Predictors of Parasitism in Wild White-Faced Capuchins (*Cebus capucinus*)

Nigel A. Parr · Linda M. Fedigan · Susan J. Kutz

Abstract Parasite infections in wildlife are influenced by many factors including host demography, behavior and physiology, climate, habitat characteristics, and parasite biology and ecology. White-faced capuchins (*Cebus capucinus*) host a suite of gastrointestinal and pulmonary parasites, yet the mechanisms affecting host susceptibility and parasite transmissibility have not been examined in this host species. We used the information-theoretic approach (Akaike's information criterion) and traditional null-hypothesis testing to determine which host characteristics, behaviors, or environmental factors affected the presence of two prevalent capuchin parasites (*Filariopsis barretoi* and *Strongyloides* sp.) as well as parasite species richness in four groups of wild capuchins from September 2007 to January 2008 and January to August 2009. Older capuchins were more likely to be infected with *Filariopsis barretoi* and had higher parasite species richness. Age-biased nematode infections may stem from age differences in capuchin behavior and physiology while high species richness likely results from long- term exposure to numerous parasite species. Infections with *Strongyloides* sp. were more likely to occur in the dry season when capuchins often descend to the forest floor to drink from terrestrial water sources, potentially increasing their risk of infection from soil-borne larvae. Capuchin behaviors were poor predictors of parasitism, as were female rank, host sex, home range size, and habitat quality. Many of our results were atypical for primate parasitology, suggesting that host–parasite interactions, and subsequently infection risk, may differ in highly seasonal habitats such as tropical dry forests where these monkeys occur.

Keywords Costa Rica · *Filariopsis* · Parasites · Parasite species richness · Platyrrhini · *Strongyloides* · Tropical dry forest

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Introduction

Parasites are important drivers of natural selection that can affect host population dynamics and social structure (Nunn and Altizer 2006). Although deaths directly attributed to parasitic infections are rarely reported in wild primates (*cf.* Huffman *et al.* 1997), parasites can affect the fitness of their hosts through a variety of mechanisms including direct energetic costs, compromising host nutrition, immune function, and fecundity, and altering reproductive opportunities and competitive ability (Coop and Holmes 1996; Dobson and Hudson 1992; Hamilton and Zuk 1982; Hudson *et al.* 2002a). Host behavior may mitigate the effects of parasitism by 1) reducing the detrimental effects of current infections on fitness and/or 2) minimizing the risk of contracting new infections (Freeland 1976; Huffman 1997; Loehle 1995). With the exception of self-medication in African apes (Dupain *et al.* 2002; Huffman 1997; Krief *et al.* 2008; McLennan and Huffman 2012), few direct responses to parasitic infections have been observed in primates. Thus, the primary focus of primate–parasite ecology research has been on the risks of contracting parasites (Nunn and Altizer 2006).

Infection risk may be influenced by host–parasite ecology, environmental conditions, and the biology/physiology of both parasite and host (Altizer *et al.* 2006; Hudson *et al.* 2002b; Loehle 1995). Parasite infections are acquired through many routes including direct transmission between hosts; contact with contaminated environmental substrates, e.g. fecal matter, soil; and indirect transmission via an intermediate host or vector. Thus, to investigate the determinants of parasite infections and parasite species richness (the number of parasite species present in an host individual or population; Bush *et al.* 1997) properly, it is advantageous to examine multiple predictor variables. For example, Stuart and Strier (1995) found that the apparent effect of host density on parasite prevalence may have been a product of differential humidity among the study sites. Thus, primate–parasite research should ideally aim to take account of the effects of demographic and life history characteristics of host populations and individuals, host behavior, as well as ecological factors that can affect the distribution and abundance of the parasites themselves, such as forest conditions and climate.

Which Factors Affect Parasite Risk?

Seasonal environmental fluctuations, specifically temperature and humidity, can affect parasite distributions because survivorship is greater for many parasites in moist environments than in arid areas (Stuart and Strier 1995). This is especially true for soil-borne parasites, such as *Strongyloides*, whose larvae may desiccate rapidly in hot, dry conditions (Hausfater and Meade 1982). Seasonal shifts in host behavior and diet may also result in seasonal differences in infection risk. Indirectly transmitted parasites infect at least one other host species before maturing in their definitive host (Poulin and Morand 2000). Infection occurs in the definitive host after they consume an intermediate or paratenic host, which is often an invertebrate. In seasonally dry forests, rainfall patterns may determine the abundance of invertebrate intermediate hosts and transmission opportunities for certain parasites (Altizer *et al.* 2006).

Infection risk for environmentally and contact-transmitted parasites increases with host density, especially for primates that form cohesive social units, because the opportunities for transmission are increased (Altizer *et al.* 2003; Anderson and May

1979; Arneberg 2001; Côté and Poulin 1995). However, large primate groups can reduce density-dependent infection risk by using a larger area, effectively reducing host density. Primate species with larger home ranges use areas less intensively and may have a reduced risk of reinfection from contact with contaminated feces (Freeland 1976), thus reducing parasite prevalence. This reduced infection risk likely influences parasite species richness in a similar manner; therefore parasite species richness should be lower in animals with larger home ranges (Bordes *et al.* 2009; Lindenfors *et al.* 2007; Nunn *et al.* 2003).

Primates living in disturbed or poor-quality habitats may have limited space, leading to range overuse and increased risk of parasite reinfection due to fecal–oral contamination (Nunn and Dokey 2006; Stuart and Strier 1995). For example, some primates living in forest fragments and on forest edges have higher parasite prevalence than those on the interior (Chapman *et al.* 2006; Gillespie and Chapman 2008). A dearth of fruit resources may force omnivorous primates to supplement their diets with more invertebrate prey and potentially put them at a higher risk of contracting indirectly transmitted parasites (Gillespie *et al.* 2005).

Nutritional, social, and physical stress can decrease immune function and reduce the host's ability to resist infection (Sapolsky 2005). In group-living primates, the relationships among dominance rank, stress levels and immunocompetence are complex (Cross *et al.* 2009). However, in primate species that exhibit stable dominance hierarchies, lower-ranking individuals may have higher stress levels because they receive more aggression from conspecifics than do dominant individuals (Janson 1985; Perry 1996; Sapolsky 2005). In addition to social stress, subordinate primates may suffer from nutritional stress and immunosuppression due to food competition (Janson 1985), especially during periods of resource scarcity.

