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Gastrointestinal Helminths of Two Species of Mouse Opossums (*Marmosa demerarae* and *Marmosa murina*) from French Guiana

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ABSTRACT: The woolly mouse opossum *Marmosa demerarae* and the murine opossum, *Marmosa murina*, occur in sympatry across most of their range; however, they are not syntopic in that *M. demerarae* is more abundant in the canopy of primary and secondary forest, while *M. murina* is scansorial and appears to be more abundant in lower forest strata. We herein present a survey and comparison of the helminths occurring in these 2 species in French Guiana based on examinations of 18 individuals of *M. murina* and 21 individuals of *M. demerarae*. At the level of the component community, species richness was established at 12 for *M. demerarae* and 14 for *M. murina*; the nematodes *Pterygodermatites* (*Paucipectines*) *elegans* and *Aspidodera raillieti* were established as the most abundant and prevalent species in *M. demerarae* and *M. murina*, respectively. Infracommunities in both species had an average species richness of 3.7 and 3.8, respectively. Both species share 12 species of parasites, yet *Phaneropsolus philanderi*, *Pterygodermatites* (*Paucipectines*) *elegans*, *Travassostrongylus paraquintus*, *Trichuris reesali*, and *Spirura trinitatis* were significantly more frequent in *M. demerarae*. Infections also included *Mathevotaenia bivittata*, an unidentified anoplocephalid, and *Viannaia venezuelensis*, all 3 species of which were more frequent in *M. murina*.

KEY WORDS: French Guiana, mouse opossums, *Marmosa demerarae*, *Marmosa murina*, *Phaneropsolus philanderi*, *Aspidodera raiilieti*, *Pterygodermatites* (*Paucipectines*) *elegans*, encounter filter.

A successful parasitic infection depends on the compatibility between the parasite and its host as well as the exposure of the host to infective stages (Combes, 1991). Thus, organisms sharing a common ancestor may share features that make them susceptible to infections by the same parasites (Brooks and McLennan, 2002), while organisms from different phylogenetic lineages and habits should be infected by different species of parasites. Thus, a precise identification of the relative roles of the compatibility and encounter between host and parasite could be studied using sympatric and phylogenetically related organisms (Meyer-Lucht et al., 2010; Jiménez et al., 2011). A prerequisite to such a study would include a detailed helminth faunal assessment and documentation of the frequency of host–parasite association. We herein present such a comparison of the helminth faunas of 2 species of mouse opossums (Didelphidae: *Marmosa*) in French Guiana.

Species of *Marmosa* are small, typically arboreal, and occur from southern Mexico to northern Argentina (Gardner, 2007). Mouse opossums are omnivorous (Voss et al., 2001), yet insects constitute a large fraction of their diet, which is supplemented by seeds and other plant materials (Pinheiro et al., 2002). Three species of *Marmosa* occur in French Guiana, including the arboreal *Marmosa demerarae* and the scansorial species *Marmosa lepida* and *Marmosa murina* (Voss et al., 2001; Steiner and Catzeflis, 2004; Hannibal and Caceres, 2010). The species are not reciprocal sister groups (Gutiérrez et al., 2010). Both *M. demerarae* and *M. murina* overlap in most of French Guiana, and their presence in the same patch of forest has been documented in the same locality (Adler et al., 2012). Field observations suggest that *M. demerarae* is a rather common species in both primary and secondary forests, whereas *M. murina* appears to be locally abundant in highly modified sites, including secondary forests. As a consequence, and even though the species are sympatric (e.g., occur in the same geographic area), they are rarely syntopic (e.g., they generally do not occur in the same microhabitat).

