 large (6 acre) corrals. One of these corrals containing approximately 700 animals was the focus of the present study. Baboons in the SNPRC colonies are naturally infected with species of *Trichuris* and *Strongyloides*, representing 2 of the 6 major genera of intestinal nematodes that infect humans. This study was designed to investigate the prevalence and intensity of *Trichuris* sp. and identity of *Strongyloides* sp. infecting these animals.

Animals are captured semi-annually for TB testing and are closely monitored so the age of animals is known. During these roundups, animals are injected with 1% Ivermectin (Merial, Duluth, GA) according to the following regimen: 0.15 ml for animals 0-5 kg, 0.45 ml for animals 5-15 kg, 0.75 ml for animals 15-25 kg, and 1 ml for animals >25 kg). Fecal samples were collected (by fecal loop) prior to treatment during these semi-annual "roundups" in October 2003 and April 2004. *Trichuris* sp. fecal egg counts (FEC) were measured using a

*Correspondence to: Tim JC Anderson, Department of Genetics, Texas Biomedical Research Institute (TBRI), San Antonio, Texas 78245. tanderso@txbiomedgenetics.org.

modification of the Kato-Katz method (WHO 1994), in which fecal material was weighed, placed on slides, and all eggs present were counted to estimate epg of feces. This approach was used as it provides more accurate measures of fecal mass than the templates used in human studies, and because very limited amounts (<10 mg) of fecal material were available from many animals. We used Harada-Mori fecal cultures to detect *Strongyloides* sp. larvae in the October 2003 survey when sufficient fecal material was available after making Kato-Katz slides.

Sufficient fecal material for FEC was sampled from 283 animals in Oct 2003 and 359 in April 2004. We found high levels of *Trichuris* sp. infection, with 79% of animals egg positive in the first survey and 69% in April 2004. The mean epg was 1,235 in Oct 2003 and 1,256 in Apr 2004. Using WHO categorization for human infections, 54% had light (1-999 epg) infections, 22% had moderate infections (1,000-9,999 epg), and 3% had heavy infections (>10,000 epg) in Oct 2003. Equivalent figures for April 2004 were 47% light, 20% moderate, and 3% heavy. Egg counts were overdispersed as found in many helminth infections (Anderson and May, 1985)(Fig. 1). The most heavily infected 20% of the animals accounted for 81% of all eggs excreted in Oct 2003 and 87% of eggs in April 2004. The sex ratio of baboons in the corral was strongly biased towards females in the older age classes. There were 9 males and 227 females >4-yr-old in Oct 2003, and 15 males and 259 females greater than 4-yr-old in Apr 2004. However, for animals <4-yr-old where both males and females were represented, no effect of host gender was observed for epg (Mann Whitney-*U*, $Z=-0.94$, $P=0.35$ in Oct 2003 and $Z=-1.19$, $P=0.24$ in Apr 2004).

In human populations, *Trichuris trichiura* show strong age dependent infection patterns, with the highest intensity of infection observed in school age children (5- to 9-yr-old). Typical patterns are illustrated using published data from a Guatemalan population (Anderson et al., 1993) (Fig. 1, inset). Patterns of prevalence and intensity in baboons are rather different. The highest epg were observed in baboons that were <1- or >15-yr-old in both surveys and differences in epg between age classes were highly significant (Kruskal Wallis test, $H=30.9$, $P<0.0001$ for Oct 2003 and $H=38.3$, $P<0.0001$ for Apr 2004). Given that adult animals produce a greater mass of fecal material per day and have higher mean infection intensities, old animals are the major contributors to *T. trichiura* transmission in these colonies. This contrasts with human populations where school age children make the largest contribution to transmission (Haswell-Elkins, et al., 1987). The reasons that underlie these differences may relate to exposure patterns or there may be differences in acquired immunity to *T. trichiura* in baboon and human populations. A cross sectional survey of parasitism in 5 olive baboon troops in Gombe, Uganda, showed a similar even age-prevalence relationship to that observed in this study (Muller-Graf et al., 1996). Young and old baboons did not show elevated intensity of infection in the Gombe baboons.