Different host demographics, e.g., age classes, sexes, often employ differing behavioral strategies (Jones 2005) that should lead to differential infection risk. Behavior rates, specifically for behaviors that involve primates interacting in contact or close proximity, e.g., allogrooming, should affect transmission opportunities for certain directly transmitted parasite species (Loehle 1995; Stuart and Strier 1995). The most social individuals should have the greatest risk of contracting and transmitting parasites within the social group (Meyers *et al.* 2005). For parasites that require time in the external environment to develop into the infective stage, it is reasonable to expect that infection risk will be higher for hosts that more frequently come into contact with "environmental reservoirs." Individuals that routinely use multiple canopy levels may be exposed to greater parasite diversity and more terrestrial individuals may be more likely to harbor infections from free-living soil-borne parasites, e.g., *Strongyloides*, or parasites that mature in terrestrial substrates (Nunn *et al.* 2000). In addition, sex differences in diet may result in sex-biased infections (Zuk and McKean 1996). Male animals, owing to their larger body size, typically consume more food than females, which may make them more prone to ingesting contaminated food (Nunn and Altizer 2006). For parasites that use insects as intermediate or paratenic hosts, variation in individual insectivory may result in skewed infections (Nunn and Altizer 2006). Finally, hosts with long lifespans tend to have higher parasite species richness because their opportunities for infection are more numerous than in shorter-lived organisms (Poulin and Morand 2000). It follows that older individual hosts should have had more encounters with infective-stage parasites than their younger conspecifics.

Capuchin Parasite Ecology

In this study we discern which risk factors affect infections with *Filariopsis* and *Strongyloides*, and which factors affect overall parasite species richness, in primates living in a seasonally dry forest. White-faced capuchins (*Cebus capucinus*) are medium-sized Neotropical primates with diverse diets and high degrees of sociality (Fragaszy *et al.* 2004). These monkeys form stable, linear dominance hierarchies (Bergstrom and Fedigan 2010) and their behavior and diet vary with sex and age, as well as seasonally (Chapman 1987; Fragaszy 1990; Gilbert and Stouffer 1995; MacKinnon 2006; Melin *et al.* 2010; Parr *et al.* 2008; Perry 1996, 1997, 1998; Rose 1994). Therefore we expect white-faced capuchins to have high intraspecific variation in parasite risk and subsequent variation in parasite infections.

   Wild white-faced capuchins are hosts to a diverse suite of gastrointestinal and pulmonary parasites (Chinchilla *et al.* 2007, 2010; Parr *et al.* 2013). The most prevalent parasite species in the capuchins of northwestern Costa Rica are the lungworm *Filariopsis barretoi* and an intestinal nematode, *Strongyloides* sp. (Parr *et al.* 2013). The transmission route of *Filariopsis* has not yet been documented. However, *Filariopsis* belongs to the same family (Filaroididae) as other parasites, e.g., *Filaroides hirthi*, *Oslerus osleri*, whose larvae are immediately infective when shed in the feces of an infected host. Therefore, larvae of *Filariopsis* may be immediately infective as well. In contrast, *Strongyloides* requires 24–48 h in the external environment for hatched rhabditiform larvae to develop into the infective third-stage filariform stage (Lok 2007). Because infections with *Filariopsis* are more likely to be acquired by host–host contact than infections with *Strongyloides*, these two parasite species should rely on different aspects of capuchin ecology for their transmission.

Methods

Study Site and Seasonality

Data collection for this study took place in Santa Rosa Sector, Área de Conservación Guanacaste, located on the northwestern coast of Costa Rica. Santa Rosa is a 108-km^2 mixture of evergreen and semideciduous tropical dry forest located at the base of the volcanic Guanacaste Cordillera. In the decades leading up to its establishment as a national park in 1971, sections of the forest were selectively logged and cleared for cattle pasture and now exist in various stages of regeneration (Fedigan and Jack 2012). Santa Rosa experiences extreme seasonal shifts in climate typical of tropical dry forests and distinct precipitation levels characterize the three seasons: dry (January–April), early wet (May–August), and late wet (September–December).

Subjects

We collected data on four habituated groups of white-faced capuchins (*Cebus capucinus*; Table I) from September 2007 to January 2008 and January to August 2009. We have studied two of the four groups intensively since the 1980s and the other two intermittently (Fedigan and Jack 2012), so the ages of most focal individuals were

Table I White-faced capuchin study group sizes, home range sizes, and habitat quality in Sector Santa Rosa, ACG, Costa Rica from September 2007 to January 2008 and January to August 2009

Group	Group size	Home range size (ha)	Home range class	Habitat quality	Habitat quality class
CP	24–26	80	Small	0.00173	Low
EX	8–11	125	Medium	0.00240	High
GN	33–35	188	Large	0.00233	High
LV	20–23	174	Large	0.00186	Low

known. We grouped individuals into one of four age classes: infants (<1 yr), small juveniles (1–3 yr), large juveniles (3–6 yr), and adults (>6 yr) and we knew the sex of all individuals. We based female dominance ranks (high/low) on matriline rank determined using dyadic aggression and submission rates (M. Bergstrom, *pers. comm.*). Aside from that of the alpha male, we could not distinguish male ranks owing to low intrasexual interaction rates. Our data collection methodology was approved by Costa Rica's Ministerio de Ambiente y Energia and complied with protocol BI 2008–03, approved by the University of Calgary's Life and Environmental Sciences Animal Care Committee.

Parasite Collection

We attempted to collect a fecal sample from each individual in the focal population during each of the three seasons. We collected samples immediately after defecation and stored them in 15-ml Corning® plastic centrifuge tubes with screw caps. Within 12 h, we filled centrifuge tubes with 10% buffered formalin, double-sealed the samples with Parafilm® laboratory film, and stored them until we transported them back to Canada.

