A Coprological Survey of Parasites in White-Faced Capuchins (*Cebus capucinus*) from Sector Santa Rosa, ACG, Costa Rica

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Key Words
Parasites · White-faced capuchins · Costa Rica · Filariopsis · Strongyloides

Abstract
Neotropical primate parasitology has been dominated by studies of howler monkeys (*Alouatta* spp.), whereas the literature on the parasites of other platyrrhines is relatively sparse. We analysed the faeces of white-faced capuchins (*Cebus capucinus*) in a Costa Rican tropical dry forest and recovered 8 parasite taxa (*Filariopsis barretoi*, *Giardia duodenalis*, *Strongyloides* sp., *Prosthenorchis* sp., a spirurid nematode, a subulurid nematode, a strongylid nematode and a cestode). *F. barretoi* and *Strongyloides* sp. were the most prevalent parasites and were recovered from 84 and 76% of the sampled individuals, respectively. Individual capuchins were infected with an average of 1.89 parasite species. Capuchins host a diverse suite of parasites belonging to several taxonomic groups (Nematoda, Cestoda, Acanthocephala, Protozoa) and including species with direct and indirect life cycles. Many capuchin parasites are transmitted through the consumption of invertebrate intermediate hosts making diet a critical component of capuchin-parasite ecology. This study represents the most intensive parasitological survey of wild capuchin monkeys to date.

Introduction
Documenting parasite diversity and abundance is an important part of monitoring and understanding the health status and disease risk of wild primate populations [Altizer et al., 2003]. Understanding host-parasite dynamics can also offer evolutionary insights into the highly variable behaviour, social organization and ecology of primates [Freeland, 1976; Møller et al., 1993]. Neotropical primate parasitology has
focused heavily on howler monkeys (Alouatta spp.) [Stuart et al., 1990; Stoner, 1996; Stuart et al., 1998; Chinchilla et al., 2005; Eckert et al., 2006; Stoner and González Di Pierro, 2006; Vitazkova and Wade, 2006; Trejo-Macias et al., 2007; Vitazkova and Wade, 2007; Kowalzik, 2009; Cristóbal-Azkarate et al., 2010]. Relatively few studies have examined the parasites of capuchin monkeys (Cebus), and most are on captive populations [Dunn, 1963; Yamashita, 1963; Garner et al., 1967; Ewing et al., 1968; Lee et al., 1996; Sanchez et al., 2009]. Parasitological studies of wild capuchin populations are nearly non-existent [but see Phillips et al., 2004; Chinchilla et al., 2010].

Parasites are highly diverse in their transmission routes, and characteristics of host behaviour and ecology can influence the number of parasite species that the host encounters. Capuchins have relatively large home ranges and group sizes, complex social behaviour, very diverse diets that include invertebrates, and use all levels of the canopy including the forest floor [Fragaszy et al., 2004]. Parasite richness, the number of parasite species infecting a population [Bush et al., 1997], should be higher in species with small home ranges, large group sizes, high population densities, greater social contact and greater dietary diversity [Nunn et al., 2003; Ezenwa, 2004; Ezenwa et al., 2006; Nunn and Dokey, 2006]. Therefore, capuchins are expected to host a large number of parasite species.

In this study, we identify the parasites of wild white-faced capuchins (Cebus capucinus) in Costa Rica and discuss their biology and prevalence. We then compare our results to those from other parasitological studies of wild capuchins and discuss the potential for cross-species parasite transmission between sympatric primate species at our study site.

