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RESEARCH ARTICLE

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A multiyear survey of helminths from wild saddleback (*Leontocebus weddelli*) and emperor (*Saguinus imperator*) tamarins

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Abstract

The establishment of baseline data on parasites from wild primates is essential to understand how changes in habitat or climatic disturbances will impact parasite–host relationships. In nature, multiparasitic infections of primates usually fluctuate temporally and seasonally, implying that the acquisition of reliable data must occur over time. Individual parasite infection data from two wild populations of New World primates, the saddleback (*Leontocebus weddelli*) and emperor (*Saguinus imperator*) tamarin, were collected over 3 years to establish baseline levels of helminth prevalence and parasite species richness (PSR). Secondarily, we explored variation in parasite prevalence across age and sex classes, test nonrandom associations of parasite co-occurrence, and assess the relationship between group size and PSR. From 288 fecal samples across 105 individuals (71 saddleback and 34 emperor tamarins), 10 parasite taxa were identified by light microscopy following centrifugation and ethyl-acetate sedimentation. Of these taxa, none were host-specific, Dicrocoeliidae and Cestoda prevalences differed between host species, *Prosthenorchis* and Strongylida were the most prevalent. Host age was positively associated with *Prosthenorchis* ova and filariform larva, but negatively with cestode and the Rhabditoidea ova. We detected no differences between expected and observed levels of co-infection, nor between group size and parasite species richness over 30 group-years. Logistic models of individual infection status did not identify a sex bias; however, age and species predicted the presence of four and three parasite taxa, respectively, with saddleback tamarins exhibiting higher PSR. Now that we have reliable baseline data for future monitoring of these populations, next steps involve the molecular characterization of these parasites, and exploration of linkages with health parameters.

KEYWORDS
baseline data, Callitrichidae, free-ranging, Neotropics, parasite infections

1 | INTRODUCTION

Parasitism has a fundamental role to play in the persistence of animal populations in nature, and the richness of parasite communities may serve as effective population- and ecosystem-level measures of health (Hudson, 1998; Hudson, Dobson, & Lafferty, 2006). In particular, helminth parasites, which can be detected through noninvasive sampling, may be ideally suited for long-term health monitoring of a primate community (Gillespie, 2006; Howells, Pruetz, & Gillespie, 2011). They are relatively easy to evaluate from fecal samples collected from habituated primate

groups, but can sometimes be acquired in the absence of habituation by scat detection dogs or by searching beneath known feeding or resting locations (Arandjelovic et al., 2015; Orkin, Yang, Yang, Yu, & Jiang, 2016). Several long-term research programs have successfully used temporal parasite data to examine ecological perturbations of threatened primate populations (Bakuza & Nkwengulila, 2009; Chapman, Gillespie, & Speirs, 2005; Gillespie & Chapman, 2008; Gillespie, Chapman, & Greiner, 2005). In contrast, in the absence of temporal data, comparative studies between isolated and more urban primate populations are effective at evaluating impacts of increased contact with humans (Salzer, Deutsch, Raño, Kuhlenschmidt, & Gillespie, 2010; Wenz, Heymann, Petney, & Taraschewski, 2009). Despite the utility of such studies, parts of the world with the highest primate diversity, such as the Neotropics, remain inadequately sampled for naturally occurring helminth parasites (reviewed in Hopkins & Nunn, 2007, but also see Solórzano-García & de León, 2018), and reliable baseline data that are required to detect changes over time and space are not commonly available.

Since the range of factors that can explain parasite–host patterns in nature is large (Clough, Heistermann, & Kappeler, 2010; Gillespie, Barelli, & Heistermann, 2013; Gillespie et al., 2010; MacIntosh, Hernandez, & Huffman, 2010; MacIntosh et al., 2012; Monteiro, Dietz, Raboy, et al., 2007; Muehlenbein & Watts, 2010; Nunn, Brezine, Jolles, & Ezenwa, 2014; Telfer et al., 2008) and often dependent on the environment and time (Clough et al., 2010; Gillespie et al., 2010), it may be best approached through longitudinal monitoring of individuals in host communities (Clutton-Brock & Sheldon, 2010; Erkenswick, Watsa, Gozalo, Dmytryk, & Parker, 2017; Stuart et al., 1998). A primary challenge has been that research on wild primates usually requires habituation to observers, which often constrains sample sizes, making it difficult to adequately analyze many of these factors (Williamson & Feistner, 2011). Thus far, a multitude of studies have offered snapshots of parasite prevalences, focused on just one or two parasites of known interest, the sampling of a single primate host, or on data from health inspections, or necropsies, after animal extraction from the wild. Collectively they have created a broad foundation of primate parasite data (see Nunn & Altizer, 2005 for a detailed compilation; Solórzano-García & de León, 2018).

The next challenge will be to determine baseline levels of prevalence and species richness, which will enable more detailed studies that incorporate host demography and development, mode of transmission, and change over time at the level of a population. As an example, for almost a half-century it has been well known that New World monkeys are broadly infected by *Plasmodium brasilianum*, a quartan malarial parasite, that may in fact be the same as the human parasite *Plasmodium malariae* (Collins & Jeffery, 2007; Lalremruata et al., 2015). However, only last year do we have the first evidence that it may persist in a highly aggregated manner among a small number of chronically infected nonhuman primate hosts (Erkenswick, Watsa, Pacheco, Escalante, & Parker, 2017). In addition, long-term studies that incorporate more than one primate host are essential to examine several longstanding hypotheses of how sociality influences parasite prevalence, intensity, and diversity (Altizer et al., 2003; Freeland, 1976, 1979), as are long-term studies of multiple sympatric species to examine species-specificity of infection dynamics.