We analyzed 1 g of each fecal sample (N = 186) at the wildlife parasitology laboratory at the University of Calgary in Calgary, Alberta, Canada. We recovered parasites using flotation (Sheather's solution) and sedimentation (tap water), and immunofluorescence (Smith *et al.* 2007). Detailed parasite recovery methods are described in Parr *et al.* (2013).

Behavioral Data Collection

During the dry and early wet seasons (January–April and May–August 2009, respectively) we collected behavioral data on all large juvenile and adult individuals with the exception of those in GN group, for which we collected data from only two adult males, three adult females, and a large juvenile male. Collecting behavioral data on all individuals in GN group was not feasible owing to its large size. We used two methods for behavioral data collection: focal animal sampling and instantaneous point sampling.

We collected 30-min focal animal samples (Altmann 1974) on all subjects (total focal time = 139 h) during which we recorded the durations of all auto- and allo-grooming bouts. We summed the grooming durations (groom–give, groom–receive, groom–self) for each focal animal by season.

At 2.5-min intervals during each focal session we recorded instantaneous point samples (Altmann 1974). In each sample we recorded the canopy height of the focal individual on a 3-point scale (ground, lower canopy, upper canopy) and the number of individuals in contact, within 1 m, and within 5 m of the focal individual. For each proximity level we included the scores for closer distances, i.e. the number of conspecifics within 5 m included all individuals ≤5 m, ≤1 m, and in contact. Before analysis, we summed the frequencies of each canopy height and proximity scores for each focal individual by season.

Ecological Measures

We collected ranging data using a Garmin GPSMAP 76CX handheld GPS unit. We recorded the group's location on each hour and half-hour, as well as at sleep sites in the morning and evening.

We calculated home range sizes (Table I) using the adaptive local convex hulls method (Getz et al. 2007) in ArcGIS Desktop v9.2 (ESRI, Redlands, CA). Home ranges represent the 95% isopleth. For statistical analysis we assigned each group an ordinal home range size of small (<100 ha), medium (100–150) and large (150+).

We assessed habitat quality by quantifying fruit availability in each group's home range and core areas (Table I). Fruit biomass is a product of the tree's trunk diameter-at-breast-height (DBH; Peters et al. 1988) and, consequently, fruit tree area. Thus, habitats with greater proportional fruit tree area will contain more available fruit. We sampled all fruit trees >1.2 m tall, i.e., breast height, along 133, 100 m × 2 m line transects (total area = 2.66 ha) spaced evenly throughout the home ranges of the four study groups (Parr and Melin unpub. data). For each tree, we recorded the DBH and the tree species. In each study group's home range we summed the area (calculated from DBH) of all sampled fruit trees and divided the value by the size of the sampled area. We included only areas from trees with a DBH greater than the minimum DBH of the smallest tree in which we had observed the capuchins feeding (Melin et al. in press). We based habitat quality on fruit availability proportions, which we classified as low (<0.002) or high (≥0.002).

In addition to group-level ecological variables, we also investigated the effects of season. To assess parasitism at the peak of each season, and to minimize the chance of detecting residual infections from the previous season, we analyzed samples from the latter half of each season: dry (March–April), early wet (July–August), and late wet (November–December).

Statistical Analyses

Our analyses involved a combination of an information-theoretic approach and traditional null hypothesis testing. We used three data sets for the analyses: 1) the main data set ($N = 186$ samples), which included data on all capuchins in the study; 2) the "dominance" subset ($N = 61$), which included only data from adult female capuchins; and 3) the "behavior" subset ($N = 74$), which included data from the adult and large juvenile capuchins on which we conducted behavioral sampling. We used the main data set to model the effects of host age, host sex, season, home range size, and habitat quality on infection presences and parasite species richness. We used the dominance

subset to examine the effect of female social rank and the behavioral subset to examine the effects of grooming rates, canopy height use, and proximity scores. Each data set included up to three entries per individual, one per season. Thus, we included "individual" and "social group" as random effects in all models. We performed all statistical analyses using R (R Core Team 2013) and significance, where applicable, was set at $P < 0.05$.

We could not statistically analyze the other six parasites that we recovered, e.g., *Giardia* sp., due to their low prevalence in the host population (Parr *et al.* 2013). In addition, we opted to test the effects of the predictor variables on parasite presence but not on prevalence, as prevalence is a group-level measurement and statistical analyses were not feasible with only four study groups.

Ecological and Demographic Factors For each dependent variable (*Filariopsis barretoi* presence, *Strongyloides* sp. presence, parasite species richness) we constructed and contrasted generalized linear mixed models that included combinations of one, two, and three of the predictor variables (host age, host sex, season, home range size, habitat quality). The models of *Filariopsis* and *Strongyloides* were fit to binomial distributions while the parasite species richness models were fit to Poisson distributions. We used Akaike's information criterion (AIC; Akaike 1974) to determine the relative strength of each candidate model. To account for small sample size we computed Akaike's second-order criterion (AIC$_c$) for each model, as described in Burnham and Anderson (2002). For each model we also computed the Akaike weight (ω_i). Candidate models were then ranked based on AIC$_c$ and ω_i, with the "best" models being those with the lowest AIC$_c$ and highest ω_i. Competing models within 2 AIC$_c$ units of the best model were considered equally strong, except for cases where the models had similar maximized log-likelihood values and differed from the best model by a single parameter (Burnham and Anderson 2002).

Female Dominance and Behavioral Factors We constructed separate generalized linear mixed models to test the effects of female hierarchical rank, grooming rates, canopy height use, and proximity scores on presence of infection with *Filariopsis barretoi*, presence of infection with *Strongyloides* sp., and parasite species richness. As with the AIC models, we specified binomial distribution for the parasite presence models and Poisson distribution for the species richness models. In the hierarchical rank models we included season, home range size, and habitat quality as covariates. We included "number of point samples" as a covariate for the canopy height and proximity scores models while we included "total focal time" as a covariate in the grooming models.

Results

Parasite Species Richness

In addition to *Filariopsis barretoi* and *Strongyloides* sp., we recovered six other parasite species from the 186 samples (Parr *et al.* 2013). Capuchin individuals were

infected with a mean ± SD of 1.29 ± 0.83 (range 0–4) parasite species and species richness increased monotonically from infant samples to those of small juveniles, to large juveniles, and finally to adults (Table II). The best AIC-selected model included host age as its single predictor variable, and host age was present in all of the top five models (Table IIIA). Thus, it is clear that host age plays an important role in capuchin parasite communities. Neither female social rank ($Z = 0.028$, $P = 0.978$) nor behavior (Table IV) affected parasite species richness.