In human studies, pre- and post-treatment worm burdens are often correlated, indicating predisposition (Haswell-Elkins et al., 1987; Bundy et al. 1987). We found strong correlations between *Trichuris* sp. epg in individual baboons sampled during the 2 cross sectional surveys, before and after ivermectin treatment ($n=144$, Kendal rank correlation, $T=0.216$, $P<0.0001$). This may be explained in part by inefficient drug treatment and does not provide strong evidence for predisposition in this case. Epg was measured in 5 animals 3 wk after treatment with ivermectin. One animal was egg negative, 2 had decreased egg counts, and 2 had increased egg counts. Hence, single dose drug treatment shows poor efficacy in these animals, consistent with results from humans (Beach et al., 1999; Belizario et al., 2003). We suggest that further evaluation of the efficacy of single dose ivermectin treatment is warranted for use in primate colonies.

Larval *Strongyloides* sp. were recovered from just 1.3% (3/236) of Harada Mori cultures from the Oct 2003 survey. This figure is likely to be a gross underestimate of *Strongyloides* sp. prevalence in this colony, because animals were sampled a single time, and limited amounts of fecal material (often <10 mg) were available from fecal loop sampling. In preliminary work, prior to the present surveys, 1 g of feces was collected from animals that were hospitalized due to injuries. In these animals, *Strongyloides* sp. was detected in fecal cultures from 4 of 5 animals, suggesting high infection levels in the colony. The Harada-Mori methods used in the present survey were inefficient due to the limited amount of fecal material available for culture.

Intact eggs were found in the feces of baboons infected with *Strongyloides* sp. in the hospitalized animals and is consistent with *S. fuelleborni* infections (Olsen et al., 2009). We amplified and sequenced 1150bp of the 18s rDNA to compare cultured larvae from SNPRC baboons with existing published *Strongyloides* sp. GenBank sequences. Two worms were sequenced from SNPRC baboon cultures; 1 exhibited morphology characteristic of a free-living generation, while the second was characteristic of the parasitic form (Olsen et al. 2009). Primers for PCR were SSUA (5' AAAGATTAAGCCATGCATG) and SSU18P (5' TGATCCWKCYGCAGGTTTCAC); an additional sequencing primer was used SSU22R (5' GCCTGCTGCCTTCCTTGA). All primers were designed following Dorris et al (2002). Sequences from both nematodes were identical (GenBank accession number HM026569). The full length sequence obtained differed from *S. stercoralis* at 25 positions; 3 indel polymorphisms were present (Fig. 2). We aligned our sequence data with the conserved 366bp region used in previous work on *Strongyloides* species and related nematodes (Dorris et al. 2002) using the software Muscle (Edgar 2004) (Supplementary material, Fig. S1). Prior to phylogenetic analysis, the best-fit nucleotide substitution model was determined using jModeltest v 0.1.1 (Posada 2008). The substitution model was chosen using the Akaike information criterion corrected for small samples. The general time reversible model (GTR, Tavaré 1986), with a gamma correction for among-site rate heterogeneity (GTR + Γ), and a shape parameter $\alpha = 0.7200$ had the highest probability. These settings were used in a maximum-likelihood (ML) phylogenetic inference, and the resulting phylogram was bootstrapped 1000 times to evaluate the statistical support for interior nodes (Fig. 3.) Phylogenetic inference and bootstrapping were carried out using PAUP v 4.0 (Sinauer Associates, Inc., Sunderland MA), and trees were constructed using Treeview (Page 1996).

While published sequences for *S. stercoralis* and *S. fuelleborni* were identical for the 366bp sequence examined, they differed from the *Strongyloides* sp. from SNPRC baboons at 5 nucleotide sites; however, the SNPRC worms resided in a monophyletic group with other *Strongyloides* species, and this group had 92% statistical support in bootstrap resampling (Fig. 3.). The SNPRC worms also differed from *S. stercoralis* and *S. fuelleborni* at an indel within the E9-2 stem-loop of the small subunit rRNA that distinguishes the “stercoralis” and “cebus” clades within *Strongyloides* genus (Dorris et al., 2002). Hence, the SNPRC *Strongyloides* sp. is divergent from published *S. fuelleborni* sequences.