The Callitrichidae (comprised of tamarins and marmosets) are small arboreal primates that are widely distributed throughout the forests of South America (Sussman & Kinzey, 1984). They are frequently found in sympatry with other New World monkeys and in some cases have proven relatively resilient and flexible in the face of encroachment by human populations (Gordo, Calleia, Vasconcelos, Leite, & Ferrari, 2013; G. C. Leite, Duarte, & Young, 2011; Soto-Calderón, Acevedo-Garcés, Álvarez-Cardona, Hernández-Castro, & García-Montoya, 2016). Part of their ecological flexibility may be due to their generalist diets that include fruits, insects, tree exudates, and fungi (Sussman & Kinzey, 1984), a characteristic that also could expose them to a wide array of parasites that are dispersed by intermediate arthropod hosts. Studies of endoparasites of callitrichids have documented overlap with other primate families including the Ateledae, Cebidae, and Aotidae (Michaud, Tantalean, Ique, Montoya, & Gozalo, 2003; Phillips, Haas, Grafton, & Yrivarren, 2004; Tantalean, Gozalo, & Montoya, 1990; Wolff, 1990). Considering the approximately 61 species and subspecies of Callitrichidae (Rylands and Mittermeier, 2009), there have been only a handful of comprehensive evaluations of helminth parasites from free-ranging populations (Monteiro, Dietz, Beck, et al., 2007; Müller, 2007; Wenz et al., 2009), and only two species in which parasites have been monitored routinely over time—the golden lion and golden-headed lion tamarins (*Leontopithecus rosalia* and *L. chrysomelas*, respectively; Monteiro, Dietz, Raboy, et al., 2007).

The principle aim of this study was to characterize the helminth assemblages from two populations of sympatric, individually identifiable, free-ranging callitrichids—the saddleback tamarin (*Leontocebus weddelli*, formerly *Saguinus fuscicollis weddelli*; Buckner, Lynch Alfaro, Rylands, & Alfaro, 2015; Matauschek, Roos, & Heymann, 2011) and emperor tamarin (*Saguinus imperator*)—from fecal samples collected noninvasively and via an annual mark-recapture program. By sampling these hosts across 3 years, we estimate the prevalence of helminth parasites, species richness, and the extent of parasite overlap between the two host species. We also summarize changes in infection status from the subset of animals that were screened for helminths in two or more consecutive years. In doing so, we establish baseline data for future comparative studies following perturbations such as changing weather patterns due to climate change, habitat loss/modification, or greater human encroachment.

Secondarily, as sampling came from an individually identifiable population, we analyzed how parasite prevalence varied by host demographic variables. As a result of greater social burdens placed on females to compete for dominant breeding opportunities, we predicted that an age–sex interaction would influence prevalence and parasite species richness. We also analyzed infection data for nonrandom associations between all pairwise parasite combinations, on the basis that blood parasite associations were detected previously in the same populations (Erkenswick, Watsa, Gozalo, et al., 2017). Lastly, prior studies have detected a potential pattern between primate group size and parasite species richness (Cote &

Poulin, 1995; Nunn, Altizer, Jones, & Sechrest, 2003; Rifkin, Nunn, & Garamszegi, 2012; Vitone, Altizer, & Nunn, 2004), but this association has not been considered within the Callitrichidae, at small taxonomic scales. We tested the hypothesis that large groups will harbor higher parasite species richness.

2 | METHODS

All sampling protocols adhered to guidelines outlined by the American Society of Mammalogists (Sikes & Gannon, 2011) and complied with the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates. Permissions for this study were obtained from the Institutional Animal Care and Use Committee at the University of Missouri-St. Louis and the Directorate of Forest and Wildlife Management (DGFFS) of Perú annually. The DGFFS also granted export permits for the samples, while the CDC and U.S. Fish and Wildlife Services approved the import of these samples into the United States.

2.1 | Field site and study subjects

Sample collection took place annually from 2012 to 2014 in the Madre de Dios Department of Southeastern Perú at the Estación Biológica Rio Los Amigos (EBLA; 12°34′07″S, 70°05′57″W), which is managed by the Asociación para la Conservación de La Cuenca Amazonica. This site was previously known as the Centro de Investigación y Capacitación Río Los Amigos (CICRA), see Watsa, Erkenswick, Rehg, and Pitman (2012) for further description of the site, including a detailed map of the location. The field station was created in 2000, and aside from selective logging, the forest remains intact. All sampling took place within a forest trail system that covers approximately 900 ha of tropical rainforest that is adjacent to the Los Amigos Conservation Concession inside the buffer zone of Manu National Park. The collection area consists of five, nonmutually exclusive, forest types including *terra firme*, primary forest, bamboo, palm swamp, floodplain, and successional/disturbed forests (Pitman, 2008). There are two distinct seasons each year at this site—the wet season from October to March (average monthly precipitation > 250 mm), and the dry season from April to September (136 mm ± *SD* 19 mm; Watsa, 2013). All sampling took place during the dry season, from May–July each year, precluding the study of the effects of seasonality on the parasite community in these primates.

Three callitrichines at this site, the saddleback tamarin, emperor tamarins, and the more cryptic Goeldi's monkey (*Callimico goeldii*; Watsa et al., 2012), share forest habitat with eight other primate species including three species of Cebidae, and two species each of Atelidae and Pithecidae, as well as owl monkeys (*Aotus nigrifrons*; Watsa, 2013). At EBLA, both *S. imperator* and *L. weddelli* have average group sizes of 5 (range of 3–8) individuals and group compositions are similar (Watsa, Erkenswick, & Robakis, 2017; Watsa et al., 2015). The primary differences between *S. imperator* and *L. weddelli* are adult weight, 515 ± 66 and 386 ± 86 g, respectively, and nuances in feeding behavior including greater amounts of fungi consumption in *S. imperator* (pers. obs.; Terborgh, 1985).