**Methods**

**Study Site**

This study took place in Sector Santa Rosa, Área de Conservación Guanacaste, located on the north-western coast of Costa Rica. Santa Rosa is a 108 km² mixture of evergreen and semi-deciduous tropical dry forest lying at the base of the volcanic Guanacaste Cordillera. In the decades leading up to its establishment as a national park in the early 1970s, sections of the forest were cleared for logging and cattle pasture and now exist in various stages of regeneration [Fedigan and Jack, 2001]. The area experiences extreme seasonal shifts in climate. Dry seasons (January to mid-May) are hot with very little precipitation. Most of the non-riparian trees shed their leaves and almost all natural water sources dry up, including many seasonal rivers. Rain begins to fall in May, but the majority of the annual precipitation (ca. 1,500 mm) comes during September and October [Janzen, 1988]. A 2- to 3-week dry period, the veranito, separates the early (May–August) and late (September–December) wet seasons.

**Subjects**

We collected faecal samples from all individuals in four habituated groups (Cerro de Piedra, Exclosure, Guanacaste, Los Valles) of white-faced capuchins (Cebus capucinus; table 1) from September 2007 to January 2008 and from January to August 2009. The study population included 95 capuchins, all of which could be individually identified.

**Faecal Collection and Analysis**

We attempted to collect a monthly faecal sample from all individuals in the study population. Our collection efficiency was approximately 75% due to the difficulties of collecting samples from certain individuals; infants rarely passed the minimum amount of faecal matter required for processing (1 g), some subordinate individuals were rarely seen as they remained on the pe-
riphery of the group, and a number of monkeys were not present in the study groups for the entirety of the study due to immigrations, emigrations, births and deaths. Samples were collected immediately after defecation and stored in 15 ml Corning® plastic centrifuge tubes. Within 12 h of collection, 1 g of faeces was extracted from each sample and stored in 10% buffered formalin. Tubes were sealed with Parafilm® laboratory film and stored until transported back to Canada.

We analysed the faecal samples in the veterinary parasitology laboratory at the University of Calgary in Alberta, Canada. We analysed 272 samples from 83 monkeys, collected during the last 2 months of each season (dry, early wet, late wet). Parasites were recovered via centrifugal flotation in Sheather’s solution, sedimentation in tap water, and immunofluorescence [Smith et al., 2007]. Faecal samples were first mixed with tap water and centrifuged for 10 min to remove small debris. After the supernatant was poured off, a 10-μl sample of the sediment was extracted and was tested for *Giardia* via immunofluorescent antibody detection using the Aqua-Glo G/C Direct Comprehensive Kit (Waterborne Inc., New Orleans, La., USA). The remaining sample was then mixed with Sheather’s solution (specific gravity = 1.27), additional Sheather’s solution was added to create a positive meniscus on the test tube, and a cover slide was placed on top of the tube which was then centrifuged again for 10 min. The cover slide was removed and analysed (flotation), the supernatant was poured off and the remaining sample mixed with tap water. After 4 min, the supernatant was poured off and all of the remaining sediment analysed (sedimentation).

**Parasite Identification**

We used a Leica DME compound microscope to detect parasites from faecal flotation and sedimentation. We used an Olympus BX51 fluorescent microscope to detect *Giardia* via immunofluorescence. Flotation and sedimentation slides were scanned on ×100 magnification, while the fluorescence slides were scanned on ×200. All slides were scanned systematically [Smith et al., 2007]. Parasite eggs, larvae and cysts were counted, measured using an ocular micrometer, and photographed with a Lumenera Infinity-1 digital microscope camera. Unless noted otherwise, parasite dimensions are reported as the average measurement of 10 eggs, larvae or cysts.

For each parasite, we report its prevalence (number of infected individuals/number of individuals sampled). Parasite species richness is defined as the number of distinct parasite species found in an individual or population [Bush et al., 1997]. As we were unable to obtain multiple samples per individual over consecutive days, we acknowledge that some infections may have been missed and therefore our reported prevalence and species richness values should be considered conservative estimates.