Few sporadic records document the parasite fauna in species of *Marmosa*. Fleas of Ctenopthalmidae (Hastriter and Peterson, 1997) and several species of *Leishmania* (Lainson and Shaw, 1969; Alexander et al., 1998) have been recorded in individuals of both *M. demerarae* and *M. murina*. In particular, parasites

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reported in the latter species include the nematodes *Viannaia bisbali*, *Viannaia minispicula*, *Viannaia hamata*, *Spirura guianensis*, the digenean *Euparadistomum paraense*, and an apicomplexan (*Sarcocystis* spp.: Shaw and Lainson, 1969; Gomes and Pinto, 1972; Gomes, 1979; Guerrero, 1985). Finally, 3 species of parasites have been reported in unidentified species of *Marmosa*; these include *Castroia inquassata*, *Pterygodermatites* (*Paucipectines*) *kozeki*, and *Trypanosoma cruzi* (Gomes and Pinto, 1972; Chabaud and Bain, 1981).

Limited numbers of publications summarize the diversity of parasites occurring in 1 or more species of marsupials (Alden, 1995; Gomes et al., 2003; Monet-Mendoza et al., 2005; Jiménez et al., 2011). These include the parasite faunas of the most common and abundant opossums, which include the larger-sized members of the tribe Didelphini (species of *Didelphis* and *Philander*). Parasites from small-sized marsupials are only known from species descriptions, and, as a consequence, the parasite fauna for more than 94% of the marsupial species of the New World remains unknown. We herein present the parasite fauna recorded in the woolly mouse opossum *M. demerarae* and the murine opossum *M. murina*.

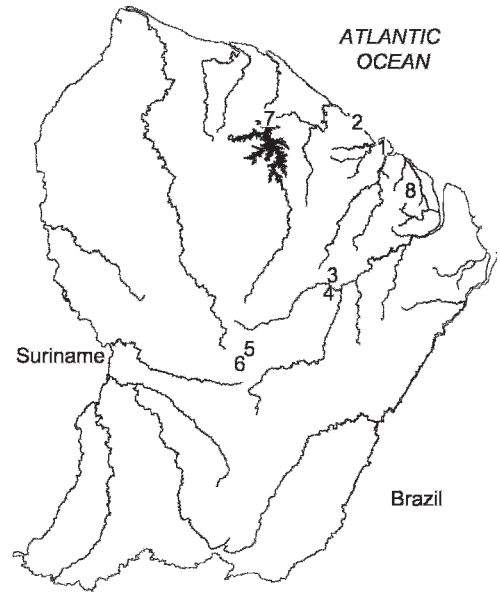


Figure 1. Location of collection sites in French Guiana. 1 = Montagne du Tigre (commune de Cayenne); 2 = Macouria (commune de Macouria); 3 = Nouragues (commune de Regina); 4 = Saut Pararé (commune de Regina); 5 = Pic Matecho (commune de Saül); 6 = Saül (commune de Saül); 7 = Petit Saut (commune de Kourou); and 8 = Route de Kaw (commune de Roura).

MATERIALS AND METHODS

Specimens were collected between April 2000 and May 2005 in 8 localities (Fig. 1), including Montagne du Tigre (04°54′N; 52°18′W); Macouria (04°55′N; 52°22′W); Nouragues (04°05′N; 52°42′W); Saut Pararé (04°02′N; 52°42′W); Pic Matecho (03°45′N; 53°02′W); Saül (03°37′N; 53°13′W); Petit Saut (05°04′N; 53°03′W); and Route de Kaw (04°37′N; 52°17′W). Nouragues, Saut Pararé, and Pic Matecho are pristine primary forests, while the remaining collection sites are secondary forests with dense understory vegetation. Mammal vouchers were deposited in the Muséum d'Histoire Naturelle de la Ville de Genève, Switzerland. Gastrointestinal contents were preserved in 70% ethanol and transported to the laboratory to be examined for helminths. Preservation, staining, clearing, and mounting of parasites followed Pritchard and Kruse (1982).

