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Verreaux's sifaka (*Propithecus verreauxi*) and ring-tailed lemur (*Lemur catta*) endoparasitism at the Bezà Mahafaly Special Reserve

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ABSTRACT

As hosts, primate behavior is responsible for parasite avoidance and elimination as well as parasite acquisition and transmission among conspecifics. Thus, host behavior is largely responsible for the distribution of parasites in free-ranging populations. We examined the importance of host behavior in acquiring and avoiding parasites that use oral routes by comparing the behavior of sympatric Verreaux's sifaka (*Propithecus verreauxi*) and ring-tailed lemurs (*Lemur catta*) inhabiting the Bezà Mahafaly Special Reserve (BMSR) in Madagascar. For each species, two groups lived in a protected parcel and two groups lived in anthropogenically-disturbed forests. Analysis of 585 fecal samples revealed that the BMSR ring-tailed lemurs harbored six species of nematode worms and three species of protistan parasites. The sifaka harbored only two nematodes. Differences in richness and prevalence appear to be linked to host behavior and the ecological distribution of their parasites. To understand the interplay between behavioral mechanisms to avoid or transmit parasites, we analyzed 683 hours of behavioral observations. BMSR ring-tailed lemurs were observed on the ground significantly more than sifaka and this terrestrial substrate use provides greater opportunities for soil-transmitted parasites to acquire a host. Ring-tailed lemurs using the anthropogenically-disturbed forests harbored parasites not found in the groups inhabiting the protected parcel which they may be acquiring via coprophagy or contact with feces. The arboreality of sifaka allows them to evade most soil-transmitted endoparasites and the patterns of parasitism exhibited by sifaka living in the anthropogenically-disturbed forests did not deviate from the patterns observed among the sifaka living in the protected parcel.

RÉSUMÉ

En tant qu'hôtes, les lémuriens interviennent dans l'acquisition et la transmission de parasites entre les individus d'une population, mais aussi sur la prévention et l'élimination de ces parasites. Leur comportement est donc largement responsable de la distribution des parasites au sein d'une population non contrôlée. Dans notre étude, nous avons examiné l'importance des facteurs comportementaux lors de l'acquisition et l'évitement des parasites transmis par voie orale en comparant le comportement des Propithèques de Verreaux (*Propithecus verreauxi*) et des Makis (*Lemur catta*) se trouvant dans la Réserve Spéciale du Bezà Mahafaly (RSBM) à Madagascar. Deux groupes de chacune de ces espèces étaient distribués dans une parcelle protégée et deux autres dans des forêts dégradées par l'activité humaine. L'analyse de 585 échantillons fécaux a révélé que les Makis de la RSBM étaient infestés par six espèces de nématodes et trois espèces de parasites protistes tandis que les Propithèques de Verreaux ne l'étaient que par deux espèces de nématodes. Les différences de densité et de fréquence auxquelles étaient trouvés les parasites semblaient être liées au comportement des hôtes et à la distribution écologique de leurs parasites. Pour comprendre la relation entre les mécanismes comportementaux et la transmission des parasites, nous avons analysé le comportement des Propithèques et des Makis lors de 683 heures d'observations. Les Makis de la RSBM ont été observés à terre beaucoup plus souvent que les Propithèques. Cette utilisation du substrat terrestre augmente les possibilités des parasites du sol de trouver un hôte. Les Makis se trouvant dans les forêts perturbées étaient infestés de parasites absents des excréments des lémuriens distribués dans la parcelle protégée. Il est possible que les parasites aient été transmis par coprophagie ou par contact avec des matières fécales. La tendance des Propithèques à vivre dans les arbres leur permet d'éviter la contagion par la plupart des parasites liés au sol et le comportement des Propithèques distribués dans les forêts perturbées ne diffère guère de celui des Propithèques distribués dans la parcelle protégée.

INTRODUCTION

It is well established that parasites influence primate behavior and socioecology (Nunn and Altizer 2006, Huffman and Chapman 2009). Parasites are a polyphyletic group of infectious organisms that rely on their host for energy, shelter, and the dispersal of their offspring (Moore 2002). Microparasites (e.g. viruses, bacteria, fungi, and protozoans) are small in size, short-lived, multiply prolifically in their host, and usually result in lifelong

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host immunity (Combes 2005). Macroparasites (e.g. helminthes and arthropods) are larger and have longer lives, disperse their offspring via their host, and their infections do not result in host immunity. As such, hosts can be reinfected with the same macroparasite species (Moore 2002).