Filariopsis Barretoi

One hundred and thirty-one of the 186 samples tested positive for *Filariopsis barretoi* (Table II), making it the most common fecal parasite in capuchins at Santa Rosa. The best AIC-selected models for *Filariopsis barretoi* infections (Table IIIB) all included host age as a predictor, suggesting that age is the primary factor influencing *Filariopsis* infections. Infections increased monotonically with age class. *Filariopsis barretoi* infections were not significantly affected by female social rank ($Z = -1.19$, $P = 0.234$) or by behavior (Table IV).

Strongyloides sp.

Strongyloides sp. was recovered from 70 of the 186 samples and the competing AIC-selected models all included season (Table IIIC). The most parsimonious model was the one solely containing *Season*. Thus, among the five predictor variables, season was the only one that strongly influenced *Strongyloides* sp. infections. Infections were most likely to occur in the dry season and least likely to occur in the late wet season (Table II). *Strongyloides* infections were not affected by female social rank ($Z = 1.19$, $P = 0.234$) or by behavior (Table IV).

Discussion

Host-intrinsic factors and seasonality affected parasite infections and species richness in white-faced capuchins. *Filariopsis barretoi* infections and parasite species richness increased monotonically with age class, whereas *Strongyloides* sp. infections were most likely to occur in the dry season. Many of the ecological and behavioral measures that we analyzed were poor predictors of parasitism.

Filariopsis Barretoi

Filariopsis barretoi infections in white-faced capuchins are strongly influenced by host age. The host-prevalence curve shows a continuous increase in infections with *Filariopsis* from the infant to adult stages, which is uncommon in primate parasitology; in most primate species, parasite prevalence typically decreases with host age. For example, prevalence of *Strongyloides* spp. was highest in young Japanese macaques (Gotoh 2000; Horii *et al*. 1982) and olive baboons (Müller-Graf *et al*. 1996) and these studies provide empirical evidence for adaptive immune function in primates. Our study supports an alternative scenario: that capuchins lack the innate immune function

Table II Parasite prevalence (%) and species richness (mean ± SD) in white-faced capuchins from Sector Santa Rosa, ACG, Costa Rica, September 2007 to January 2008 and January to August 2009

	All	Sex		Age class				Season			Home range size			Habitat quality	
		Male	Female	I	SJ	LJ	A	Dry	Early wet	Late wet	Small	Medium	Large	Low	High
Number of samples	186	75	111	3	20	56	107	73	68	45	47	18	121	90	96
Nematoda (%)															
Filariopsis barretoi	70	61	77	0	30	64	83	77	63	71	74	78	68	70	71
Strongyloides sp.	38	29	43	0	25	41	39	53	34	18	45	28	36	40	35
Unidentified subulurid	5	1	8	33	5	9	3	7	3	7	11	6	3	8	3
Unidentified spirurid	2	3	2	0	0	2	3	1	3	2	0	0	3	1	3
Unidentified strongylid	1	0	1	0	0	0	1	1	0	0	0	0	1	0	1
Cestoda (%)															
Unidentified cestode	1	0	1	0	0	0	1	0	1	0	0	0	1	0	1
Acanthocephala (%)															
Prosthenorchis sp.	1	3	0	0	0	2	1	1	1	0	0	0	2	1	1
Protozoa (%)															
Giardia sp.	2	3	1	0	0	5	0	1	0	4	2	0	2	1	2
Parasite species richness	1.29± 0.83	1.17± 0.94	1.37± 0.73	0.33± 0.58	0.62± 0.80	1.30± 0.82	1.45± 0.76	1.44± 0.75	1.25± 0.89	1.11± 0.83	1.36± 0.76	1.22± 0.94	1.27± 0.84	1.33± 0.78	1.25± 0.87

I = infant, SJ = small juvenile, LJ = large juvenile, A = adult.

Table III Competitive generalized linear mixed models comparing ecological and demographic parameters that affect parasite species richness (A), *Filariopsis barretoi* infections (B), and *Strongyloides* sp. infections (C) in white-faced capuchins (*Cebus capucinus*) from Sector Santa Rosa, ACG, Costa Rica, September 2007 to January 2008 and January to August 2009

	Log(L)	K	AIC$_c$	Δ$_i$	ω$_i$	ω$_1$/ω$_i$
A. Parasite species richness						
Model	Log(L)	K	AIC$_c$	Δ$_i$	ω$_i$	ω$_1$/ω$_i$
AgeClass	−65.75	1	133.52	0.00	0.3342	1.0000
AgeClass + Sex	−65.60	2	135.27	1.74	0.1398	2.3915
AgeClass + Season	−65.70	2	135.47	1.94	0.1265	2.6430
AgeClass + HabitatQuality	−65.70	2	135.47	1.94	0.1265	2.6430
GLOBAL (All variables)	*−66.50*	*5*	*143.33*	*9.81*	*0.0025*	*135.0705*
B. *Filariopsis barretoi*						
Model	Log(L)	K	AIC$_c$	Δ$_i$	ω$_i$	ω$_1$/ω$_i$
AgeClass + Season	−100.60	2	205.27	0.00	0.2404	1.0000
AgeClass + Sex + Season	−99.85	3	205.83	0.57	0.1812	1.3273
AgeClass	−102.20	1	206.42	1.16	0.1349	1.7826
AgeClass + Sex	−101.25	2	206.57	1.30	0.1255	1.9155
GLOBAL (All variables)	*−100.40*	*5*	*211.13*	*5.87*	*0.0128*	*18.8004*
C. *Strongyloides* sp.						
Model	Log(L)	K	AIC$_c$	Δ$_i$	ω$_i$	ω$_1$/ω$_i$
Sex + Season	−115.55	2	235.17	0.00	0.2796	1.0000
AgeClass + Sex + Season	−114.85	3	235.83	0.67	0.2004	1.3954
Season	−117.40	1	236.82	1.66	0.1222	2.2889
Sex + Season + HabitatQuality	−115.50	3	237.13	1.97	0.1046	2.6729
AgeClass + Season	−116.55	2	237.17	2.00	0.1029	2.7183
GLOBAL (All variables)	*−115.40*	*5*	*241.13*	*5.97*	*0.0141*	*19.7643*