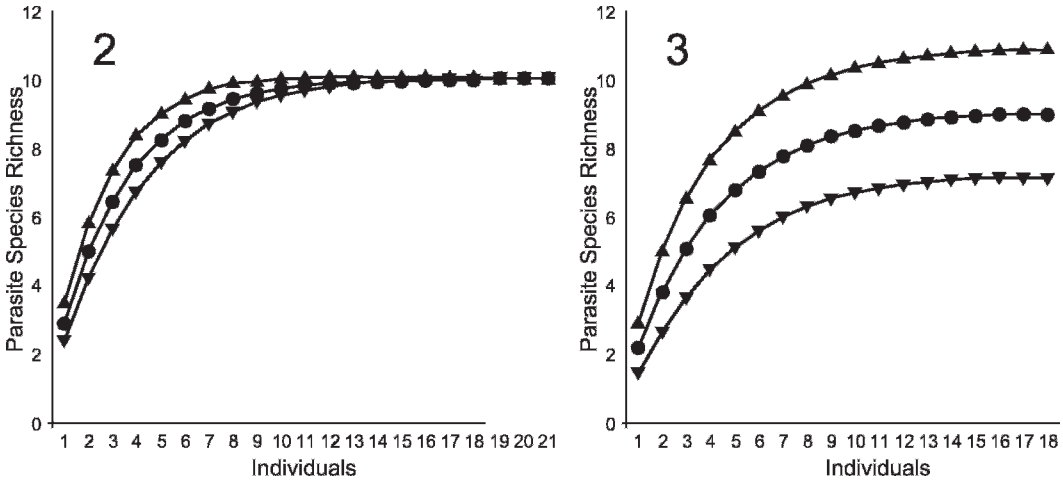
Vouchers for this study were deposited in the Harold W. Manter Laboratory (HWML) of the University of Nebraska (Lincoln, Nebraska, USA) and the Collection Parasitologique du Museúm National d'Histoire Naturelle (Paris, France). All helminths were preserved in 70% ethanol and kept refrigerated. Digenetic trematodes, cestodes, and acanthocephalans were stained in Semichon's acetocarmine, dehydrated in a graded series of ethanol, cleared in xylene, and mounted in Canada balsam. Nematodes were cleared in lactophenol and mounted on temporary slides.

Definitions of prevalence, mean abundance, mean intensity, and other ecological descriptors follow Bush et al. (1997). Nonrandomized area accumulation curves were constructed to evaluate species recovered per sampling unit using an incidence-based approach (Colwell et al., 2004). With the purpose of eliminating the confounding effect of rare species, these curves were constructed with the inclusion of species present at a prevalence of >10% (Fig. 2) using EstimateS version 8.2.0 for Macintosh (Colwell, 2009).

The qualitative taxonomic similarity of parasite infracommunities was measured by using the Jaccard similarity index as implemented in SAS (SAS Institute Inc., 2009). Differences in species richness and the total number of helminths between *M. demerarae* and *M. murina* were tested using χ^2 tests for independence.

RESULTS

In total, 12 species of helminths were recovered from 21 individuals of *M. demerarae* collected over 4 different localities: 15 in Montagne du Tigre; 2 in Pic Matecho; 1 in Saül; and 3 in Nouragues. In total, 14 species of helminths were recovered from 18 specimens of *M. murina* collected over 7 different localities, including: 4 in Montagne du Tigre; 1 in Macouria; 4 in Nouragues; 1 in Petit Saut; 5 in Saül; 1 in Saut Pararé; and 2 in Route de Kaw (Table 1). Individuals of *M. demerarae* and *M. murina* had an average species richness of 3.7 and 3.8, respectively.



Figures 2–3. Nonrandomized rarefaction curve of species recovery per infracommunity using prevalence data for parasites present in prevalence <10% for *Marmosa demerarae* ($n = 21$) and *Marmosa murina* ($n = 18$). The Mao τ index was employed to estimate confidence intervals for observed species (observed parasite species richness [Mao τ], circles; upper bound of the 95% confidence interval, triangles; lower bound of the 95% confidence interval, inverted triangles). **2.** *Marmosa demerarae*. **3.** *Marmosa murina*.

Digenea

Phaneropsolus philanderi Caballero and Grocott, 1952. This digenean infected 33.3% of *M. demerarae* and 11.1% of *M. murina* (Table 1). Murine opossums were infected in Montagne du Tigre, whereas in woolly mouse opossums, the infection was recorded in the same locality and in Saül.