Theoretical models and field studies have demonstrated the impact of parasites on primate dietary patterns, home range size, resource utilization, group size, social organization, and mating system (Nunn and Altizer 2006). Diet is critically important for those parasite species that gain access to their host by way of the consumption of contaminated food or water, feces, or via intermediate hosts. Omnivorous primates may acquire a wider breadth of parasites including those species that use intermediate hosts in comparison to folivorous primates that circumvent these infections by consuming a diet consisting of leaves (Vitone et al. 2004). Thus, the dietary preferences of a primate species should profoundly impact their patterns of parasitism. Another critical variable is daily ranges and habitat utilization. Primates using large home ranges should theoretically be exposed to more microhabitats and a wider breadth of parasite species living in those habitats (Nunn and Altizer 2006, Vitone et al. 2004). Group size, social organization, and degree of sociality result in differences in contact patterns and dyadic behavior among primates, and this may increase the probability of acquiring parasites that use transmission routes dependent on host contact or close proximity between hosts (Altizer et al. 2003). Thus, specific primate behaviors are used by parasites for transmission and aspects of their socioecology may facilitate their spread throughout a group or population. Initial parasite acquisition by a host and its subsequent spread to other hosts is dependent on the life cycle stage of the parasite, as well as its mode of transmission.

Anthropogenic disturbance may alter parasite richness and prevalence. Among the Malagasy primates, changes in parasite dynamics have been found within *Propithecus edwardsi* (Wright et al. 2009), *Eulemur flavifrons* (Schwitzer et al. 2010), and *Indri indri* (Junge et al. 2011) communities inhabiting disturbed forests. Loss of habitat requires primates to use smaller forest plots and may force a primate population to utilize regions of their home range that are soiled with parasites that they would otherwise avoid (Hausfater and Meade 1982). Simulations by Nunn et al. (2011) demonstrated that the intensity of range use by mammals is a primary measure impacting parasite prevalence for fecally transmitted parasites. Overcrowding due to habitat loss can result in higher degrees of overlap, higher probabilities of contact, and closer proximity to conspecifics, theoretically increasing the transmission of communicable parasites (Anderson and May 1992). Furthermore, primate habitats are frequently cleared for crops or used as grazing grounds for livestock, increasing the likelihood for the transmission of generalist parasites (Pedersen et al. 2005).

Here we compare the gastrointestinal parasite richness and prevalence between sympatric Verreaux's sifaka (*Propithecus verreauxi*) and ring-tailed lemurs (*Lemur catta*) inhabiting the Bezà Mahafaly Special Reserve (BMSR) in southwestern Madagascar. We examine the impacts of host behavior and socioecology on the patterns of parasitism for each primate over a nine month period. We collected parasite and behavioral data on groups of ring-tailed lemurs and sifaka which inhabited a protected parcel and anthropogenically-disturbed forests. These different habitats are useful for showing the importance of host behavior regarding parasite acquisition and how habitat disturbance may change primate-parasite dynamics or introduce primates to novel parasites (Chapman et al. 2005). However this study focuses on interspecific comparisons of parasitism between the BMSR ring-tailed lemurs and sifaka and not on intraspecific comparisons between social groups living in the protected parcel against those groups inhabiting the anthropogenically-disturbed forests. The BMSR sifaka and ring-tailed lemurs act as good models for testing how primate behavior and socioecology impact primate parasite patterns. Verreaux's sifaka and ring-tailed lemurs share a common phylogenetic history, with the indriids (i.e. *Propithecus*) and lemurids (i.e. *Lemur*) having diverged approximately 40 million years ago (Roos et al. 2004). This split is quite old, yet indriids and lemurids constitute sister taxa that share a number of morphological and behavioral traits. Sifaka and ring-tailed lemurs both groom orally via a mandibular toothcomb, increasing the likelihood of acquiring parasites that utilize oral transmission routes. Sifaka and ring-tailed lemurs also live in multi-male multi-female groups that are characterized by short, distinct mating seasons that are strongly linked to ecological variables (Richard et al. 2002, Sauther et al. 1999). Stark differences also exist between these species. Ring-tailed lemurs are omnivorous (Sauther et al. 1999) and spend approximately 16-19% of their time on the ground foraging or traveling (Sauther 1994, Loudon 2009). In contrast, sifaka consume a nearly exclusive folivorous diet precluding the need to descend to the forest floor, although they infrequently do so to consume terrestrial herbs (Loudon 2009). The BMSR ring-tailed lemurs are also more gregarious than the sifaka as they engage in more dyadic behavior including allogrooming, sitting in contact, chasing, displacements, and playing (Loudon unpublished data). Based on these behavioral and socioecological differences, we expect that the BMSR ring-tailed lemurs will harbor a greater richness of parasite communities and a higher prevalence for (a) soil-transmitted parasites and (b) socially-mediated parasites in comparison to the sifaka (Table 1).