**Necropsy**

A necropsy was performed on an adult female capuchin that was hit by a car and died on the Pan American Highway just outside the border of Sector Santa Rosa. We stored the lungs,

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**Table 1. Group compositions of *C. capucinus* in Sector Santa Rosa, ACG, Costa Rica**

<table>
<thead>
<tr>
<th>Group</th>
<th>Adults</th>
<th>Large juveniles</th>
<th>Small juveniles</th>
<th>Infants</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>♂/♀</td>
<td>♂/♀</td>
<td>♂/♀</td>
<td>♂/♀</td>
<td>♂/♀</td>
</tr>
<tr>
<td>CP</td>
<td>2/7–9</td>
<td>0–3/4</td>
<td>1–3/2–4</td>
<td>4–5/1–2</td>
<td>24–26</td>
</tr>
<tr>
<td>EX</td>
<td>1/4</td>
<td>1/0</td>
<td>1/0</td>
<td>0–3/1–2</td>
<td>8–11</td>
</tr>
<tr>
<td>GN</td>
<td>8/10–11</td>
<td>2–5/1</td>
<td>4–7/1–2</td>
<td>1–2/1–2</td>
<td>33–35</td>
</tr>
<tr>
<td>LV</td>
<td>4/6</td>
<td>1/3</td>
<td>2–4/2</td>
<td>0–2/1–2</td>
<td>20–23</td>
</tr>
</tbody>
</table>

CP = Cerco de Piedra; EX = Exclosure; GN = Guanacaste; LV = Los Valles.
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We recovered 8 parasite species (fig. 1a–h) from the 272 faecal samples: 5 nematodes (Filariopsis barretoi, Strongyloides sp., unidentified subulurid, unidentified spirurid, and unidentified strongylid), 1 cestode (unidentified), 1 acanthocephalan (Prosthenorchis sp.) and 1 protozoan (Giardia duodenalis). All parasites identified to the genus or species level have been previously reported in capuchins. The prevalence for each parasite is shown in table 2. We also identified a number of non-primate parasites (e.g. a Syphacia-like pinworm, invertebrate cestode egg capsules, a Habronema-like spirurid nematode) and parasites in developmental stages too advanced to have been recently passed in the host’s faeces (e.g. sporulated Isospora sp. oocyst). We did not consider these as parasites of capuchins due to their morphologies and low prevalence.

Parasites were recovered from 76 of 83 individuals (91.6%) and average individual parasite species richness was 1.89. Almost all of the capuchins from which no parasites were detected were immature individuals less than 3 years of age, although this may be due to sample size as only one sample was processed for each. All but 1 individual over the age of 3 were infected with at least 1 parasite species during the course of the study.

We recovered only 1 parasite species from the necropsied female capuchin. Coiled, long-tailed larvae were present in the intestinal contents and adult nematodes were widespread in the lung parenchyma. We identified these as the lungworm

Table 2. Prevalence of the 8 parasite species recovered from wild C. capucinus in Sector Santa Rosa, ACG, Costa Rica

<table>
<thead>
<tr>
<th>Parasite</th>
<th>Prevalence, %</th>
<th>Transmission route</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthocephala</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prosthenorchis sp.</td>
<td>2.4</td>
<td>indirect-invertebrate</td>
</tr>
<tr>
<td>Cestoda</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unidentified cestode</td>
<td>1.2</td>
<td>indirect-invertebrate</td>
</tr>
<tr>
<td>Nematoda</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Filariopsis barretoi</td>
<td>84.3</td>
<td>direct-contact¹</td>
</tr>
<tr>
<td>Strongyloides sp.</td>
<td>75.9</td>
<td>direct-environmental</td>
</tr>
<tr>
<td>Unidentified subulurid</td>
<td>13.3</td>
<td>indirect-invertebrate</td>
</tr>
<tr>
<td>Unidentified spirurid</td>
<td>6.0</td>
<td>indirect-invertebrate</td>
</tr>
<tr>
<td>Unidentified strongylid</td>
<td>2.4</td>
<td>direct-environmental</td>
</tr>
<tr>
<td>Protozoa</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Giardia duodenalis</td>
<td>6.0</td>
<td>direct-contact</td>
</tr>
</tbody>
</table>

¹ The transmission route of F. barretoi is unknown, but has been inferred.
Filariopsis barretoi (syn. F. arator, F. cebi) based on adult nematode morphology [Rego and Schaeffer, 1988; Santa Cruz et al., 1998]. Due to the fragility of the adult nematodes, we were unable to extract them intact from the lung tissue and, therefore, were unable to determine the infection intensity.