2.2 | Sample collection and storage

Since 2009, an annual mark-recapture program has been implemented on ~70 saddleback and emperor tamarins by Field Projects International (Watsa et al., 2015). During capture, each individual is permanently tagged with a microchip (Microchip ID Systems, Covington, LA), and was made visually identifiable by unique patterns of bleached rings around the tail, as well as a tricolor beaded necklace that signified group, sex and individual identity (for the full capture protocol see Watsa et al., 2015). In addition to collecting fecal samples at the time of capture, we used radio telemetry to track tamarins in 14 groups each year via a radio collar placed on the breeding female in each group (Wildlife Materials, Murphysboro IL). We also used both full (sleep-site to sleep-site, spanning ~11 hr) and half-day (minimum 5 hr) follows to opportunistically collect fecal samples from all group members as they were produced.

Each animal in the study was classified into one of three age classes based on dental eruption patterns (Watsa, 2013). Juveniles were defined as individuals whose adult teeth were absent or not fully erupted (<11 months old). Subadults were animals with adult teeth, but that were juveniles in the preceding year. All remaining individuals were assigned to the adult age class. Due to small sample sizes from the subadult class, the juveniles and subadult classes were combined to analyze the effects of age on parasite prevalence.

Upon sample collection during mark-recapture and follows, all fecal samples were transferred using sterile technique into numbered plastic bags and stored in a chilled thermos. Upon return to basecamp, each sample was fixed in 10% neutral buffered formalin (1:2, feces to preservative ratio). For each sample, we recorded species, individual ID, group, date, time of day, and type of collection (follow or trapping event). Only samples produced by identified individuals were included in this study. All samples were exported to the University of Missouri-St. Louis for analyses.

2.3 | Laboratory analysis

Isolation of parasite cysts, eggs, and larvae from fecal samples followed a two-step process based on sedimentation procedures as per MacIntosh et al. (2010) and Zajac and Conboy (2012). In Step 1, we used a fecal straining procedure in which fecal samples were (a) diluted in 10% neutral buffered formalin, (b) strained of large debris through cheese cloth into a plastic cup, (c) transferred to a 15-ml falcon tube with an empty weight already recorded, (d) centrifuged at 800*g* for 5 min to form a fecal pellet, (e) removed of the supernatant and weighed, (f) resuspended and homogenized in 5 ml of 10% formalin. In Step 2, we followed the centrifugal sedimentation test outlined by Zajac and Conboy (2012) with 1 ml of the homogenized suspension from Step 1. Sedimentations from Step 2 were resuspended in exactly 1 ml of preservative, and 80 µl aliquots were placed onto clean slides with 22 × 22 mm coverslips for full evaluation with an

Olympus CX31 light microscope (Center Valley, PA) using ×200 magnification (micrographs were taken at higher power). Evaluations of parasites were timed and tabulated using a free online data counter, COUNT (http://erktime.github.io/count/), and each unique infection/sample was documented with multiple micrographs taken with a Leica ICC50 HD camera (Allendale, NJ). Three separate aliquots per sample were evaluated with each evaluation taking an average of 10 min.

Unless infections were too rare, standard length and width measurements from 10 representative micrographs per parasite per species were recorded with a calibrated ruler in Image J (https://imagej.nih.gov/ij/) to the nearest 1 μm. Sizes and measurements of all parasite forms were compared with known references values in the literature and identified to the lowest taxonomic scale possible.

2.4 | Statistical analysis

For each animal and for each year of the study, if a parasite was detected in one or more fecal samples it was considered a positive parasite infection. Average prevalence, as well as the proportion of individuals that acquired infection, lost infection, or showed no change in infection status, was calculated for each helminth identified by microscopy across the 3-year study period. Average change in infection status was determined by selecting all instances where an individual was sampled across a 2-year period, either 2012–2013 or 2013–2014, and computing the mean number of individuals that acquired, lost, or did not change infection status. Differences in annual helminth prevalence between host species were tested with a two-tailed Fisher's Exact Test, followed by *p*-value adjustment for multiple comparisons using the Holm–Bonferroni method, α level of .05 (Holm, 1979). To test for variation in the presence of parasitic infections across host variables we used mixed-effect logistic regression models with a binary response variable and binomial errors. Fixed effects included "sex," "age class," and "species" and random effects included "animal identity" and "year" to accommodate individual resampling and possible interannual variation. We also incorporated the number of samples collected per animal per year as an offset to account for temporal sampling bias (Walther, Cotgreave, Price, & Gregory, 1995). Parasite species richness, which was a discrete numerical response variable, was analyzed with an identical model formula but using Poisson errors. Model selection for all models was carried out with step-wise term deletion by removing nonsignificant factors and comparing nested models with a likelihood ratio test.

To test for significant correlations between group size and parasite species richness we calculated rarified parasite community richness estimates per group. The use of species accumulation curve estimates are advocated by Walther et al. (1995), because raw values of parasite community richness are easily biased by uneven sampling. We used Spearman's rank correlations to test if parasite community richness estimates with similar sampling effort were associated with group size.

To identify any nonrandom parasite co-occurrences, we compared the prevalence of all observed pairwise co-infections with expected estimates of co-infection (calculated as prevalence of A × prevalence of B). We then plotted expected against observed values to identify discordant levels of co-infection, and if applicable, used a two-sample *z*-test to compare proportions. All statistical analyses were performed in R (R Development Core Team, 2015).