METHODS

STUDY SITE. We collected data from November 2005 to July 2006 at the Bezà Mahafaly Special Reserve (BMSR) (E°44°34'20", S23°41'20", 150 m; Figure 1) in southwestern Madagascar. This region is extremely dry, experiencing approximately 550 mm of annual rainfall (Sauther 1998). Throughout this study, BMSR consisted of two noncontiguous parcels of land, approximately 600 ha in size, and a small research camp. In 1986, BMSR was decreed a special reserve by the government of Madagascar (Ratsirarson 2003). The size of each parcel was originally estimated using conventional cartographic methods but has since been measured using a handheld Global Positioning System (GPS) unit (Axel and Maurer 2010). Parcel 1 is an 80 ha riparian forest bordering the Sakamena River. This parcel has been protected against grazing for over twenty years through a local accord with the surrounding Mahafaly villagers. A barbed wire fence surrounds the parcel and facilitates the prevention of livestock grazing. As such, the parcel has remained relatively un-modified and is characterized by a multi-leveled canopy with a rich understory of terrestrial vegetation. The parcel is monitored and managed by the BMSR

TABLE 1. Parasite richness, prevalence, and mode of transmission for each of the gastrointestinal parasites recovered from the Bezà Mahafaly Special Reserve ring-tailed lemurs *(Lemur catta*) and Verreaux's sifaka (*Propithecus verreauxi*) populations. Prevalence refers to the number of individuals infected not the number of samples analyzed.

Parasite species (richness)	Ring-tailed lemur (n = 39)	Verreaux's sifaka (n = 26)	Transmission	Soil-transmitted	Socially-mediated
Balantidium sp.	100.0%	0.0%	direct fecal-oral route	yes	no
Entamoeba sp.	51.3%	0.0%	direct fecal-oral route	yes	no
Coccidia	12.8%	0.0%	direct fecal-oral route	yes	no
Oxyuridae	87.2%	38.5%	direct fecal-oral route	yes	yes
Lemurostrongylus sp.	38.5%	11.5%	unknown	yes	no
Trichostrongyloidea	7.7%	0.0%	direct fecal-oral route	yes	no
Subulura sp.	7.7%	0.0%	intermediate host	no	no
Trichuris sp.	5.1%	0.0%	direct fecal-oral route	yes	no
Unidentified brown nematode	10.3%	0.0%	unknown	unknown	unknown

Ecological Team, which maintains an extensive color-coded trail system that consists of 100 m x 100 m forest plots.

As one travels westward, the vegetation becomes xerophytic and the trees become smaller with a wider distribution (Sussman 1991). The dominant tree species near the river is *Tamarindus indica* (*kily* or tamarind). The vegetation near the Sakamena riverbank is a mosaic of tall trees (~30 meters in height) and thick curtains of vines. Here the forest floor is characterized by a thick leaf litter. The westward, drier region of Parcel 1 is dominated by *sasavy* (*Salvadora angustifolia*) and *famata* (*Euphorbia tirucalli*) trees (Sussman and Rakotozafy 1994). This region of the parcel is more open and less humid. The forest floor in this portion of the reserve is characterized by thick mats of terrestrial herbs (*Metaporana parvifolia*). Surrounding Parcel 1 are landscapes that we refer to as 'anthropogenically-disturbed forests.' The anthropogenically-disturbed forests consist of the same plants species that are found in Parcel 1. However, the structure of the forest differs. The Mahafaly have traditionally used the forests outside of the parcel for fuel and building materials resulting in less tree density and wider spaces between adult trees. The Mahafaly also use these forests as grazing grounds for their livestock which continuously consume many of the bushes, seedlings, and terrestrial herbs (Loudon et al. 2006). As a result, the structure of many of these anthropogenically-disturbed forests is characterized by wide expanses with sparse vegetation or forests with large adult trees lacking an understory. Habitat structural comparisons between the floral communities in Parcel 1 and the surrounding forests also revealed significantly more grazing and fecal contamination by livestock and free-ranging domestic dogs in the anthropogenically-disturbed forests (Whitelaw et al. 2005).