Acanthocephala

Family Oligacanthorhynchidae. Acanthocephalan eggs (fig. 1a) resembling Prosthenorchis sp. were recovered from sedimentation in 2 samples, both from male capuchins. Eggs contained an acanthor and measured 68.4 ± 4.2 by 46.1 ± 6.5 μm (n = 3). Size and morphology were consistent with Prosthenorchis elegans and Prosthenorchis spirula.
Cestoda

*Family Anoplocephalidae.* Cestode eggs containing hexacanth embryos (fig. 1b) were recovered in 1 sedimentation sample from an adult female capuchin. The eggs measured 54.7 ± 1.6 by 46.4 ± 3.0 μm and the oncosphere measured 38.0 ± 1.5 by 29.6 ± 7.1 μm (n = 2). We were unable to identify the cestode beyond the family level based on size and morphology.

Nematoda

*Family Filaroididae.* The most commonly recovered parasite was *Filariopsis barretoi*, with larvae measuring 381.4 ± 39.4 by 10.4 μm. Larvae were found in 191 samples representing 70 individuals. The larvae were often coiled with very long tails (fig. 1c) and were commonly recovered by both flotation and sedimentation.

*Family Strongyloidae.* We recovered eggs (fig. 1d) and first-stage rhabditiform larvae of *Strongyloides* sp. in both flotation and sedimentation samples. Eggs (54.9 ± 4.8 by 34.4 ± 2.2 μm) were thin-shelled and embryonated. The larvae averaged 244.3 ± 22.7 μm in length and 10.0 ± 1.1 μm in width. The morphology and size of both eggs and larvae were characteristic of *S. cebus* [Little, 1966; Cogswell, 2007]. *Strongyloides* sp. was found in 134 samples collected from 62 capuchins.

*Family Subuluridae.* Subulurid nematode eggs (fig. 1e) containing visible larvae were recovered in faecal flotation. We found subulurid eggs in single samples from 11 different capuchins. Eggs measured 39.5 ± 1.4 by 36.1 ± 2.0 μm (n = 6).

*Order Spirurida.* We recovered thick-shelled spirurid nematode eggs (fig. 1f) in 10 samples from 6 individuals. Eggs contained larvae and measured 42.5 ± 1.5 by 28.3 ± 2.7 μm (n = 9). We recovered the spirurid predominantly by flotation.

Suborder Strongylida. Strongyle nematode eggs were recovered by sedimentation from 2 capuchins. The species could not be identified as it is extremely difficult to distinguish nematode species by egg size and morphology alone. The eggs measured 61.7 ± 1.4 by 38.4 ± 0.9 μm (n = 2) and were thin-shelled (fig. 1g).

Protozoa

*Family Hexamitidae.* Using immunofluorescence, *Giardia* sp. cysts (fig. 1h) were identified in 6 samples representing 5 individuals. No trophozoites were found. Cysts measured 12.4 ± 1.0 by 8.7 ± 0.7 μm and fall within the range of *G. duodenalis* [Cogswell, 2007]. This species (syn. *G. lamblia, G. intestinalis*) is the only *Giardia* species reported in primate hosts [Nunn and Altizer, 2005].