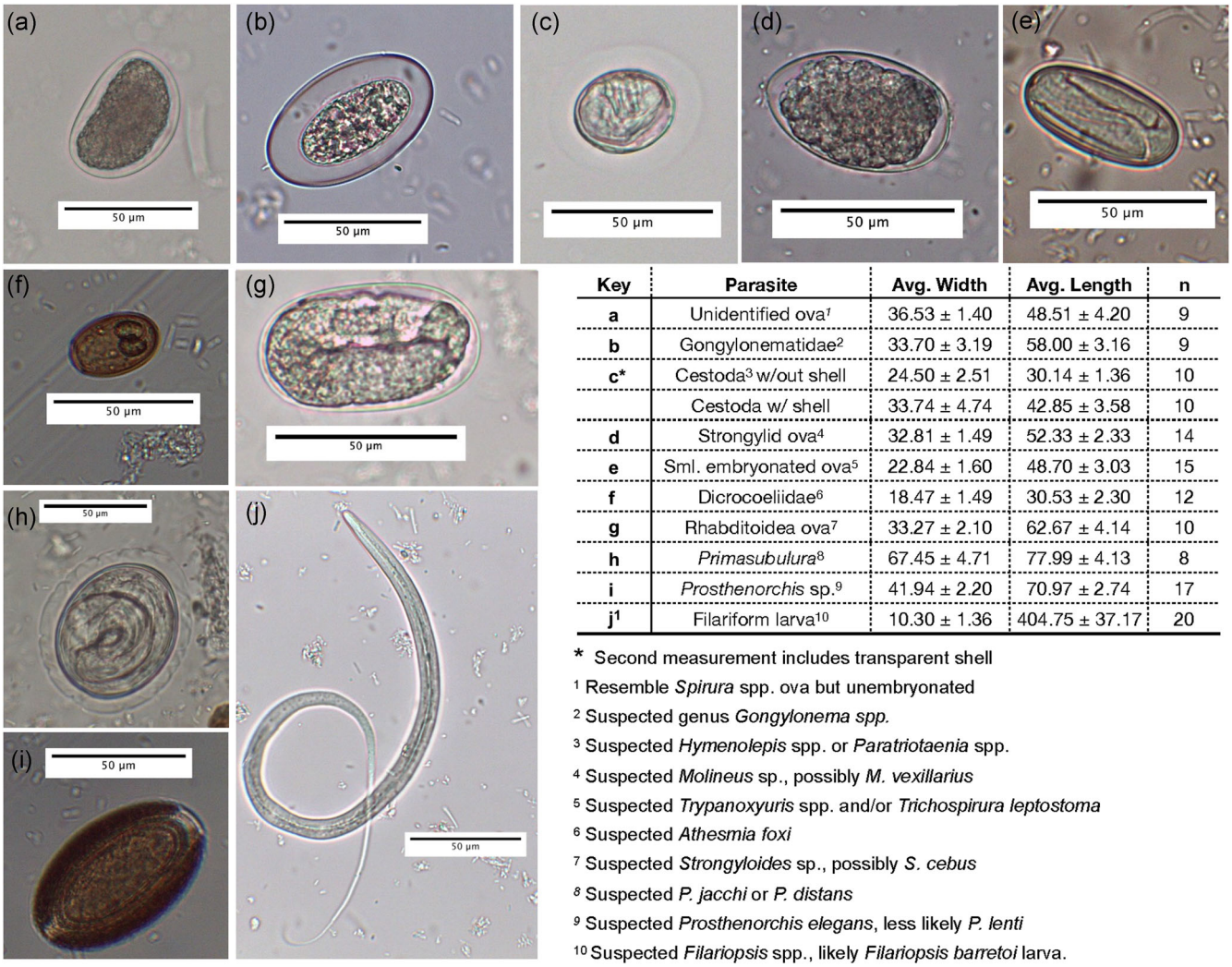
TABLE 1 Numbers of individuals sampled by species, sex, age class, and year

	L. weddelli			*S. imperator*		
Year	2012	2013	2014	2012	2013	2014
Sex	36	46	34	18	23	19
Male	19	28	17	7	14	10
Female	17	18	17	11	9	9
Age class						
Juvenile	8	9	3	6	3	3
Subadult	4	6	1	2	3	1
Adult	24	31	30	10	17	15

3 | RESULTS

In total, we collected 288 individually identified fecal samples from 105 unique tamarins (71 *L. weddelli*, 34 *S. imperator*) distributed across 13 groups of *L. weddelli* and 7 groups of *S. imperator*. The number of samples collected per individual per year ranged from 1 to 7, with a mean of 1.6 ± 0.98. The average fecal sample weight, following Step 1 in sample processing (see Methods), was 0.41 ± 0.22 g. Across the study period, we were able to assess individual infection status from two or more fecal samples 40% ($n = 71$) of the time. Within this 40%, redetection of a parasite infection is significantly correlated with parasite prevalence for both species (for *L. weddelli* r (8) = .95, $p < 0.05$, for *S. imperator* r (7) = .69, $p < 0.05$), meaning that common infections were relatively easy to redetect but rare parasites were difficult. This pattern held for all resampling within a year, whether obtained from a trapping event or collected during a primate follow. Considering all sex and age classes, our sampling included slightly more males than females across years, and subadults of both host species were the least sampled age group (Table 1).

We were able to differentiate 10 helminth parasites by morphology (Figure 1). The parasite ova were grouped based on morphology, length, width, color, shell, and internal characteristics, and compared with New World nonhuman primate helminth ova descriptions reported in the literature. Suspect genus and/or species for each morpho-group was suggested based on ova characteristics and their similarity to those of parasites known to affect Callitrichidae in the wild (Table 2). All but one rare parasitic infection, an unidentified ova (Group A, Table 2), were found in both host species, although prevalence profiles varied (Tables 3 and S2 for post-hoc adjusted *p*-values). Prevalence for the Dicrocoeliidae was significantly higher in *S. imperator* (Fisher's test mean-adjusted $p < 0.05$), and Cestoda was significantly higher in *L. weddelli* (Fisher's test mean-adjusted $p < 0.05$; Table 3). Our rarest parasite infections for both host species were the unidentified ova and large larvated ova (Group H, likely *Primasubulura* spp.), and also Cestoda for *S. imperator*. Out of



Key	Parasite	Avg. Width	Avg. Length	n
a	Unidentified ova[1]	36.53 ± 1.40	48.51 ± 4.20	9
b	Gongylonematidae[2]	33.70 ± 3.19	58.00 ± 3.16	9
c*	Cestoda[3] w/out shell	24.50 ± 2.51	30.14 ± 1.36	10
	Cestoda w/ shell	33.74 ± 4.74	42.85 ± 3.58	10
d	Strongylid ova[4]	32.81 ± 1.49	52.33 ± 2.33	14
e	Sml. embryonated ova[5]	22.84 ± 1.60	48.70 ± 3.03	15
f	Dicrocoeliidae[6]	18.47 ± 1.49	30.53 ± 2.30	12
g	Rhabditoidea ova[7]	33.27 ± 2.10	62.67 ± 4.14	10
h	*Primasubulura*[8]	67.45 ± 4.71	77.99 ± 4.13	8
i	*Prosthenorchis* sp.[9]	41.94 ± 2.20	70.97 ± 2.74	17
j[1]	Filariform larva[10]	10.30 ± 1.36	404.75 ± 37.17	20

* Second measurement includes transparent shell

[1] Resemble *Spirura* spp. ova but unembryonated

[2] Suspected genus *Gongylonema spp.*

[3] Suspected *Hymenolepis* spp. or *Paratriotaenia* spp.