Cestoda

Mathevotaenia bivittata (Janicki, 1904) Yamaguti, 1959. This anoplocephalid was found infecting 19% of woolly mouse opossums and 27.8% of murine opossums (Table 1). In the latter, this tapeworm was recorded in Montagne du Tigre, Nouragues, and Saut Pararé, whereas it was documented in woolly mouse opossums from Montagne du Tigre and Pic Matecho. Infection by an unidentified anoplocephalid cestode was recorded in a single murine opossum in Montagne du Tigre.

Nematoda

Aspidodera raillieti Travassos, 1914, was recorded in woolly mouse opossums from Nouragues and Montagne du Tigre; in addition to those localities, the worm was detected in the murine opossum in Petit Saut, Route de Kaw, and Saül. *Pterygodermatites* (*Paucipectines*) *elegans* Travassos, 1928, infected the woolly mouse opossum in Montagne du Tigre, Pic Matecho, and Saül, and the murine opossum in Montagne du Tigre and Nouragues. *Travassostrongylus paraquintus* Durette-Desset, 1974, and *Viannaia venezuelensis* Guerrero, 1985, were recovered from both species of mouse opossums in Montagne du Tigre and Saül. While both trichostrongyles were recorded in the murine opossum at Route de Kaw, only *V. venezuelensis* was found in this host at Nouragues. An unidentified species of *Travassostrongylus* was detected in both marsupials at Montagne du Tigre and in murine opossums from Nouragues, Route de Kaw, and Saül. *Hoinneffia simplicispicula* Navone, Suriano, and Pujol, 1991, infected the woolly opossum in both Montagne du Tigre and Saül and the murine opossum in Route de Kaw. *Skrjabinofilaria philanderi* (Foster, 1939) was exclusively found at Montagne du Tigre, Saut Pararé, and Saül. Finally, the species *Trichuris reesali* Wolfgang, 1951, *Spirura guianensis* (Ortlepp, 1924), and *Subulura trinitatis* Wolfgang, 1951, infected both species of marsupials from Montagne du Tigre and Saül, while *T. reesali* and *S. trinitatis* were also recorded from Nouragues in the woolly mouse opossum and *S. trinitatis* from the murine opossum in Route de Kaw.

Acanthocephala

Oligacanthorhynchus microcephala (Rudolphi, 1819) was collected from both species of mouse

Table 1. Characterization of the infection of *Marmosa demerarae* ($n = 21$), and *M. murina* ($n = 18$) in French Guiana. Numbers under Locality: 1 = Montagne du Tigre (commune de Cayenne); 2 = Macouria (commune de Macouria); 3 = Nouragues (commune de Regina); 4 = Saut Pararé (commune de Regina); 5 = Pic Matecho (commune de Saül); 6 = Saül (commune de Saül); 7 = Petit Saut (commune de Kourou); and 8 = Route de Kaw (commune de Roura).

Parasite taxa	Site of infection*	*Marmosa demerarae*			*Marmosa murina*		
		HWML no.	Prev† (%)	Locality	HWML no.	Prev† (%)	Locality
Digenea							
Phaneropsolus philanderi	SI	49768	33.3	1, 6	—	11.1	1
Cestoda							
Mathevotaenia bivittata	SI	—	19.0	1,5	49769	27.8	1, 3, 4
Unidentified cestode	LI	—	—	—	—	5.6	1
Nematoda							
Aspidodera raillieti	Cecum	67205, 11	38.1	1, 3		44.4	1, 3, 6, 7, 8
Pterygodermatites (*Paucipectines*) *elegans*	SI	67202, 04	42.9	1, 5, 6	67210	16.7	1, 2
Travassostrongylus paraquintus	SI	67214, 15, 17	38.1	1, 6	67216, 18	38.9	1, 6, 8
Travassostrongylus sp.	SI	67223 -27	28.6	1	67228	44.4	1, 2, 6
Viannaia venezuelensis	SI	67220	28.6	1, 6	67219, 67221, 22	38.9	1, 3, 6, 8
Hoinneffia simplicispicula	SI	67213	14.3	1	67212	5.56	8
Trichuris reesali	LI	67207	14.3	1, 6	—	5.56	2
Spirura guianensis	Stomach	67208	4.8	1	—	5.56	1
Skrjabinofilaria philanderi	VC	—	—	—	67203	16.7	1, 6
Subulura trinitatis	LI	67206	38.1	1, 6, 8	67209	11.1	1, 6, 2
Acanthocephala							
Oligacanthorhynchus microcephala	SI	—	23.8	1,5	—	22.2	1, 2

* SI, small intestine; LI, large intestine; VC, visceral cavity.