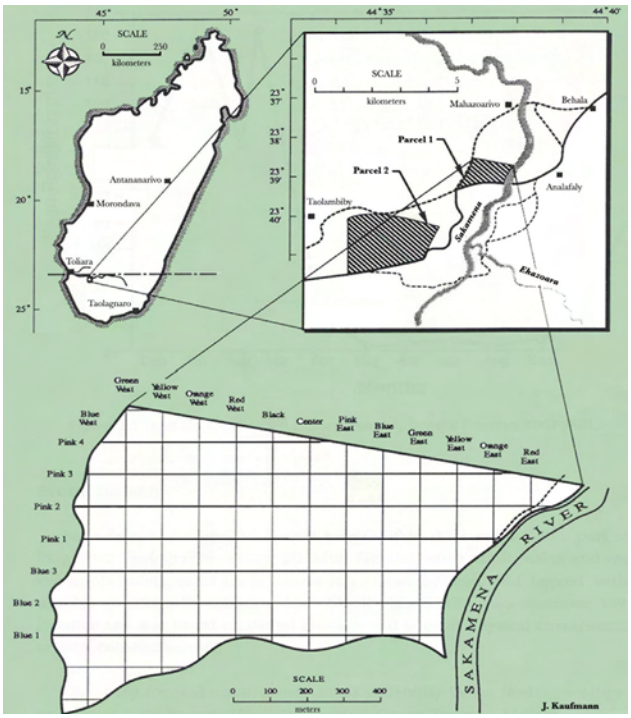

FIGURE 1. Map of Madagascar indicating the location of the Bezà Mahafaly Special Reserve. Map by Jeffrey Kaufmann.

Directly south of Parcel 1 lies the BMSR camp which is surrounded by the anthropogenically-disturbed forests. The camp consists of administrative buildings, a museum, two pit latrines, two shower facilities, a well, an outdoor kitchen, and an area for researchers to set up their tents. The camp is an important component to this study because it is encompassed by the home ranges of two ring-tailed lemur groups, and one sifaka group which we observed during this study. These BMSR ring-tailed lemur groups regularly fed on food scraps within the camp (Loudon et al. 2006) and occasionally ate human fecal matter from traditional open-air latrines used by the Mahafaly that were located just outside the camp during this study (Fish et al. 2007), but which have subsequently been removed.

STUDY GROUPS. We collected behavioral and parasitological data on four groups of sifaka and ring-tailed lemurs. For each species, two groups lived in the protected Parcel 1 and two groups lived in the anthropogenically-disturbed forests. In total, we collected data on 65 animals, of which 39 were ring-tailed lemurs and 26 were sifaka. Each BMSR ring-tailed lemur and sifaka group is fitted with a color-coded collar and an identification tag (Sauther et al. 1999). Collared sifaka also have notched ears to assist identification (Richard et al. 2002).

BEHAVIORAL DATA AND FECAL SAMPLE COLLECTION. We used twenty-minute focal follows with a one-minute interval (Altmann 1974) to record the general behavior of the BMSR Verreaux's sifaka and ring-tailed lemurs. Each focal follow was accompanied with *ad libitum* notes to record behavior that occurred between intervals and follows. We collected behavioral data from 0700h to 1700h. As a consequence of the larger