Models are ranked by Akaike's second-order criterion (AIC$_c$) and are presented with the maximized log-likelihood (Log(L)), number of parameters (K), AIC difference (Δ$_i$), Akaike weight (ω$_i$), and evidence ratio (ω$_1$/ω$_i$).

to combat infections with *Filariopsis* and rarely acquire complete immunity as they age (Wilson *et al*. 2002). However, a number of capuchins were infection-free during the early wet season despite having infections only months earlier during the dry season. Thus, infections with *Filariopsis* are not perpetually maintained and capuchin immune defenses do appear to play some role in mitigating infections.

If immune function cannot explain the age-biased infections we observed, other factors may have affected differential infection risk among capuchin age classes. For example, young capuchins allo-groom less often than adults (Parr, *pers. obs*.). Despite being an effective defence mechanism against ectoparasitosis (Altizer *et al*. 2003; Møller *et al*. 1993), grooming has been proposed as a facilitative behavior for endoparasite transmission via the fecal–oral route (MacIntosh *et al*. 2012; Nunn and Altizer 2006). Although grooming rates did not predict infection with *Filariopsis* in our study, we did not collect behavioral data on infants and small juveniles. Thus, possible age variations in grooming behavior would not have been fully revealed by our analysis but may affect *Filariopsis* transmission nonetheless. However, the effects of grooming

Table IV Results of generalized linear mixed models examining the effects of white-faced capuchin (*Cebus capucinus*) behavior on *Filariopsis barretoi* and *Strongyloides* sp. infections, as well as parasite species richness, in Sector Santa Rosa, ACG, Costa Rica from September 2007 to January 2008 and January to August 2009

	Filariopsis barretoi		Strongyloides sp.		Parasite species richness	
	Z	P	Z	P	Z	P
Grooming rates						
Groom–give	0.123	0.902	−0.188	0.851	−0.556	0.578
Groom–receive	0.947	0.344	−0.842	0.400	0.296	0.767
Self-groom	−0.009	0.993	1.340	0.180	0.338	0.735
Canopy use						
Ground	−0.833	0.405	−0.240	0.811	−0.552	0.581
Middle canopy	0.806	0.420	−1.220	0.223	−1.184	0.237
Upper canopy	0.336	0.737	−1.625	0.104	−1.273	0.203
Proximity scores						
Contact	1.158	0.100	−0.111	0.912	0.060	0.952
<1 m	0.489	0.625	0.580	0.562	0.218	0.828
<5 m	−0.688	0.492	0.082	0.935	0.062	0.951

on lungworm transmission cannot be investigated further until more is known about the biology and life cycle of *Filariopsis barretoi*.

Strongyloides sp.

Despite increased nematode survivorship in warm, humid climates (Hausfater and Meade 1982), infections with *Strongyloides* sp. in Sector Santa Rosa were more common in the dry season than in the wet seasons. Although prevalence with *Strongyloides* sp. was significantly higher in the dry season for black howlers (Stoner and González Di Pierro 2006), this pattern is contrary to what has generally been observed in other primate species. For example, *Strongyloides fuelleborni* prevalence increased during the warm, humid summer months and decreased during the winter in Japanese macaques (Horii *et al.* 1982). Other primate studies have shown no seasonality to *Strongyloides* infections (Huffman *et al.* 1997; Petrželková *et al.* 2010).

The dry season bias we observed could not be explained by host variation in terrestriality. However, we collected behavioral data only in the dry and early wet seasons, not in the late wet season when infections with *Strongyloides* were least common. Therefore, any seasonal variation in infections with *Strongyloides* due to behavior, i.e., canopy height usage, may not have been adequately represented in our study.

Alternatively, risk of infection with *Strongyloides* may not be a function of *when* capuchins spend time on the ground, but *where*. A lack of available rainfall on leaves and in tree holes during the dry season forces capuchins to the ground to find drinking water (Freese 1978). During these dry months, capuchins congregate daily around limited and widely spaced waterholes (Chapman 1988). *Strongyloides* is able to bypass oral infection by burrowing directly into the host's skin (Cogswell 2007), so if densities of

Strongyloides are high in the moist soil surrounding terrestrial water holes, infection risk in these areas could be substantial. For black howlers, higher protozoan prevalence in the dry season was attributed to increased drinking from tree holes in the dry season (Stoner and González Di Pierro 2006). Therefore, areas containing contaminated water pose a threat not only to capuchins, but also to other species that share these few water sources.

Seasonality may also *indirectly* alter a host's parasite risk by causing environmental, physiological, and behavioral changes that can affect host health. For example, food availability fluctuates dramatically between the seasons at Sector Santa Rosa. Fruit availability is lowest during the latter half of the late wet season and the first half of the dry season (November–February; Melin 2011). During this time capuchins invest more time in invertebrate foraging, often on the forest floor. Increased contact with the terrestrial substrates should increase capuchin susceptibility to soil-borne parasites and may contribute to increased infections with *Strongyloides* during the dry season. Nutritional stress caused by decreasing food availability can lead to suppressed immune function and increased susceptibility to parasitic diseases (Chapman *et al.* 2005). Since the peak of *Strongyloides* infections followed the period of fruit scarcity in Santa Rosa, it is possible that nutritional stress affected capuchin resistance to this parasite. Food scarcity led to decreased health of chimpanzees in Gombe National Park, Tanzania and may have resulted in higher *Strongyloides fuelleborni* prevalence during the dry season when fruit availability was lowest (Bakuza and Nkwengulila 2009). Similarly, directly transmitted nematode infection intensities were higher for chacma baboons during the winter when nutritional stress was most likely (Appleton and Henzi 1993). Drier environments also tend to have hotter temperatures. In Santa Rosa, average daily temperatures increase by up to five degrees from the wet to the dry seasons (Campos and Fedigan 2009). Therefore, thermoregulatory costs should differ seasonally and immune function may be further compromised as a result of temperature stress on the host.