There are 2 possible explanations for the results obtained. First, the nematode infecting SNPRC baboons may be unrelated to *S. fuelleborni* and was acquired from a local source. Such cross species transfer events are not unprecedented, i.e., in Papua New Guinea, people are infected with a *Strongyloides* species (*S. fuelleborni kellyi*) that is morphologically distinct from either *S. stercoralis* or *S. fuelleborni* (Smith et al., 1991). Ribosomal sequences from *S. f. kellyi* are identical to those from *S. papillosus*, which parasitizes a wide range of domestic animals, suggesting a zoonotic source for *S. fuelleborni kellyi* in Papua New Guinea. Second, the published sequences of *S. fuelleborni* may be incorrect. The sequences *S. fuelleborni* used for phylogenetic analysis (Dorris et al., 2002) were obtained from formalin fixed archived material, and it is conceivable that the sample was mislabeled. We

suggest that further specimens of *Strongyloides* species should be sequenced from both wild and captive baboons to differentiate between these 2 explanations and to clarify the relationships within the genus *Strongyloides*.

Species of both *Trichuris* and *Strongyloides* are important parasitic helminths of humans. *Trichuris trichiura* infects an estimated 1 billion people worldwide causing morbidity in 220 million people and an estimated 10,000 deaths per yr (Savioli and Albonico, 2004). Severe infections are responsible for a range of pathology, including colitis, growth stunting, and, in severe cases, a dysentery-like syndrome and rectal prolapse (Cooper et al., 1990; Cooper et al., 1995). Medical interest in *T. trichiura* also stems from this parasite's use as a treatment for Crohn's disease (Summers et al., 2003). *Strongyloides* spp. infect an estimated 100-200 million individuals, causing diarrhea, and is a particular problem in immunocompromised patients where the parasite may invade the tissues. *Strongyloides stercoralis* is the principal species infecting humans, although infections with a primate parasite (*S. fuelleborni fuelleborni*) have been recorded in Africa (Hira and Patel, 1980), and infection with *S. fuelleborni kellyi* occurs in the Papua New Guinea (Smith et al., 1991). Mice and pigs are the model systems of choice for work on *Trichuris* spp. (Boes and Helwich, 2000). Mice have many advantages as experimental animals, and are ideal for some research questions. However, their distant relationship from humans and differing physiology severely limits the utility of mouse models for understanding human infections. The use of pigs stems from the importance of *Trichuris suis* in swine production systems, and similar criticisms apply. For *Strongyloides* spp., insights on many aspects of the complex life cycle and basic biology have come from *S. ratti* infection in rats (Harvey et al., 2000), while the human parasite *S. stercoralis* has been studied extensively within a dog model system (Mansfield and Schad, 1992). Again, however, the physiological and phylogenetic distance between dogs and humans make this system less than ideal as a model for many aspects of human infection. A baboon model for studying both *Trichuris* sp. and *Strongyloides* sp. would be useful for a number of reasons. First, the parasites infecting baboons are closely related, or identical, to those infecting humans. Second, baboon immune systems are closely comparable to our own, having the full complement of IgG subclasses (Hefty et al., 2002). Finally, the baboon genome organization is similar to our own and genetic maps are contiguous (Rogers et al. 2000).

Acknowledgments

We thank Peter Nejsum and three anonymous referees for helpful comments on the manuscript and the staff of the Southwest National Primate Research Center for assistance.

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FIGURE 1.

Epidemiology of *Trichuris* sp. in the baboon colony. (a) Age prevalence and (b) age intensity profiles in October 2003 (open circles, dashed lines, n=283) and April 2004 (filled circles, solid lines, n=359). Mean intensities include those from egg negative animals. The insets show comparable profiles from a human population in Guatemala (Anderson et al., 1993). (c) The frequency distribution of infection intensity (epg) in the baboon colony.