ring-tailed lemur groups, we collected more behavioral data on ring-tailed lemurs (ring-tailed lemurs: 370 hours, sifaka: 313 hours). We analyzed sifaka and ring-tailed lemur behavior that could potentially increase the likelihood of acquiring or avoiding a parasitic infection. These included the frequency of allogrooming, autogrooming, sitting in contact, scent marking, and terrestrial substrate use. Sifaka and ring-tailed lemurs allo- and autogroom orally via mandibular toothcombs and the frequency of this behavior may increase the likelihood of acquiring parasites using fecal-oral transmission routes. Sitting in contact may also facilitate the spread of parasites which rely on host contact or close proximity. Sifaka and ring-tailed lemurs rely heavily on olfactory communication and lay scent via scent glands throughout their environment. Male and female ring-tailed lemurs lay scent via ano-genital glands and scent marking may result in the inadvertent spread of fecally-transmitted parasites throughout their home range. Terrestrial behavior increases the likelihood of acquiring fecal borne parasites harbored by the sifaka and ring-tailed lemurs as well as those carried by the Mahafaly livestock and the Mahafaly themselves who frequently defecate directly on the ground (Muehlenbein et al. 2003). Given the dietary and socioecological differences between each species some behaviors could not be compared. For example, the ring-tailed lemurs that utilized the camp frequently drank well water from discarded basins and buckets and the groups in Parcel 1 and in the anthropogenically-disturbed forests drank water from naturally occurring puddles (Figure 2). Verreaux's sifaka were not observed drinking water from anthropogenic or naturally occurring sources such as arboreal cisterns or puddles. Furthermore, some BMSR ring-tailed lemurs consume human, canine, and livestock feces (Fish et al. 2007) a behavior not observed in the sifaka.

We collected fecal samples from each individual directly after defecation to preclude contamination. Fecal samples were collected in the morning hours (0700h-0900h) at the end of each month. In this study, we analyzed 585 fecal samples (ring-tailed lemurs: 351, sifaka: 234). Fecal matter was placed in 50ml tubes filled with formalin.

PARASITE PROTOCOLS. Parasite abundances were detected using conventional gastrointestinal parasitology protocols. Given our methods, we acknowledge that we are underestimating the parasite diversity and prevalence for each primate species. We used fecal smear, fecal flotation, and fecal sedimentation methods. The fecal smear technique was used to detect the presence of non-buoyant parasites within each animal's feces (Gillespie 2006). For this protocol, fecal matter was placed directly on a slide and homogenized with distilled water. Fecal floatation methods were used to identify buoyant endoparasites and eggs (Gillespie 2006). For each floatation, we placed 2 g of fecal matter in a centrifuge tube containing a solution of sodium nitrate with a specific gravity of 1.2 (Zajac and Conboy 2006). The solution and feces were then homogenized with a wooden applicator and each sample was centrifuged at approximately 1,800 RPM for five minutes. Each test tube was placed in a test tube rack and topped off to a meniscus using more floatation solution. A coverslip was placed on the meniscus for five minutes. Each cover slip was then removed and placed on a microscope slide for viewing. We used the remaining 2 g of fecal matter at the bottom of the centrifuge tube for fecal sedimentation analysis (Gillespie 2006). Fecal matter was placed in a soapy water solution and filtered through a wire strainer. The sediment was left to settle for five minutes. The supernatant was removed, and the fecal sediment was pippetted onto a microscope slide and topped with a cover slip (Gillespie 2006). For each protocol, the fecal sample was scanned and parasites were counted using the 10x objective. The 40x objective was used to identify parasites. Parasites were photographed, measured, and logged into a computer database.

FIGURE 2. Ring-tailed lemurs drinking discarded well water in the camp (a) and rainwater from puddles on the road adjacent to the camp (b).

DATA ANALYSIS. We analyzed the parasite richness and prevalence for each primate host. Parasite richness is the number of parasite species harbored by each host. Prevalence is the number of hosts infected with a specific parasite species divided by the total number of hosts. For this paper, we used interval data to investigate how each primate host used behavior to acquire or eliminate and avoid parasites. We define 'soil-transmitted parasites' as those parasites that are acquired by the host through consumption of contaminated soil, water, or fecal matter that is lying on the ground, and those parasites on the ground which have an active host seeking life cycle stage in which they come in contact with their host while they are terrestrial (Table 1). We define 'socially-mediated parasites' as species whose transmission from one host to the next is facilitated by host social behavior (i.e. allogrooming, huddling, and smelling scent markings). Since parasite infections are generally found in Poisson distributions and do not adhere to the assumptions of parametric tests, we used only nonparametric statistics for all comparisons. Due to unequal sample sizes we also used nonparametric Mann-Whitney *U* tests for all behavioral analysis. Statistical tests were performed on Sigma Plot 11.0.