[4] Suspected *Molineus* sp., possibly *M. vexillarius*

[5] Suspected *Trypanoxyuris* spp. and/or *Trichospirura leptostoma*

[6] Suspected *Athesmia foxi*

[7] Suspected *Strongyloides* sp., possibly *S. cebus*

[8] Suspected *P. jacchi* or *P. distans*

[9] Suspected *Prosthenorchis elegans*, less likely *P. lenti*

[10] Suspected *Filariopsis* spp., likely *Filariopsis barretoi* larva.

FIGURE 1 Micrographs and measurements for each parasite

176 parasite screening events (animal-years), at least one parasite was detected all but five times.

With caution due to the error associated with redetecting rare parasites, we report that individual infections status remained primarily unchanged (Figure 2). Among *S. imperator*, this pattern differed slightly for strongylid ova and Dicrocoeliidae (Figure 2 and Table S1). Among *L. weddelli*, we only detected slightly more frequent changes in individual infection status for Cestoda.

Considering each year separately, we did not detect any significant deviations between expected and observed prevalence of co-infection (Figure 3); the largest absolute difference in prevalence across all parasite combinations throughout the study period was 0.07. We also found no evidence of a relationship between group size (ranged 3–8) and estimated parasite species richness within groups after controlling for sampling effort (Spearman's rank correlation = −0.08, $p = .665$, $n = 30$).

Out of the 10 helminths identified, 6 were common enough to evaluate their distributions across host species, sex and age class variables; the unidentified ova, Gongylonematidae, and the large larvated ova (*Primasubulura* sp.) were too rare to analyze prevalence patterns using statistical models. No parasitic infection exhibited a significant sex bias; however, age and species did predict the presence of 4 and 3 parasites, respectively (Table 4). Relative to *L. weddelli*, *S. imperator* was positively associated with Dicrocoeliidae but negatively associated with cestode and strongylid ova. Relative to adults, juveniles and subadults were negatively associated with *Prosthenorchis* and filariform larva, but positively associated with cestode and the Rhabditoidea ova. Our models of parasite species richness identified host species as the only significant predictor considered in this study (Table 4), which had a significantly negative estimate for *S. imperator*.

4 | DISCUSSION

The results provided here, in combination with recent works on hemoparasites at the same site (Erkenswick, Watsa, Gozalo, et al., 2017), represent a benchmark against which future parasitological surveys can be compared. Included in the parasite assemblages found here were parasites that could be transmitted directly/indirectly or

TABLE 2 Parasite ova and larva characterization and classification

Group	Name	Characterization
A	Unidentified ova	Eggs are subglobose with a slightly flattened side and a smooth and thick transparent shell. Eggs morphologically resemble *Spirura guianensis* ova but are unembryonated (Cosgrove, Nelson, & Jones, 1963; Thatcher and Porter, 1968). A new species, *S. delicata*, was reported in a tamarin but the ova not described (Vicente, Pinto, & Faria, 1992).
B	Gongylonematidae	Eggs are ovoid with a thick smooth transparent shell and larvated. Suspect genus *Gongylonema* spp. (Orihel & Seibold, 1972; Strait et al., 2012).
C	Unidentified cestoda ova	Eggs are spherical with a clear mucus thick layer and embryonated, morphologically similar, but smaller, than *Hymenolepis spp.* and *Paratriotaenia* spp. (Guerrero, Serrano-Martínez, Tantaleán, Quispe, & Casas, 2012; Müller, 2007).
D	Strongylid ova	Eggs are ellipsoidal, slightly tapered at one end, with a smooth thin shell and are unembryonated. Suspect genera *Molineus* spp. Possibly *M. vexillarius* (Cogswell, 2007; Cosgrove et al., 1968; Dunn, 1961; Stone, Conga, & Santos, 2016).
E	Small embryonated ova	Eggs are ellipsoidal, symmetrical, with a smooth, relatively thick shell and larvated. Two common nematodes in tamarins with similar egg morphology are *Trypanoxyuris* spp. (Carrasco, Tantaleán, Gibson, & Williams, 2008; Conga et al., 2014; Guerrero et al., 2012; Stone et al., 2016; Thatcher & Porter, 1968) and *Trichospirura leptostoma* (Orihel & Seibold, 1971; Vicente et al., 1992; Vicente, de Oliviera Rodrigues, Corrêa Gomes, & Pinto, 1997). Other parasites with similar ova occasionally reported in New World nonhuman primate species are *Physaloptera dilatata* and *Longistriata dubia*. However, Ortlepp (1922) describes *P. dilatata* eggs as oval, thick-shelled, and measuring on average 39 × 27 μ, and Vicente et al. (1997) and Gibbons and Kumar (1980) describe *L. dubia* as having thin-shelled ova measuring 62–79 × 31–41 μ. *P. dilatata* eggs are not ellipsoidal and are smaller than the ova found in the current study and *L. dubia* eggs are larger and with a thinner shell compared with the ova found in the current study. Hence, the ova found are most likely *Trypanoxyuris spp.* and/or *Trichospirura leptostoma*.
F	Dicrocoeliidae ova	Eggs are ovoid, golden-brown with a thick shell and operculum. Based on ova morphology and size the suspect species is *Athesmia foxi = heterolecithoides* (Cogswell, 2007; Thatcher & Porter, 1968).
G	Rhabditoidea ova	Eggs are ellipsoidal, with a smooth thin shell, and larvated. Suspect genus *Strongyloides*, possibly *S. cebus* (Cogswell, 2007; Conga et al., 2014; Guerrero et al., 2012; Mati, Junior, Pinto, & de Melo, 2013; Parr, Fedigan, & Kutz, 2013; Stone et al., 2016).
H	Large larvated ova (*Primasubulura*)	Eggs are large, globular, with a thick irregular transparent shell and embryonated. Ova morphology is characteristic for *Primasubulura spp.* Possibly *P. jacchi* or *P. distans* (Rocha, 2014; Tavela et al., 2013; Thatcher and Porter, 1968; Vicente et al., 1997).
I	Acanthocephala ova (*Prosthenorchis* sp.)	Characteristic eggs are ovoid, brown, thick walled with three layers, the outer shell has fine reticular sculpting, contains an acanthor. Suspect species *Prosthenorchis elegans*. Other species occasionally reported in Callitrichidae is *P. lenti*, however, the ova for this species are much larger than the ones found in the current study (Cogswell, 2007; Müller, 2007; Orihel & Seibold, 1972; Thatcher & Porter, 1968).
J	Filariform larva	Translucent larvae with a very long, sometimes coiled, thin tail. Tiny notch on tip of tail, characteristic of *Strongyloides* larvae, was not observed. In addition, larvae were larger than reported *Strongyloides* rhabditiform larvae. Little (1966) describes all stages of *S. cebus* larvae which are morphologically very different from the larvae found in the tamarins.*S. cebus* larvae have a short and very muscular esophagus, something we did not observe in the larvae found in the tamarins, and a shorter tail. Moreover, *S. cebus* eggs do not hatch until they leave the body of the host and since the feces were collected immediately post defecation, chilled and within 6 hr placed in fixative, it is unlikely these larvae are *Strongyloides* spp. The morphology of the larvae found in the tamarins agree with previous descriptions of *Filariopsis barretoi* larvae in South American monkeys. Suspect genus *Filariopsis spp*, possibly *F. barretoi* (Lee, Boyce, & Orr, 1996; Orihel & Seibold, 1972; Parr et al., 2013; Stone et al., 2016).