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stercor1      CTGATTAAACAGCTATAGACTACACGGTAAATTTAGTGTGATACTAGGTAATTC
stercor2      CTGATTAAACAGCTATAGACTACACGGTAAATTTAGTGTGATACTAGGTAATTC
SNPRC Str.    CTGATTAAACAGCTATAGACTACACGGTAAATTTAGTGTGATACTAGGTAATTC
*****

stercor1      TTGAGCTAATACAGCTATTATACACATTAGTGTGCTTTATTGATTAAACATT
stercor2      TTGAGCTAATACAGCTATTATACACATTAGTGTGCTTTATTGATTAAACATT
SNPRC Str.    TTGAGCTAATACAGCTATTATACACATTAGTGTGCTTTATTGATTAAACATT
*****

stercor1      TATATGGTTGACTCAAAATATCTCGCTGATTTTGTACTAAACATACCGTATGTGA
stercor2      TATATGGTTGACTCAAAATATCTCGCTGATTTTGTACTAAACATACCGTATGTGA
SNPRC Str.    TATATGGTTGACTCAAAATATCTCGCTGATTTTGTACTAAACATACCGTATGTGA
****

stercor1      TCTGTTTATCACTTCGATGGTAGGGTATTGGCTACCATGTTGTGACGGATAACGG
stercor2      TCTGTTTATCACTTCGATGGTAGGGTATTGGCTACCATGTTGTGACGGATAACGG
SNPRC Str.    TCTGTTTATCACTTCGATGGTAGGGTATTGGCTACCATGTTGTGACGGATAACGG
*****

stercor1      AGAATTAGGTTGACTCGGAGGGAGGCTGAGAACGGCTACCATCAAGGAAG
stercor2      AGAATTAGGTTGACTCGGAGGGAGGCTGAGAACGGCTACCATCAAGGAAG
SNPRC Str.    AGAATTAGGTTGACTCGGAGGGAGGCTGAGAACGGCTACCATCAAGGAAG
*****

stercor1      CAGCAGGCGGAAATACCAATTTAGTTAAAGAGGTAGTACGAAATGACAAC
stercor2      CAGCAGGCGGAAATACCAATTTAGTTAAAGAGGTAGTACGAAATGACAAC
SNPRC Str.    CAGCAGGCGGAAATACCAATTTAGTTAAAGAGGTAGTACGAAATGACAAC
*****

stercor1      AATATATTATTATATTGATTGAAATCTCAAGTTAAATACTGTTGGTAAAG
stercor2      AATATATTATTATATTGATTGAAATCTCAAGTTAAATACTGTTGGTAAAG
SNPRC Str.    AATATATTATTATATTGATTGAAATCTCAAGTTAAATACTGTTGGTAAAG
*****

stercor1      GAAAGGCAAGCTCTGTGCGCAGCAGCGCGTAATACAGCTTCCAGTGCTATAAATG
stercor2      GAAAGGCAAGCTCTGTGCGCAGCAGCGCGTAATACAGCTTCCAGTGCTATAAATG
SNPRC Str.    GAAAGGCAAGCTCTGTGCGCAGCAGCGCGTAATACAGCTTCCAGTGCTATAAATG
*****

stercor1      ATTGTGTGGTTAAAGCTGTAGTTGGATTAAAGATTGTATAAGACATCTTGA
stercor2      ATTGTGTGGTTAAAGCTGTAGTTGGATTAAAGATTGTATAAGACATCTTGA
SNPRC Str.    ATTGTGTGGTTAAAGCTGTAGTTGGATTAAAGATTGTATAAGACATCTTGA
*****

stercor1      TGTATTATATCATCATCTTAT-ATTTTATATAT- ---TAGAATAATAATAA
stercor2      TGTATTATATCATCATCTTAT-ATTTTATATAT- ---TAGAATAATAATAA
SNPRC Str.    TGTATTATATCATCATCTTAT-ATTTTATATAT- ---TAGAATAATAATAA
*****

stercor1      -CTGTACTTTGAATAAATCAGAGGTTTAAACAGACATT-ATATGTTGTATGGTCTA
stercor2      -CTGTACTTTGAATAAATCAGAGGTTTAAACAGACATT-ATATGTTGTATGGTCTA
SNPRC Str.    -CTGTACTTTGAATAAATCAGAGGTTTAAACAGACATT-ATATGTTGTATGGTCTA
*****