Discussion

White-faced capuchins in our study had a rich parasite fauna. We recovered parasites from Nematoda, Cestoda and Acanthocephala as well as one protozoan species. However, we must be cautious about labelling the parasites occurring at low prevalence as ‘capuchin parasites’. Terrestrial primates may accidently ingest parasite material from incidental contact with the faeces of other animals [Lindsay et al., 1997] and primates who consume other animals may also pass the prey’s parasites in their faeces [Vitazkova, 2009]. Capuchins consume dozens of vertebrate [Rose, 1997] and invertebrate species and the non-primate parasites that we recovered were likely parasites of capuchin prey species (e.g. rodents, birds).
F. barretoi and Strongyloides sp. were the most prevalent parasites found in white-faced capuchins in Sector Santa Rosa. Interestingly, Filariopsis and Strongyloides were also the 2 most prevalent parasites found in a captive colony of Cebus apella in Argentina [Santa Cruz et al., 2000] suggesting that both parasites have well-developed evolutionary relationships with the genus Cebus.

Parasites Transmitted via an Intermediate Host

The consumption of an infected intermediate host (e.g. cockroach) is the most common transmission route for capuchin parasites in Sector Santa Rosa. Four of the parasites we recovered are transmitted indirectly: Prosthenorchis sp., the spirurid nematode, the subulurid nematode and the cestode.

Prosthenorchis is a common parasite of capuchins and other Neotropical primate species [Dunn, 1963; Cogswell, 2007] and is transmitted to monkeys through consumption of infected cockroach intermediate hosts [Cogswell, 2007]. Two species of Prosthenorchis have been reported in primates: P. elegans and the less common P. spirula. Both species occur naturally in capuchins [Yamashita, 1963; Garner et al., 1967; Cogswell, 2007], but only the former has been previously reported in C. capucinus [Nunn and Altizer, 2005]. Adult worms embed themselves deep into the intestinal mucosa and can cause significant pathology. Mucosal inflammation, necrosis and ulcers can occur at the site of attachment [Whitney, 1974] and fatal infections are common [Kuntz and Myers, 1972; Kuntz, 1982; Müller et al., 2010]. Heavy infections of this parasite have been reported in squirrel monkeys (Saimiri), titi monkeys (Callicebus spp.), and marmosets and tamarins (Callitrichidae), with the deaths of many animals attributed to bowel obstruction caused by the embedded worms [Dunn, 1963; Richart and Benirschke, 1963].

Spirurid nematodes have been recovered from the faeces of New and Old World primates and infections occur through consumption of an infected intermediate host, often a cockroach, cricket or beetle [Bowman, 2007]. Physaloptera cebi has previously been described from C. capucinus in Panama [Nunn and Altizer, 2005] and from captive C. apella [Yamashita, 1963]. Physaloptera dilatata has been reported in C. apella [Hershkovitz, 1977] and Protospirura muricola has been reported in captive C. capucinus in Japan [Yamashita, 1963]. Because spirurid eggs are similar in size, molecular analysis is required to identify the spirurids recovered in this study to the species level.

Few subulurid nematodes infect non-human primates. Subulurids are transmitted by arthropod intermediate hosts [Anderson, 1988] and typically have a wide host range, including mammals, birds and reptiles [Vicente et al., 2000]. These parasites reside in the large intestines and caeca of their hosts [Baker, 2007] and although they can cause intestinal perforation [de Melo, 2004], they are not known to be highly pathogenic [Petzelkova et al., 2006]. Species from the genus Subulura have been recovered from baboons, vervet monkeys and mouse lemurs [Myers and Kuntz, 1965; Nunn and Altizer, 2005], while Tarsubulura perarmata has been recovered from tarsiers [Nunn and Altizer, 2005]. No subulurid has been found previously in a capuchin host. Primasubulura jacchi is the only subulurid reported in Neotropical primates, infecting callitrichids [Michaud et al., 2003; Santos Sales et al., 2010] and squirrel monkeys [Nunn and Altizer, 2005]. The subulurid we recovered is too small to be P. jacchi, so it may either be a previously undescribed primate subulurid species or one that infects a capuchin prey species rather than the capuchins themselves.
Tapeworms rarely cause death in non-human primates [Kuntz, 1982]. The unidentified cestode eggs in our study resembled those of Mathevotaenia megastoma, which has been recovered from numerous Neotropical primate genera including Alouatta and Cebus [Yamashita, 1963; Kuntz and Myers, 1972; Stuart et al., 1998; Michaud et al., 2003; Beveridge, 2008]. It is also morphologically similar to an unidentified anoplocephalid cestode recovered from captive C. apella in Argentina [Santa Cruz et al., 2000].