† Prev, Prevalence.

opossums from Montagne du Tigre. It was also recorded infecting the woolly opossum in Pic Matecho and the murine opossum in Macouria.

Overall, *Pterygodermatites* (*Paucipectines*) *elegans* exhibits the highest prevalence in *M. demerarae*, whereas *P. philanderi* exhibits the highest mean intensity and mean abundance. In *M. murina*, *A. raillieti* shows the highest prevalence, and *M. bivittata* exhibits both the highest mean intensity and mean abundance. *Aspidodera raillieti* occurs in both species of marsupials at relatively similar prevalences (Table 1).

For *M. demerarae*, the values for the Mao τ and both lower and upper confidence intervals predict the same number of parasite species, at 15 (Fig. 2). For *M. murina*, the estimate for Mao τ and values of lower and upper confidence intervals do not predict the same number of species (Fig. 2).

Qualitative taxonomic similarity analysis resulted in values of similarity of 0.20 among infracommunities of *M. demerarae* (SD $\pm$ 0.17, 153 pairs) and 0.19 in *M. murina* (SD $\pm$ 0.17, 91 pairs). Values of interspecific similarity were 0.18 (SD $\pm$ 0.17, 252 pairs).

Results of the χ^2 tests suggest that 5 species of parasites occur more frequently in *M. demerarae* than in *M. murina*, including *P. philanderi* ($P < 0.001$), *P.* (*Paucipectines*) *elegans* ($P < 0.001$), *T. paraquintus* ($P < 0.01$), *Tr. reesali* ($P = 0.03$), and *Su. trinitatis* ($P < 0.001$). In turn, infections caused by *M. bivittata* ($P < 0.001$), an unidentified anoplocephalid ($P < 0.001$), and *V. venezuelensis* ($P < 0.001$) are more frequent in *M. murina*. No differences were detected in the infections caused by the nematodes *A. raillieti*, *H. simplicispicula, S. guianensis*, *Travassostrongylus* sp., and the acanthocephalan *O. microcephala*.

DISCUSSION

To our knowledge, this study is the first characterization of helminth infections in any species of mouse opossum from French Guiana. It is also the first comparison of helminth parasites in 2 sympatric species of mouse opossums, which in this case includes *M. demerarae* and *M. murina*. In total, 14

species of helminths were recovered between both species; of this total, 12 were shared. With the exception of *S. guianensis* collected in *M. murina*, all species of parasites represent new records of infections for both species of mouse opossums. Species of parasites that represent new records for the country include *P. philanderi*, *P.* (*Paucipectines*) *elegans*, *V. venezuelensis*, *H. simplicispicula*, and *S. trinitatis*.

The species richness of the component communities for both species of *Marmosa* was higher than the species richness reported for *Philander opossum* and *Didelphis marsupialis* in the same localities (Jiménez et al., 2011). Moreover, larger-bodied opossums and mouse opossums share 6 species of parasites. The finding of the same parasite species in 4 sympatric species of marsupials suggests that all didelphid marsupials are exposed to the same sources of infection and that they are compatible with the parasites. Because all helminths were recovered as adults, these findings also suggest that all shared parasites are compatible with these marsupial hosts. However, the parasites found in mouse opossums show relatively low prevalence values, mean intensities, and mean abundances. The predilection of *M. demerarae* and *M. murina* to move through different strata in the forest may explain their different exposure to parasites from different layers or habitats. The murine opossum, *M. murina*, is scansorial and uses lower forest strata, whereas *M. demerarae* is arboreal and primarily uses the canopy. This difference in use of habitat may help to explain the more diverse helminth fauna (14 species) of *M. murina* relative to *M. demerarae*, because murine opossums may be exposed to infective stages of parasites localized in the ground and in the lower canopy (young and/or small trees) levels, whereas *M. demerarae* may be exposed to infective stages present exclusively in the canopy. The infections of *P. philanderi* are consistent with this phenomenon, since this species of digenean is only found in arboreal animals, including the woolly opossum, *Caluromys derbianus*, and the woolly mouse opossum, *M. demerarae*.