trophically, which may be differentially impacted by anthropogenic disturbance and climate change. Worth noting, we also detected differences from previous studies of parasites in congeneric callitrichids. In northern Peru, both Müller (2007) and Wenz et al. (2009) conducted snapshot surveys on sympatric callitrichids, *S. fuscicollis* and *S. mystax*, and reported a parasite assemblage that overlaps with our findings (including *Prosthenorchis*, *Hymenolepis*, large and small spirurids, *Primasubulura*, and strongylid larvae). Phillips et al. (2004) screened a group of *S. fuscicollis* in the nearby Tambopata National Reserve and identified four parasites (*Trichuris*, *Iodamoeba*, *Entamoeba*, and an unidentified strongyle), none of which could be confirmed in our study. In this study, all samples were fixed in formalin, which is not always preferred for screening of protozoan parasites (Zajac & Conboy, 2012). Müller (2007) and Wenz et al. (2009) also recorded higher prevalence than our study for every helminth except *Prosthenorchis*, which was considerably less common. These differences could be explained to some extent by, for instance, the small sample size of four individuals in the study by Phillips et al.

TABLE 3 Average annual prevalence by host species and parasite

		Leontocebus weddelli		*Saguinus imperator*				
Class	**Parasite**	**%**	***SD***	**%**	***SD***	**Diff**	**Dispersal**	**Pathogenic**
Acanthocephala	*Prosthenorchis* sp.	85	0.04	78	0.08	0.07	Trophic	Yes
Cestoda	*Hymenolepis* or *Paratriotaenia*	44	0.02	7	0.02	0.37[a]	Trophic	Unknown
Nematoda	Unidentified ova	6	0.06	0	0	0.06	Trophic	Possibly[b]
	Primasubulura	4	0.05	7	0.08	0.03	Trophic	Unknown
	Rhabditoidea ova	16	0.08	21	0.07	0.05	Trophic	Unknown
	Gongylonematidae	15	0.09	13	0.06	0.02	Trophic	No
	Sml embryonated ova	19	0.1	39	0.04	0.2	Trophic	Unknown
	Filariform larva	43	0.11	4	0.16	0.03	Direct	Unknown
	Strongylid ova	83	0.07	76	0.22	0.07	Direct	No
Trematoda	Dicrocoeliidae	8	0.1	4	0.12	0.32[a]	Trophic	Unknown

Note: Pathogenic classification reviewed in Müller (2007) with hosts appearing to tolerate well helminthic infections in the wild.
Abbreviations: %, average prevalence across the study period; Diff, difference in average prevalence between the host species; *SD*, standard deviation.
[a]Significant differences (Fisher's exact $p < .05$).
[b]*Spirura guianensis* has been documented as pathogenic (See Group A, Table 2).

(2004), but broader differences are possibly explained by ecologically distinct sites, including a higher helminth diversity due to increased primate species diversity (11 species compared with 4). However, an additional factor could be a consequence of prior human activities (such as hunting), which increased the densities of small primate species at EBLA (Pitman, 2008; Rosin & Swamy, 2013).