RESULTS

Table 1 illustrates the parasite richness and prevalence exhibited by each primate host at BMSR. Verreaux's sifaka did not harbor any protistan endoparasites and only two species of nematode worms. In contrast, ring-tailed lemurs harbored three species of protistan parasites and six species of nematodes (Figure 3). Each primate host harbored an oxyurid pinworm. The pinworm harbored by the ring-tailed lemurs was identified as *Lemuricola bauchoti* (del Rosario Robles et al. 2010; Figure 4) and the sifaka harbored *Biguetis trichuroides*. Both primate hosts harbored *Lemurostrongylus* sp. worms. The prevalence for oxyurid pinworms and *Lemurostrongylus* sp. infections was significantly higher in the ring-tailed lemur population (oxyurids: X^2= 22.370; P < 0.0001; *Lemurostrongylus* sp.: X^2 = 4.793; P < 0.05). The BMSR ring-tailed lemurs spent 4241 (19.1%) intervals on the ground and Verreaux's sifaka were terrestrial for only 1138 (6.1%) intervals and this difference was significant (*U* =

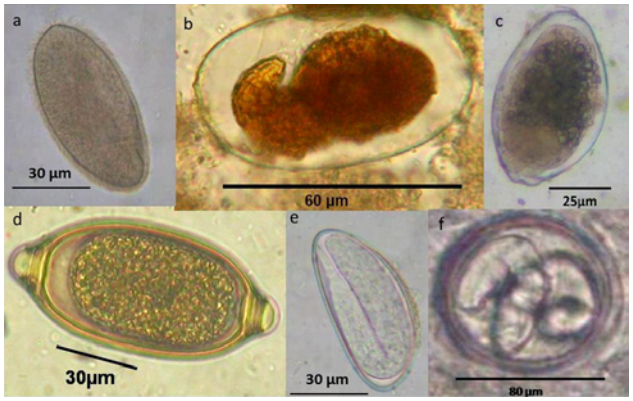

FIGURE 3. Photos of the protistan parasite (a) *Balantidium* sp. and helminth eggs harbored by the Bezà Mahafaly ring-tailed lemurs (b) *Lemurostrongylus* sp. (c) Unidentified trichostrongylid egg (d) unembryonated *Trichuris* sp. (e) *Lemuricola bauchoti* and (f) *Subulura* sp.

1.0; P < 0.001). Ring-tailed lemurs also allogroomed (U = 7.5; P < 0.01), autogroomed (U = 16.0; P < 0.05), and scent marked (U = 12.0; P < 0.05) significantly more frequently than sifaka. No significant differences in the frequency of sitting in contact with conspecifics were found between the BMSR ring-tailed lemur and sifaka populations (U = 32.0; P = 0.48).

DISCUSSION

The BMSR ring-tailed lemurs exhibited a greater endoparasite richness than the sympatric sifaka. The ring-tailed lemur population also exhibited a greater prevalence of infection for those parasites that were soil-transmitted and socially-mediated (Table 1). Furthermore, the BMSR ring-tailed lemurs had a higher prevalence for the two nematodes (oxyurids and *Lemurostrongylus* sp.) that each primate harbored. The BMSR ring-tailed lemurs and sifaka are both group-living, gregarious primates. However, the ring-tailed lemur population was observed on the ground significantly more often. Throughout this study, the sifaka spent 93.9 % of all intervals in the trees. This degree of arboreality decreases the likelihood of acquiring soil-transmitted parasites (Muehlenbein et al. 2003). In contrast, the ring-tailed lemurs were observed on the ground in 19.1 % of all intervals. The extent of their terrestrial behavior may be responsible for the wide diversity of nematode worms harbored by the BMSR ring-tailed lemurs, as *Lemuricola bauchoti*, *Trichuris* sp., and trichostrongylids use direct fecal-oral transmission routes. The prevalence of *Lemurostrongylus* sp. infections were significantly higher among the ring-tailed lemurs and this may be linked to their ground use. The life cycle of *Lemurostrongylus* sp. has yet to be identified and this nematode may use direct fecal-oral route or penetrate the skin of the host via direct contact like some other strongylid nematodes. Both sifaka and ring-tailed lemurs defecate directly onto the ground and are careful not to soil their sleeping trees and core areas (Loudon, per. obs). However, the high degree of terrestriality observed among the ring-tailed lemur population (Sauther 1994, Loudon 2009) increases the probability of acquiring these soil-transmitted parasites that require host ingestion or perhaps physical contact for acquisition and establishment (Anderson 2000).