Parasite Species Richness

Our data strongly supported host age as an important factor affecting parasite species richness in white-faced capuchins. Species richness, like infections with *Filariopsis barretoi*, increased with age class suggesting species richness is a function of exposure (Cross *et al.* 2009). The majority of parasites we recovered were not present in individuals <3 yr of age (small juveniles and infants) and all parasite species were found in individuals >3. For capuchins, it appears that older individuals have exposure to a wider range of parasites and that by the age of 3, capuchins have been exposed to the entire spectrum of parasites. Parasite species richness has been well documented as a function of host age; primate species with longer lifespans have significantly higher species richness (Nunn *et al.* 2003) and this pattern could be expected within a single species or population as well.

In addition to allogrooming less than their adult counterparts, young capuchins (<3 yr of age) spend less time on the forest floor (Fragaszy 1990; Gilbert and Stouffer 1995) and consume fewer large insects, e.g., cockroaches (MacKinnon 2006). Thus, they should be less likely to harbor infections of contact, environmentally and indirectly transmitted parasites. The lesser risk of contracting parasites across all transmission routes may explain the lower parasite species richness in younger capuchins.

Adult capuchins should have a greater risk of infection if infective stage parasites contaminate food (Nunn and Altizer 2006). Larger individuals have greater metabolic demands and must consume greater amounts of food than younger, smaller individuals. Greater parasite diversity in older, larger reef fish was attributed to these greater nutritional requirements, which resulted in the more frequent consumption of intermediate hosts (Lo *et al.* 1998). Larger individuals should also be able to support a larger parasite community, as they represent a "larger parasite habitat" (Wilson *et al.* 2002). This relationship between host body size and parasite species richness is consistent across the order Primates (Nunn *et al.* 2003).

Conclusions

While the relationship between parasite species richness and capuchin age is consistent with previous findings in primate parasitology, the patterns we revealed for infections with *Filariopsis barretoi* and *Strongyloides* sp. are markedly different than those seen in other studies of primates. Primates living in highly seasonal environments such as tropical dry forests may face different challenges, e.g., water availability, than rain forest primates and, thus, the infection patterns we observed may result from habitat-specific interactions among primate behavioral ecology, climate, and parasite risk.

References

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control, 19*(6), 716–723.

Altizer, S., Nunn, C. L., Thrall, P. H., Gittleman, J. L., Antonovics, J., Cunningham, A. A., et al. (2003). Social organization and parasite risk in mammals: integrating theory and empirical studies. *Annual Review of Ecology, Evolution, and Systematics, 34*, 517–547.

Altizer, S., Dobson, A., Hosseini, P., Hudson, P., Pascual, M., & Rohani, P. (2006). Seasonality and the dynamics of infectious diseases. *Ecology Letters, 9*(4), 467–484.

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour, 49*(3/4), 227–267.

Anderson, R. M., & May, R. M. (1979). Population biology of infectious diseases: Part I. *Nature, 280*(5721), 361–367.

Appleton, C. C., & Henzi, S. P. (1993). Environmental correlates of gastrointestinal parasitism in montane and lowland baboons in Natal, South Africa. *International Journal of Primatology, 14*(4), 623–635.

Arneberg, P. (2001). An ecological law and its macroecological consequences as revealed by studies of relationships between host densities and parasite prevalence. *Ecography, 24*(3), 352–358.

Bakuza, J., & Nkwengulila, G. (2009). Variation over time in parasite prevalence among free-ranging chimpanzees at Gombe National Park, Tanzania. *International Journal of Primatology, 30*(1), 43–53.

Bergstrom, M. L., & Fedigan, L. M. (2010). Dominance among female white-faced capuchin monkeys (*Cebus capucinus*): Hierarchical linearity, nepotism, strength and stability. *Behaviour, 147*(7), 899–931.

Bordes, F. r., Morand, S., Kelt, D. A., & Vuren, D. H. V. (2009). Home range and parasite diversity in mammals. *The American Naturalist, 173*(4), 467–474.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York: Springer Science+Business Media.

Bush, A. O., Lafferty, K. D., Lotz, J. M., & Shostak, A. W. (1997). Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *Journal of Parasitology, 83*(4), 575–583.

Campos, F. A., & Fedigan, L. M. (2009). Behavioral adaptations to heat stress and water scarcity in white-faced capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica. *American Journal of Physical Anthropology, 138*(4), 101–111.

Chapman, C. (1987). Flexibility in diets of three species of Costa Rican primates. *Folia Primatologica, 49*, 90–105.

Chapman, C. (1988). Patterns of foraging and range use by three species of Neotropical primates. *Primates, 29*(2), 177–194.

Chapman, C. A., Gillespie, T. R., & Goldberg, T. L. (2005). Primates and the ecology of their infectious diseases: how will anthropogenic change affect host-parasite interactions? *Evolutionary Anthropology, 14*(4), 134–144.

Chapman, C. A., Speirs, M. L., Gillespie, T. R., Holland, T., & Austad, K. M. (2006). Life on the edge: gastrointestinal parasites from the forest edge and interior primate groups. *American Journal of Primatology, 68*, 397–409.

Chinchilla, M., Guerrero, O. M., Gutiérrez-Espeleta, G. A., Sánchez, R., & Campos, I. V. (2007). Parásitos en monos carablanca *Cebus capucinus* (Primates: Cebidae) de Costa Rica. *Parasitología Latinoamericana, 62*(3–4), 170–175.

Chinchilla, M., Urbani, B., Valerio, I., & Vanegas, J. C. (2010). Parasitosis intestinal en monos capuchinos cariblancos Cebus capucinus (Primates: Cebidae) de un área protegida en la provincia de Limón, noreste de Costa Rica. *Revista de Biología Tropical, 58*(4), 1335–1346.

Cogswell, F. (2007). Parasites of non-human primates. In D. G. Baker (Ed.), *Flynn's parasites of laboratory animals* (2nd ed., pp. 693–743). Ames: Blackwell.

Coop, R. L., & Holmes, P. H. (1996). Nutrition and parasite interaction. *International Journal for Parasitology, 26*(8/9), 951–962.