stercor1      GCATGGAATAACACTAGAAAAATTTAGTGTGTTTCACTAA- TTTTCTGATTAT
stercor2      GCATGGAATAACACTAGAAAAATTTAGTGTGTTTCACTAA- TTTTCTGATTAT
SNPRC Str.    GCATGGAATAACACTAGAAAAATTTAGTGTGTTTCACTAA- TTTTCTGATTAT
*****

stercor1      AGGAACAAAGGGGCTTGTATCGCTAGCTTAGAGGTGAATCTTGGACGTAGCGA
stercor2      AGGAACAAAGGGGCTTGTATCGCTAGCTTAGAGGTGAATCTTGGACGTAGCGA
SNPRC Str.    AGGAACAAAGGGGCTTGTATCGCTAGCTTAGAGGTGAATCTTGGACGTAGCGA
*****

stercor1      GACGTCTACTCGGAAGCATTGCGCAGATGTTTTCATTATCAGAACGAAGTAG
stercor2      GACGTCTACTCGGAAGCATTGCGCAGATGTTTTCATTATCAGAACGAAGTAG
SNPRC Str.    GACGTCTACTCGGAAGCATTGCGCAGATGTTTTCATTATCAGAACGAAGTAG
*****

stercor1      AGGTTCAAGGGGATCAGATACCGCTAGTTTACCGTAACTATGCTACTAGATGT
stercor2      AGGTTCAAGGGGATCAGATACCGCTAGTTTACCGTAACTATGCTACTAGATGT
SNPRC Str.    AGGTTCAAGGGGATCAGATACCGCTAGTTTACCGTAACTATGCTACTAGATGT
*****

stercor1      ATGAATTATTAGTTATAAATTTATGCACTCTTGGAAACGAAGCTTTGGTTCGG
stercor2      ATGAATTATTAGTTATAAATTTATGCACTCTTGGAAACGAAGCTTTGGTTCGG
SNPRC Str.    ATGAATTATTAGTTATAAATTTATGCACTCTTGGAAACGAAGCTTTGGTTCGG
*****

stercor1      GGGAGATGATGTTGCAAGCTGAACTTAAGGAATTACGGAAGGACACACAGGAG
stercor2      GGGAGATGATGTTGCAAGCTGAACTTAAGGAATTACGGAAGGACACACAGGAG
SNPRC Str.    GGGAGATGATGTTGCAAGCTGAACTTAAGGAATTACGGAAGGACACACAGGAG
*****

stercor1      TGGAGCTCGGCTTAATTGACTCAACAGGGAATCTACCGGCGGACACTATAA
stercor2      TGGAGCTCGGCTTAATTGACTCAACAGGGAATCTACCGGCGGACACTATAA
SNPRC Str.    TGGAGCTCGGCTTAATTGACTCAACAGGGAATCTACCGGCGGACACTATAA
*****

stercor1      GGATTGACAGATTGATAGCTTTTCATGATTAGTGGTTGGTGTGATGGCGTCTTA
stercor2      GGATTGACAGATTGATAGCTTTTCATGATTAGTGGTTGGTGTGATGGCGTCTTA
SNPRC Str.    GGATTGACAGATTGATAGCTTTTCATGATTAGTGGTTGGTGTGATGGCGTCTTA
*****

stercor1      GTTCGTGGAT
stercor2      GTTCGTGGAT
SNPRC Str.    GTTCGTGGAT
*****

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FIGURE 2.

Multiple sequence alignment of SNPRC *Strongyloides* (SNPRC Str.) with 2 *Strongyloides stercoralis* sequences (Genbank AF279916 and AJ407023). The asterisks mark similarity. Accession number for the *Strongyloides sp.* from SNPRC is HM026569.

FIGURE 3.

Phylogeny of *Strongyloides* spp. showing position of the species infecting baboons. We constructed a maximum likelihood tree bootstrapped 1000 times over 366 characters. This tree includes all the taxa included in Dorris et al. (2002) and the full alignment based on that of Dorris et al. (2002) is shown in Fig S1. Numbers at major nodes are bootstrap support (bootstrap < 40% not shown). The nematode infecting baboons in the SNPRC (gray font) in San Antonio is distinct from published sequences from *S. fuelleborni*, and is monophyletic with other *Strongyloides* sp. with 92% bootstrap support.