Our study underscores that wild animals generally maintain multiple parasitic infections during their lives (Cox, 2001; Petney & Andrews, 1998), and that the combination of parasites may be particularly important. Of the 10 helminths documented in this study, 6 are of unknown pathogenicity, 2 are probably non-pathogenic, and 2 are known to be pathogenic (Table 2). In this study population, *Prosthenorchis* sp. (Phylum Acanthocephala) is among the most prevalent, and has been hosted by some individuals for upwards of 12 years (Erkenswick, unpublished data) despite numerous reports of high pathogenicity (King, 1993; Strait, Else, & Eberhard, 2012): the thorny-headed worms attach themselves to the intestinal mucosa of a primate host and cause inflammatory responses, obstruction of the lumen, and lesions and ulcers that lead to secondary infections or even peritonitis in the worst cases. Infections with Acanthocephala have been frequently reported in wild callitrichids (Müller, 2007; Tantalean, Gozalo, & Montoya, 1990; Wenz et al., 2009) and occasionally in other New World primates such as the Cebidae and Atelidae (King, 1993; Phillips et al., 2004; Wenz et al., 2009). This suggests that observations of particularly pathogenic parasites should be taken in the context of the broader parasite community and changes in the environment, which may be best achieved with longitudinal data collection (Haukisalmi, Henttonen, & Tenora, 1988).

Although our analysis did not identify nonrandom associations between co-infecting parasites, it is still possible that within-host parasite interactions are at play. Presence-absence infection data is less sensitive

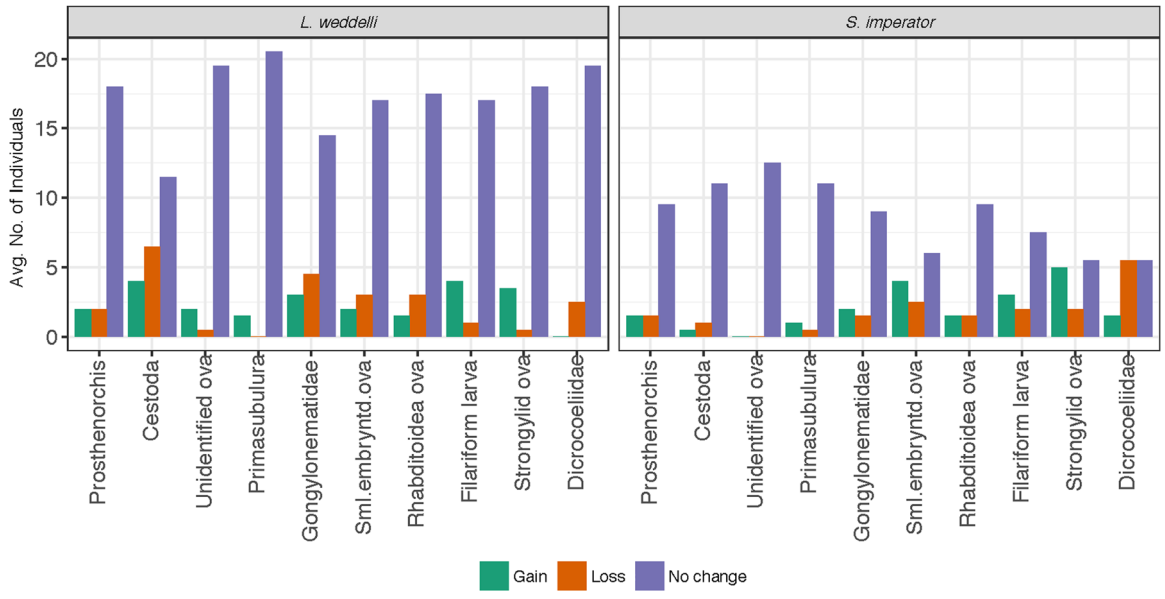


FIGURE 2 Averaged number of changes in individual infection status by host species across the study period

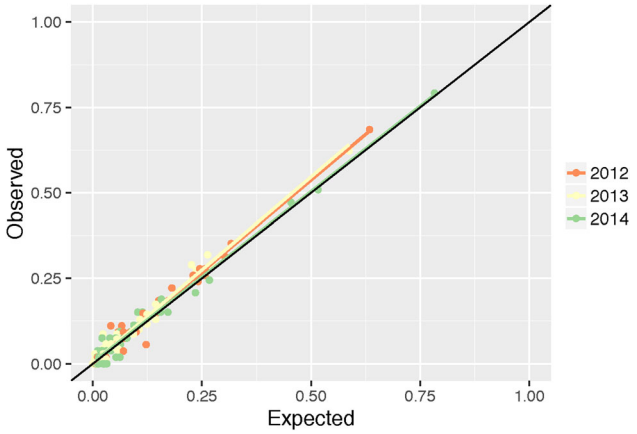


FIGURE 3 Observed versus expected prevalence of parasite co-infection. Each dot represents a unique pairwise combination of parasites

at detecting relationships than quantitative measures of parasite intensity or burden (Knowles et al., 2013; Lello, Boag, Fenton, Stevenson, & Hudson, 2004). Estimates of parasite intensity were omitted from the present study as it remains uncertain how well eggs per quantity of feces actually represents intensity of infection (Gillespie, 2006). Our hypothesis that larger groups would show higher parasite species richness was not supported. This finding is consistent with observations of blood parasites in these primates (Erkenswick, Watsa, Gozalo, et al., 2017), and may be a consequence of low group size variation (3–8 inds.). Some callitrichids can occur in larger groups, for example, *Callithrix* at 15 members (Pontes & da Cruz, 1995; Watsa et al., 2017), but it is also possible that group size and parasite diversity cannot be linked within the Callitrichidae. Alternatively, the majority of parasite taxa in this study are trophically transmitted, rather than directly transmitted, which may not be influenced by group size to the same extent.