Côté, I. M., & Poulin, R. (1995). Parasitism and group size in social animals: a meta-analysis. *Behavioral Ecology, 6*(2), 159–165.

Cross, P. C., Drewe, J., Patrek, V., Pearce, G., Samuel, M. D., & Delahay, R. J. (2009). Wildlife population structure and parasite transmission: implications for disease management. In R. J. Delahay, G. C. Smith, & M. R. Hutchings (Eds.), *Management of disease in wild mammals* (pp. 9–29). Tokyo: Springer Science+Business Media.

Dobson, A. P., & Hudson, P. J. (1992). Regulation and stability of a free-living host-parasite system: *Trichostrongylus tenuis* in red grouse. II. Population models. *Journal of Animal Ecology, 61*(2), 487–498.

Dupain, J., Van Elsacker, L., Nell, C., Garcia, P., Ponce, F., & Huffman, M. A. (2002). New evidence for leaf swallowing and *Oesophagostomum* infection in Bonobos (*Pan paniscus*). *International Journal of Primatology, 23*(5), 1053–1062.

Fedigan, L., & Jack, K. (2012). Tracking neotropical monkeys in Santa Rosa: lessons from a regenerating Costa Rican dry forest. In P. M. Kappeler & D. P. Watts (Eds.), *Long-term field studies of pgrimates* (pp. 165–184). Berlin and Heidelberg: Springer Science+Business Media.

Fragaszy, D. M. (1990). Sex and age differences in the organization of behavior in wedge-capped capuchins, *Cebus olivaceus. Behavioral Ecology, 1*(1), 81–94.

Fragaszy, D. M., Visalberghi, E., & Fedigan, L. M. (2004). *The complete capuchin: The biology of the genus Cebus*. Cambridge: Cambridge University Press.

Freeland, W. J. (1976). Pathogens and the evolution of primate sociality. *Biotropica, 8*(1), 12–24.

Freese, C. H. (1978). The behavior of white-faced capuchins (*Cebus capucinus*) at a dry-season waterhole. *Primates, 19*(2), 275–286.

Getz, W. M., Fortmann-Roe, S., Cross, P. C., Lyons, A. J., Ryan, S. J., & Wilmers, C. C. (2007). LoCoH: Nonparameteric kernel methods for constructing home ranges and utilizaton distributions. *PLoS ONE, 2*(2), e207.

Gilbert, K., & Stouffer, P. (1995). Variation in substrate use by white-faced capuchins. *Human Evolution, 10*(4), 265–269.

Gillespie, T. R., & Chapman, C. A. (2008). Forest fragmentation, the decline of an endangered primate, and changes in host–parasite interactions relative to an unfragmented forest. *American Journal of Primatology, 70*(3), 222–230.

Gillespie, T. R., Chapman, C. A., & Grenier, E. C. (2005). Effects of logging on gastrointestinal parasite infections and infection risk in African primates. *Journal of Applied Ecology, 42*, 699–707.

Gotoh, S. (2000). Regional differences in the infection of wild Japanese macaques by gastrointestinal helminth parasites. *Primates, 41*(3), 291–298.

Hamilton, W. D., & Zuk, M. (1982). Heritable true fitness and bright birds: a role for parasites? *Science, 218*(4570), 384–387.

Hausfater, G., & Meade, B. J. (1982). Alternation of sleeping groves by yellow baboons (*Papio cynocephalus*) as a strategy for parasite avoidance. *Primates, 23*(2), 287–297.

Horii, Y., Imada, I., Yanagida, T., Usui, M., & Mori, A. (1982). Parasite changes and their influence on the body weight of Japanese monkeys (*Macaca fuscata fuscata*) of the Koshima troop. *Primates, 23*(3), 416–431.

Hudson, P. J., Dobson, A. P., & Newborn, D. (2002a). Parasitic worms and population cycles of red grouse. In A. Berryman (Ed.), *Population cycles*. New York: Oxford University Press.

Hudson, P. J., Rizzoli, A., Grenfell, B. T., Heesterbeek, H., & Dobson, A. P. (Eds.). (2002b). *The ecology of wildlife diseases*. New York: Oxford University Press.

Huffman, M. A. (1997). Current evidence for self-medication in primates: a multidisciplinary perspective. *American Journal of Physical Anthropology, 104*(S25), 171–200.

Huffman, M. A., Gotoh, S., Turner, L. A., Hamai, M., & Toshida, K. (1997). Seasonal trends in intestinal nematode infection and medicinal plant use among chimpanzees in the Mahale mountains, Tanzania. *Primates, 38*(2), 111–125.

Janson, C. (1985). Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology and Sociobiology, 18*(2), 125–138.

Jones, C. (2005). *Behavioral flexibility in primates: Causes and consequences*. New York: Springer Science+ Business Media.

Krief, S., Jamart, A., Mahé, S., Leendertz, F. H., Mätz-Rensing, K., Crespeau, F., et al. (2008). Clinical and pathologic manifestation of oesophagostomosis in African great apes: does self-medication in wild apes influence disease progression? *Journal of Medical Primatology, 37*(4), 188–195.

Lindenfors, P., Nunn, C. L., Jones, K. E., Cunningham, A. A., Sechrest, W., & Gittleman, J. L. (2007). Parasite species richness in carnivores: effects of host body mass, latitude, geographical range and population density. *Global Ecology and Biogeography, 16*(4), 496–509.

Lo, C. M., Morand, S., & Galzin, R. (1998). Parasite diversity/host age and size relationship in three coral-reef fishes from French Polynesia. *International Journal for Parasitology, 28*(11), 1695–1708.

Loehle, C. (1995). Social barriers to pathogen transmission in wild animal populations. *Ecology, 76*(2), 326–335.

Lok, J. B. (2007). *Strongyloides stercoralis*: a model for translational research on parasitic nematode biology. In *WormBook*: *The online review of* C. elegans *biology*. Available at: http://www.ncbi.nlm.nih.gov/books/NBK19663/.

MacIntosh, A. J. J., Jacobs, A., Garcia, C., Shimizu, K., Mouri, K., Huffman, M. A., et al. (2012). Monkeys in the middle: parasite transmission through the social network of a wild primate. *PLoS ONE, 7*(12), e51144.