Differences in the feeding behavior of each primate may also be responsible for the higher parasite richness found among the BMSR ring-tailed lemurs. Ring-tailed lemurs are omnivorous

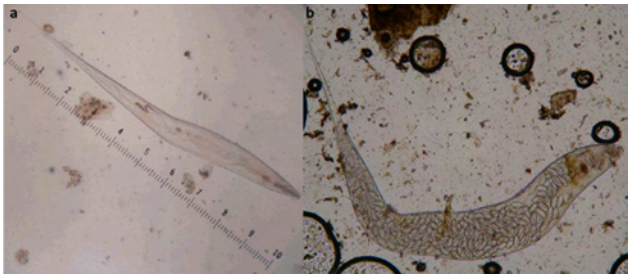

FIGURE 4. Photos of two adult *Lemuricola bauchoti* worms (a) sex unknown (b) gravid female.

and opportunistically feed on leaves, flowers, fruit, and invertebrates (Sauther et al. 1999). Verreaux's sifaka are primarily folivorous but incorporate small amounts of unripe kily fruits (*Tamarindus indica*) and kotipoke fruits (*Grewia grevei*) into their diet (Loudon 2009). The insectivory observed among the BMSR ring-tailed lemurs is most likely responsible for *Subulura* sp. infections. Worms within the genus *Subulura* use invertebrates as intermediate hosts (Anderson 2000), but as of now the identification of this intermediate host eludes us. Potential intermediate hosts include caterpillars or cockroaches. The caterpillars consumed by the BMSR ring-tailed lemurs live in the forest canopy and presumably consume leaves. To date, researchers have not observed this ring-tailed lemur community consuming cockroaches despite over 25 years of field research at BMSR, suggesting that cockroaches are unlikely intermediate hosts for this nematode. *Subulura* infections are rare among Malagasy primates and have only been documented in mouse lemurs (Chabaud et al. 1965, Raharivololona and Ganzhorn 2009). Since the life cycle of *Subulura* is not understood it remains unknown if the ring-tailed lemurs are somehow acquiring these infections from the sympatric mouse lemur (*Microcebus griseorufus*) population at BMSR.

Host behavior may also be responsible for the oxyurid (*Biguetis trichuroides*) infections we found among the BMSR sifaka. Male sifaka possess scent glands on their neck, which are used to mark the trees in their home ranges (Petter 1962). Male sifaka frequently incorporate fresh female feces into these scent marks. As a female defecates, a male will position himself directly underneath the female and capture the female's fecal pellets between his neck and tree trunk. The feces are smeared onto the trunk, resulting in a mark that includes the male's scent and the female's fecal matter (Loudon 2009). During this process, fecal pellets fall on the male, increasing the likelihood of acquiring a *B. trichuroides* infection. In a similar vein, ring-tailed lemurs may acquire some of their nematode and protistan infections via smelling and licking scent marks left by conspecifics. Ring-tailed lemurs use ano-genital glands to scent mark on substrates within their home ranges. These chemical cues function as a means to maintain home range boundaries and resource ownership, assert group status and intragroup dominance hierarchies, and mediate reproductive behavior (Drea and Scordato 2008). Ring-tailed lemurs that smell, ingest, or lick the scent marks left by a parasitized conspecific may acquire their parasites. Thus, these parasites are potentially utilizing each host's system of olfactory communication to facilitate their transmission to a new host. The BMSR ring-tailed lemurs were observed scent marking significantly more often than sifaka and this may result in the ring-tailed lemur environ-

ments that are more saturated with oxyurid eggs leading to the significantly higher oxyurid infections among the ring-tailed lemur population. The specific dynamics between each BMSR primate host and their oxyurids remains unresolved but are perhaps linked to the characteristics of oxyurid eggs which are infective almost immediately after being laid, which can lead to host auto-infection (Roberts and Janovy 2008). Oxyurid eggs are also sticky and adhere to the host's skin and fur (Sengbusch 1970), and bouts of contact by parasitized ring-tailed lemurs and sifaka may facilitate oxyurid transmission among group members. Ring-tailed lemurs and sifaka may acquire oxyurid infections from their oral allo- and autogrooming bouts that focus on the ano-genital region (i.e. genital grooming). Towards this end, the significantly higher prevalence of the socially-mediated oxyurids in the BMSR ring-tailed lemur population may be linked to differences in host behavior, as the ring-tailed lemurs allogroomed and autogroomed more frequently than sifaka.