The infracommunities of mouse opossums consist of an average of 3 species that each occur in low abundance (Table 1). The composition of these infracommunities may be explained by different factors, including the arboreal and scansorial habits of the mouse opossums, which decrease the chances of an individual opossum encountering contaminated feces (Püttker et al., 2008). The low species richness per infracommunity in mouse opossums may suggest that a single individual is not exposed to the infective stages of several parasites throughout its life span due to its limited local movements. Vagility, as defined by Kennedy et al. (1986), refers to a host's movement over its habitat and is relevant because movement patterns explain the exposure of the potential host to a variety of risk factors for helminth infection. Animals with lower vagility show local movements over a smaller area that usually consists of a single type of habitat. Such localized area movement contrasts with that seen in animals with greater vagility and could be the case for larger-bodied opossums, which are able to move though a larger area that may include varying habitats (Sunquist et al., 1987).

The resulting area accumulation curves show no convergence in the predicted values of species richness and confidence intervals for *M. murina*. This suggests that it would be possible to recruit more common species of parasites by increasing sample size. The area accumulation curves for *M. demerarae* show that the predicted value of species richness and its confidence intervals predict the same number of species (convergence) at 15 individuals, suggesting that the sample of 21 individuals of *M. demerarae* was sufficient to recover the common parasite species infecting this mouse opossum. This finding also appears to be congruent with the apparent habitat specialization of *M. demerarae* (Julien-Laferrière, 1991; Guillemin et al., 2001; Cáceres et al., 2002; Pinheiro et al., 2002; Vieira and Monteiro-Filho, 2003), and it suggests that individuals may be exposed to a limited pool of parasites, perhaps within in the canopy.

Intra- and interspecific similarity is lower than 18% among infracommunities of *M. demerarae* and *M. murina*. These low values of similarity are the result of the poor species richness per infracommunity. Overall, considering only infected individuals, the average species richness was similar in both species (3.8 in *M. murina* vs. 3.7 in *M. demerarae*). Although individuals of *M. murina* can become infected by all 14 species present in the sample, 28% of the infracommunities of *M. murina* had a species richness of zero, which may suggest that these marsupials have a low chance of encountering their parasites. The case of *M. demerarae* may be different in that these opossums might never encounter certain species of parasites or that they may be incompatible with them. The latter is derived from the observation that both the unidentified anoplocephalid and *S. philanderi* were not present in *M. demerarae*. Nevertheless, this phenomenon could be the result

of the marsupial's specialization to forage in the canopy, which translates into a relatively lower vagility and limited exposure to the infective stages of those parasites.

The differences in foraging behavior and habitat between *M. demerarae* and *M. murina* may account for the statistically significant differences in the intensity of the infection by some species of helminths. Five species of parasites occurred more frequently in *M. demerarae*, compared to 3 species of parasites that occurred more frequently in *M. murina*. The causes for the different structures of these parasite communities, as well as a number of their attributes, remains yet to be elucidated, and phylogeny may likely play a considerable role in doing so. *Marmosa demerarae* and *M. murina* are not reciprocal sister taxa (Gutiérrez et al., 2010), which suggests that a phylogenetic component may contribute to these differences, including immune system differences, different physiological adaptations, and different foraging behaviors. Other studies have demonstrated that both parasite load and the diversity of helminth morphotypes are dependent on the number of alleles involved in the immune response of the marsupials, and that this variability is host-species dependent (Meyer-Lucht et al., 2010). Our results document differences in the helminth fauna composition of closely related taxa, which may be a reflection of the different exposure and compatibility of marsupials towards their parasites.

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