Interpreting these findings in light of parasite mode of transmission, direct or trophic, is challenging because although the majority of the parasites detected were trophically transmitted via an intermediate host (usually an arthropod), these intermediates are unknown in most cases. While a comprehensive study of feeding ecology is a good next step in our host populations, two studies on sympatric *S. fuscicollis* and *S. mystax* (closely related to *S. imperator*) in Northern Perú agree that *S. fuscicollis* spends significantly more time foraging in the lower strata and on the ground, while the opposite was true of *S. mystax* (Heymann, Knogge, & Tirado Herrera, 2000; Smith, 2000). Smith (2000) documented distinct feeding preferences based on color and size of prey, a niche specialization, if present at our site, that might account for observed host differences in Dicrocoeliidae and *Hymenolepis* infections. This could also explain variation in parasite species richness among these hosts via differences in intermediate host encounter rates or the persistence of parasite free-living phases on the ground or in certain forest strata. Consistent with the pattern of prevalence of blood parasites in this population (Erkenswick, Watsa, Gozalo, et al., 2017), age class predicted the presence of two trophically transmitted parasites, though we obtained both positive and negative relationship estimates from our models. We suspect that differences in diet and foraging efficiency between younger and older individuals underlie different parasite encounter rates, but differences in immune status, and cumulative parasite exposure as animals age are also possibilities.

By tracking prevalence of parasitic infections over time in wild populations it is possible to infer the stability of natural parasite communities; however, longitudinal data at the level of the individual provides insights into the source, or lack thereof, of population stability

TABLE 4 Generalized linear mixed model outcomes for each parasite and parasite species richness

Parasite	Fixed effect	*B*	*SE*	Wald (χ^2)	*DF*	*p*-Value
Prosthenorchis	Intercept	0.7772	0.4963			
	Age: Subadult	−1.4417	0.5459	6.9742	1	<0.05
Cestoda	Intercept	−2.4263	0.3764			
	Species: *Simp*	−4.1473	0.8134	25.998	1	<0.05
	Age: Subadult	1.9867	0.6172	10.36	1	<0.05
Rhabditoidea ova	Intercept	−4.2509	0.5863			
	Age: Subadult	1.3999	0.5733	5.9619	1	<0.05
Filariform larva	Intercept	−1.7792	0.3472			
	Age: Subadult	−1.5110	0.6875	4.8303	1	<0.05
Strongylid ova	Intercept	0.4347	0.4500			
	Species: *Simp*	−0.8282	0.4322	3.6726	1	0.055
Dicrocoeliidae	Intercept	−4.4469	0.7193			
	Species: *Simp*	2.0681	0.4903	17.794	1	<0.05
PSR	Intercept	−0.4953	0.1528			
	Species: *Simp*	−0.6648	0.1874	12.577	1	<0.05
Sml. embryonated ova	Could not reject null models					

Note: Minimal, best-fit models for the presence of each parasite and parasite species richness (PSR). Model selection began with fixed factors host "sex," "age class," and "species," while "individual identity" and "year" were incorporated as random effects, and the number of fecal samples collected for each individual/year was included as a model offset. Infection data were insufficient to analyze the distribution of Unidentified ova, Gongylonematidae, and *Primasubulura*. *Simp* denotes *S. imperator*.

(Knowles et al., 2013). In some cases, it could even aid in identification of parasites that have negative health consequences. For example, if parasite prevalence is consistently low relative to the incidence of new infections across years, and there is little evidence that individuals clear infections, then previously infected hosts must be disappearing regularly. In this study, we report few disparities in the rate of acquisition or loss of parasites, and considered in concert with observed prevalence, we see no obvious signs of negative health consequences for these parasites. However, consideration of individual infection status should be mindful of the high correlation between redetection and parasite prevalence when using data derived from microscopic evaluations.

Molecular parasite identifications will be critical to assure data comparisons over time, geographic distance, across multiple laboratories, and to differentiate between species whose eggs or other reproductive stages are identical morphologically (Solórzano-García & de León, 2018). Microscopy-based detection of parasites can lack sensitivity (Garamszegi, 2009) and be prone to bias. For example, we observed a strong positive correlation between redetection of parasite infections across multiple samples from the same individuals of the same year and overall parasite prevalence. Moreover, it is possible that the same parasite population across two closely related hosts can exhibit higher or lower levels of subpopulation structure (Levin & Parker, 2013; McCoy, Boulinier, & Tirard, 2005), reflecting more or less cross species sharing of parasites. On the other hand, complete reliance on parasite molecular markers ignores variation in parasite life stages and the discovery of unexpected parasite infections, although the latter may be addressed if reliable universal eukaryotic markers are developed (Hadziavdic et al., 2014; Hugerth et al., 2014). Also, accessing the tools necessary to employ molecular methods is still much more difficult than those for light microscopy, though new efforts are underway to address the technology disparity in locations were primate biodiversity is highest (Watsa, Erkenswick, Pomerantz, & Prost, 2019). Hence, a dual approach of utilizing molecular and microscopy methods to screen for parasite infections is the current ideal (Valkiūnas et al., 2008).

This study provides the first description of the helminth parasite assemblage of free-ranging *S. imperator*, alongside a new comparative data set from *L. weddelli* (formerly *S. fuscicollis weddelli*; Buckner et al., 2015; Matauschek et al., 2011). Although the IUCN currently classifies both species as "least concern" (Rylands & Mittermeier, 2008), *S. imperator* has a vastly smaller species range than *L. weddelli*, and the core of its distribution in Peru overlaps with a rapidly expanding illegal gold mining hub (Asner, Llactayo, Tupayachi, & Luna, 2013), threatened by forest fragmentation and mercury contamination. *S. imperator* is currently one of the most valuable Peruvian monkeys in the illegal wildlife trade (Watsa, 2015). These factors emphasize the importance of this data set for this region and its comparative nature allows us to dig deeper into factors that could affect parasite distributions in wild primates.

In conclusion, we maintain that reliance on baseline parasite infection data may become increasingly important to understand how a fast changing physical and climatic environment is impacting natural wildlife populations. The Callitrichidae are nearly ubiquitous across South American rainforests, have a propensity to be found in sympatry with other New World primates, and some species readily exist in and around human-altered landscapes. They also evidence flexible, omnivorous diets that include autotrophs, fungi, insects, and small vertebrates. As such, regular study of the parasites from this family could serve as a potential flagship for the regional detection of ecological changes, or even environmental threats.

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DATA AVAILABILITY STATEMENT

The data that have been used in the production of this article are available upon request. For a copy of the raw data, send an inquiry email to the corresponding author.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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