The ecological challenges provided by the anthropogenically-disturbed forests appear to have little effect on the patterns of parasitism exhibited by the sifaka. Groups of sifaka living in these forests are required to descend to the ground more frequently but do so only to bipedally hop from one forest fragment to the other. The strict vegetarian diet of sifaka appear to circumvent the acquisition of those nematode worms that use invertebrates as intermediate hosts and their arboreal lifestyle evades soil-transmitted parasites that require physical contact or use fecal-oral transmission routes (Muehlenbein et al. 2003). It should be noted that an arboreal existence and a folivorous diet is only effective against evading those parasites that use the aforementioned transmission routes. Opportunistic necropsies of naturally deceased BMSR sifaka demonstrate that this species harbors *Paulianfilaria pauliani*, a filarial worm that uses an insect vector for transmission to new hosts (Chabaud et al. 1961). It is likely that this unidentified insect vector is a biting fly that can obtain a blood meal from animals utilizing arboreal substrates.

The anthropogenically-disturbed forests that surround the protected Parcel 1 present each primate with an entire suite of ecological challenges but it appears to only be influencing the patterns of parasitism among the BMSR ring-tailed lemurs. Our previous work at the site has demonstrated that the anthropogenically-disturbed forests exhibit significantly more tree cutting, grazing and livestock paths, and livestock manure compared to Parcel 1 (Whitelaw et al. 2005).

Furthermore, the ring-tailed lemur groups that utilized the anthropogenically-disturbed forests were observed consuming dog, cattle, and human feces during this study. Coprophagy in this population appears to be a feeding strategy to obtain calories and/or nutrients for those ring-tailed lemurs suffering from tooth loss (Fish et al. 2007). Although coprophagy may confer benefits (Soave and Brand 1991, Graczyk and Cranfield 2003), it also provides an avenue for acquiring new hosts for those parasites that utilize a fecal-oral transmission route. The coprophagic tendencies of these groups may be responsible for whipworm (*Trichuris*) infections, as these nematodes were only recovered among individuals living in the disturbed forests who were observed eating human and cattle feces. During the study, we identified *Trichuris vulpis* infections among the feral dogs living in the forests surrounding Parcel 1 (Loudon 2009). Many nematodes are host species-specific and the whipworm infections found among the BMSR ring-tailed lemurs are probably *T. lemuris*. On rare occasions *T. vulpis* has been known to use other hosts (Kagei et al. 1986, Dunn et al. 2002) and ring-tailed lemurs can act as alternative hosts for species-specific helminths (Shahar et al. 1995). However, further parasitological field research at BMSR is required to determine if the ring-tailed lemurs are in fact parasitized by *T. vulpis* and if these infections are acquired via coprophagy.

Host-parasite evolutionary relationships may also explain differences in the patterns of parasitism exhibited by the BMSR ring-tailed lemurs and sifaka. The ring-tailed lemur and sifaka helminths are likely species-specific and have co-evolved with their hosts (Brooks and Glen 1982, Glen and Brooks 1985). Previous investigations of BMSR sifaka parasitism found no evidence that this population harbored any fecal parasites (Muehlenbein et al. 2003) although we identified two nematode species. The different outcomes between our results and Muehlenbein et al. (2003) are puzzling but may be linked to differences in methodologies and/or ecology. We conducted fecal smear and sedimentation protocol, and for our fecal floatation method we used a sodium nitrate solution while Muehlenbein et al. (2003) report that they conducted fecal floatations with a zinc sulfate solution. Furthermore, Muehlenbein et al. (2003) only sampled sifaka groups inside Parcel 1 while we sampled groups within the parcel (although these may have been different groups) and groups inhabiting the anthropogenically-disturbed forests. Our study was also conducted at least two years later, in a region that is characterized by unpredictable environmental conditions (Dewar and Richard 2007) that may influence parasite abundances and distributions.

Another striking difference between the parasitic burdens of each host is the presence or absence of protistan infections. No sifaka harbored a protistan parasite. In contrast, all the BMSR ring-tailed lemurs harbored *Balantidium* sp. infections and 51.3% of the population harbored *Entamoeba* sp. infections. These stark differences are arguably rooted in the durable, evolutionary relationships between the BMSR ring-tailed lemurs and their protistan burdens. However, the ubiquitous distribution of these protistan parasites increases the likelihood of accidental infection by hosts, and the BMSR ring-tailed lemurs may be acquiring these parasites by drinking from contaminated arboreal cisterns, puddles or neglected basins of well water within the camp.

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