MacKinnon, K. C. (2006). Food choice by juvenile capuchin monkeys (*Cebus capucinus*) in a tropical dry forest. In A. Estrada, P. A. Garber, M. S. M. Pavelka, & L. Luecke (Eds.), *New perspectives in the study of Mesoamerican primates: Distribution, ecology, behavior, and conservation* (pp. 349–365). New York: Springer Science+Business Media.

McLennan, M. R., & Huffman, M. A. (2012). High frequency of leaf swallowing and its relationship to intestinal parasite expulsion in "village" chimpanzees at Bulindi, Uganda. *American Journal of Primatology, 74*(7), 642–650.

Melin, A. D. (2011). *Polymorphic colour vision and foraging in white-faced capuchins: Insights from field research and simulations of monkey vision*. Unpublished Ph.D. Dissertation, University of Calgary.

Melin, A. D., Fedigan, L. M., Young, H. C., & Kawamura, S. (2010). Can color vision variation explain sex differences in invertebrate foraging by capuchin monkeys? *Current Zoology, 56*(3), 300–312.

Melin, A. D., Hiramatsu, C., Parr, N., Matsushita, Y., Kawamura, S., & Fedigan, L. M. (in press). The behavioural ecology of colour vision: frugivory as a selective force. *International Journal of Primatology*.

Meyers, L. A., Pourbohloul, B., Newman, M. E. J., Skowronski, D. M., & Brunham, R. C. (2005). Network theory and SARS: predicting outbreak diversity. *Journal of Theoretical Biology, 232*(1), 71–81.

Møller, A. P., Dufva, R., & Allander, K. (1993). Parasites and the evolution of host social behavior. *Advances in the Study of Behavior, 22*, 65–102.

Müller-Graf, C. D. M., Collins, D. A., & Woolhouse, M. E. J. (1996). Intestinal parasite burden in five troops of olive baboons (*Papio cynocephalus anubis*) in Gombe Stream National Park, Tanzania. *Parasitology, 112*(5), 489–497.

Nunn, C. L., & Altizer, S. (2006). *Infectious diseases in primates*. New York: Oxford University Press.

Nunn, C. L., & Dokey, A. T.-W. (2006). Ranging patterns and parasitism in primates. *Biology Letters, 2*(3), 351–354.

Nunn, C. L., Gittleman, J. L., & Antonovics, J. (2000). Promiscuity and the primate immune system. *Science, 290*(5494), 1168–1170.

Nunn, C. L., Altizer, S., Jones, K. E., & Sechrest, W. (2003). Comparative tests of parasite species richness in primates. *The American Naturalist, 162*(5), 597–614.

Parr, N., Campos, F., Childers, A., Fedigan, L., & Jack, K. (2008). Dry season ranging behaviour and intergroup relations in white-faced capuchins (*Cebus capucinus*) at Santa Rosa National Park, Costa Rica [abstract]. *American Journal of Primatology, 70*(S1), 53.

Parr, N. A., Fedigan, L. M., & Kutz, S. J. (2013). A coprological survey of parasites in white-faced capuchins (*Cebus capucinus*) from Sector Santa Rosa, ACG, Costa Rica. *Folia Primatologica, 84*(2), 102–114.

Perry, S. (1996). Female-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. *American Journal of Primatology, 40*(2), 167–182.

Perry, S. (1997). Male–female social relationships in wild white-faced capuchins (*Cebus capucinus*). *Behaviour, 134*(7/8), 477–510.

Perry, S. (1998). Male-male social relationships in wild white-faced capuchins, *Cebus capucinus. Behaviour, 135*(2), 139–172.

Peters, R. H., Cloutier, S., Dubé, D., Evans, A., Hastings, P., Kaiser, H., et al. (1988). The allometry of the weight of fruit on trees and shrubs in Barbados. *Oecologia, 74*(4), 612–616.

Petrželková, K. J., Hasegawa, H., Appleton, C. C., Huffman, M. A., Archer, C. E., Moscovice, L. R., et al. (2010). Gastrointestinal parasites of the chimpanzee population introduced onto Rubondo Island National Park, Tanzania. *American Journal of Primatology, 72*, 307–316.

Poulin, R., & Morand, S. (2000). The diversity of parasites. *Quarterly Review of Biology, 75*(3), 277–293.

R Core Team. (2013). *R: A language and environment for statistical computing. (Version 3.0.1)*. Vienna: R Foundation for Statistical Computing.

Rose, L. (1994). Sex differences in diet and foraging behavior in white-faced capuchins (*Cebus capucinus*). *International Journal of Primatology, 15*(1), 95–114.

Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. *Science, 308*, 648–652.

Smith, P. H., Wiles, S. E., Malone, J. B., Jr., & Monahan, C. M. (2007). Collection, preservation, and diagnostic methods. In D. G. Baker (Ed.), *Flynn's parasites of laboratory animals* (2nd ed.). Ames, IA: Blackwell.

Stoner, K. E., & González Di Pierro, A. M. (2006). Intestinal parasitic infections in *Alouatta pigra* in tropical rainforest in Lacandona, Chiapas, Mexico: implications for behavioral ecology and conservation. In A. Estrada, P. A. Garber, M. Pavelka, & L. Luecke (Eds.), *New perspectives in the study of Mesoamerican primates* (pp. 215–240). New York: Springer Science+Business Media.

Stuart, M. D., & Strier, K. B. (1995). Primates and parasites: a case for a multidisciplinary approach. *International Journal of Primatology, 16*(4), 577–593.

Wilson, K., Bjørnstad, O. N., Dobson, A. P., Merler, S., Poglayen, G., Randolph, S. E., et al. (2002). Heterogeneities in macroparasite infections: patterns and processes. In P. Hudson, A. Rizzoli, B. T. Grenfell, H. Heesterbeek, & A. P. Dobson (Eds.), *The ecology of wildlife diseases* (pp. 6–44). New York: Oxford University Press.

Zuk, M., & McKean, K. A. (1996). Sex differences in parasite infections: patterns and processes. *International Journal for Parasitology, 26*(10), 1009–1024.