Parasites Transmitted via Environmental Contamination
Two of the 8 parasites recovered require time in the external environment to develop into the infective stage: Strongyloides sp. and the unidentified strongylid nematode. The Strongyloides eggs and larvae we recovered were likely from Strongyloides cebus, the only Strongyloides species known to infect New World monkeys [Little, 1966]. Therefore, we believe that the capuchins in our study were infected with S. cebus. Adult Strongyloides can survive and reproduce in a free-living state as well inside the body of the host. Infective stage larvae can enter the host’s body by two routes, skin penetration or ingestion. Infective larvae mature to adult female Strongyloides within 48 h and reside in the proximal half of the small intestine, producing eggs within 5 days [Little, 1966; Whitney, 1974]. Strongyloides is unique among the parasites we recovered as it also has the ability to autoinfect the host. Autoinfection occurs when the perianal region becomes contaminated with faeces and newly hatched larval burrow into the skin. Due to the risk of autoinfection and the short developmental period within the host, immunocompromised individuals may incur hyperinfections of Strongyloides. S. cebus has been reported in numerous Neotropical primates including woolly monkeys, spider monkeys, howler monkeys and squirrel monkeys [Nunn and Altizer, 2005].

The morphology and size of the recovered strongylid eggs are similar to many recognized primate strongyloid species (e.g. Oesophagostomum spp., Molineus spp.). Molecular analysis or coprocultures with detailed morphological comparisons of larvae would have been required to identify these eggs to the genus or species level.

Parasites Transmitted via Direct Contact
Only 2 of the 8 recovered parasites, F. barretoi and G. duodenalis, are infective immediately after being shed in the host’s faeces. The life cycle of Filariopsis is undescribed. However, first-stage larvae of the Filarioidea spp. are immediately infective after passing in the faeces of the host. Since Filarioidea and Filariopsis are closely related mammalian lungworms [Webster, 1978], it is possible that they share the same transmission route. In addition to white-faced capuchins, F. barretoi infections have been found in squirrel monkeys, marmosets, tamarins, owl monkeys and howlers [Rego and Schaeffer, 1988; Stuart et al., 1998; Michaud et al., 2003]. Pathogenicity of the parasite may be low as observable signs of infection were absent in 6 Argentinian capuchins despite the high intensity of adult worms within their lungs [Santa Cruz et al., 1998]. Similarly, we found a high prevalence of this parasite in our study population and observed high intensity and significant pulmonary lesions in the lungs of the necropsied female capuchin. However, we never observed clinical signs of pulmonary disease, such as coughing, in our study animals.

The Giardia species recovered in this study is most likely G. duodenalis based on size and this species’ common association with non-human primates. Giardia is a
protozoan parasite of the small intestine. Cysts are excreted in the faeces, are immediately infective, and are transmitted through consumption of contaminated food or water. The major symptom of giardiasis is severe diarrhoea and, although rarely fatal, can lead to dehydration, weight loss and cognitive impairment [Kuntz, 1982; Cogswell, 2007]. Many strains and substrains of *G. duodenalis* are known, at least 2 of which (assemblages A and B) are able to infect human and non-human primates, among other mammals [Hunter and Thompson, 2005]. Further genotyping is required to definitively identify the *Giardia* sp. recovered in this study.

**Capuchin Parasite Diversity**

The Santa Rosa capuchins were infected with more gastro-intestinal parasite species than other wild capuchins throughout Costa Rica [Chinchilla et al., 2007, 2010] and in Peru [Phillips et al., 2004]. In contrast to the Santa Rosa capuchins, many of the parasite species recovered in those 3 prior studies were protozoan. However, the capuchins across these 3 studies did share similar macroparasitic infections; *Strongyloides* infections were reported in all 3 studies and the Costa Rican studies report an acanthocephalan parasite, although it is unknown whether this was the same species.

The capuchins of Sector Santa Rosa host a greater diversity of parasites than has been reported for most wild howler monkey populations. Although the difference in parasite species richness between the current capuchin study and the majority of the howler studies [Stuart et al., 1990; Stoner, 1996; Stuart et al., 1998; Phillips et al., 2004; Chinchilla et al., 2005; Eckert et al., 2006; Stoner and González Di Pierro, 2006; Trejo-Macías et al., 2007; Kowalzik, 2009; Cristóbal-Azkarate et al., 2010; Valdespino et al., 2010] may be a result of differential sampling intensity, it seems that different howler species and populations are infected with the same small set of directly transmitted parasites (*Giardia*, *Entamoeba*, *Trypanoxyuris*, *Strongyloides*). Conversely, capuchins appear to be exposed to a wide range of directly and indirectly transmitted parasites. The variation in parasites between the 2 monkey genera may be attributed to substrate use and diet. In Santa Rosa, howler monkeys are exclusively arboreal while capuchins spend small amounts of time on the forest floor [Gebo, 1992] and may be more prone to infections from soil-borne parasites. Whereas howlers consume predominantly plant material, 20–50% of the capuchin diet comprises invertebrates including beetles, katydids, crickets and cockroaches [Chapman, 1987; Fragaszy et al., 2004]. Howler monkeys do, however, maintain at least one indirectly transmitted parasite, *Controrchis bilophilus*, a trematode that is thought to be transmitted through consumption of infected ants living in *Cecropia peltata* trees [Kowalzik et al., 2010]. Interestingly, capuchins, like howlers, consume the fruit from *Cecropia* trees yet we did not find any *Controrchis* eggs in capuchin faeces, despite the parasite being prevalent in Santa Rosa’s howler monkey population [Stuart et al., 1998]. Future parasitological studies should aim to identify the intermediate host species that are responsible for transmitting complex life cycle parasites to the definitive capuchin host.

**Cross-Species Transmission Risk**

In addition to mantled howler monkeys (*Alouatta palliata*), capuchins in Sector Santa Rosa live sympatrically with black-handed spider monkeys (*Ateles geoffroyi geoffroyi*). Wild *Cebus* and *Alouatta* are hosts to a number of the same parasite genera including *Strongyloides* and *Giardia* [Stuart et al., 1998; Chinchilla et al., 2005; Stoner
and González Di Pierro, 2006; Chinchilla et al., 2007; Cristóbal-Azkarate et al., 2010; Kowalzik et al., 2010], and although the parasites of spider monkeys are not well known, they are hosts for Strongyloides as well [Karesh et al., 1998; Carrasco et al., 2008].

Cross-species parasite transmission may be possible in Santa Rosa’s primates due to their shared habitats, substrates and food sources, but also because the monkeys often come into close proximity or contact with each other [e.g. Chapman, 1987]. However, we cannot definitively say if the parasite species we recovered from the capuchins were the same species that have been reported from howler and spider monkey populations due to the indistinguishable morphology of the eggs, larvae and cysts that we recovered. To truly assess the cross-species transmission risk, future studies should identify parasites to the species and strain levels through coprocultures and DNA-based techniques [MAFF, 1979; Hyde, 1993].

In summary, white-faced capuchins in Sector Santa Rosa are hosts to at least 8 gastro-intestinal and pulmonary parasite species that are diverse both taxonomically and in their transmission routes. This high species richness is arguably influenced by the capuchins’ diverse diet and subsequent risk of contracting parasites that use invertebrate intermediate hosts. Despite their susceptibility to indirectly transmitted parasites, the 2 most prevalent capuchin parasites (F. barretoi, Strongyloides sp.) are directly transmitted and the infection risk for these species is likely dependent on social or ecological factors rather than diet.

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