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Parasites of Wild Howlers (*Alouatta* spp.)

Michael Stuart,[1] Vickie Pendergast,[1] Susan Rumfelt,[1] Suzanne Pierberg,[1] Lisa Greenspan,[1] Kenneth Glander,[2] and Margaret Clarke[3]

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*A literature review of howler parasites provides the basis for an overview of the ecological significance of parasite surveys in primates. Within this framework, we have added insights into the interactions between primate hosts and their parasites from a long-term study in Costa Rica. We collected fecal samples from mantled howlers (*Alouatta palliata*) over a 9-year period (1986–1994 inclusive) and analyzed them for parasite eggs, larvae, cysts, and oocysts. We found many misperceptions inherent in the typical methodology of primate parasite surveys and in the reporting of the findings. Our work in Costa Rica suggests that a snapshot effect occurs with most surveys. A static view does not reflect the dynamic and changing ecological interaction between host and parasite. We describe some problems with parasite data analyses that emphasize the need for long-term longitudinal surveys in wild primate groups.*

KEY WORDS: primates; parasites; survey; Costa Rica; *Alouatta*.

INTRODUCTION

Like all other organisms, howlers exist and evolve within a framework established by an interaction with the physical aspects of the environment and the intra- and interspecific relationships with other organisms. Para-

[1]Department of Biology, University of North Carolina at Asheville, Asheville, North Carolina 28804.
[2]Department of Biological Anthropology & Anatomy, Duke University, Durham, North Carolina 27706.
[3]Tulane Regional Primate Research Center, Covington, Louisiana.

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sites—members of a different species that exist at the expense of the host species—clearly influence host ecology in a variety of ways (Price *et al.,* 1986, 1988). The parasites themselves are faced with major ecological problems in getting their offspring from one host island to another. Many parasitic species have evolved elaborate life cycles to accomplish this goal. The life cycles usually interface with the host's feeding or behavioral patterns in some manner that enhances probability of transmission. Parasites should not be surveyed simply as discrete passengers or invaders within an innocent primate, but as members of a functional ecosystem in which the monkey and the parasite are interrelated elements. From this perspective, parasites can provide clues about host feeding patterns, frequency of contact with intermediate hosts, host distribution patterns, and competitive interactions. Primatologists are in a unique position to collect and utilize parasites as ecological indicator species that provide insight into primate ecology (Stuart and Strier, 1995).

Unfortunately, our knowledge of the parasitic fauna of howlers is fragmentary. Parasitologists often work with a single parasitic group, usually one of medical or economic importance to humans. A researcher surveying large numbers of animals for the presence of blood parasites is unlikely to invest the considerable time and effort required for an examination of gut contents that contain nothing of interest to that particular research project. Access to many of the more obscure South and Central American journals can also be a problem. In some cases, even the presence of papers of interest in those journals is difficult to ascertain. Overviews of parasites in a particular group of animals (Dunn, 1968; Fiennes, 1972; Toff, 1986) may include reports of parasites that are artifacts of captivity or experimental research and which have little bearing on wild populations other than noting susceptibility. Taxonomic confusion over host and parasite nomenclature adds to the problem. A parasitologist looking at a report of worms in *Alouatta ursina* has little way of knowing if the author was discussing *A. fusca* or *A. seniculus*. A similar problem exists for the identity of *Alouatta villosa*. Here we follow Smith (1970) and Hall (1981) in considering the Guatemalan howler to be *Alouatta pigra* rather than *A. villosa*. However, reports of *Alouatta villosa* from Panama (Sousa *et al.,* 1974) are considered to refer to *A. palliata*. The same nomeclatural situation applies to many of the parasitic species, particularly nematodes which are notoriously difficult to identify. We follow Anderson *et al.* (1974) for taxonomic organization of this complex and confusing phylum.

Primate populations are so reduced in many regions that sacrifice of adequate numbers for a comprehensive parasite survey is not an ethically viable alternative. Coprological examination of the host for parasitic eggs and larvae offers an excellent means to sample parasitic presence quickly

and cheaply, provided the parasite producing the egg is known. The methodology is well established and standardized (Long *et al.,* 1985). Although coprological examinations produce helpful information and are not invasive to the host, the effectiveness is limited in many wild species, including howlers by the similarity in appearance of eggs or cysts from related parasites and the lack of adult helminths to confirm identification. Howler species in areas with major research facilities (Panama, Brazil, Argentina) have received a disproportionate amount of attention over species in other countries. Finally, no parasitic survey of any group of Neotropical primates can be definitive without considering other species of monkeys that are either sympatric or have been sympatric in recent history. The desirability of spider monkeys, capuchins, and squirrel monkeys for food by human populations has eliminated them in some areas, leaving only the relatively unpalatable howlers. Ongoing fieldwork in Costa Rica suggests that this selective culling of primate species can allow exploitation of new resources and exposure to new parasites, leading to the presence of a parasite in an otherwise abnormal host such as a howler. Few investigators, aside from Dunn (1968), have attempted to establish an overall picture of parasitism and host specificity in Neotropical primates. Simply because a particular parasite has been reported in one group of howlers does not establish that species as part of the normal parasitic fauna or that it is likely to be found in all parts of the range of that species, much less in another howler species.

The combination of these problems prompted us to attempt a compilation of significant parasite/host reports form the literature as a baseline from which future investigations may begin. Tables I and II list previous reports on howler parasites by host species and by parasite classification, respectively. The taxonomic classifications used in the tables reflect the present state of contradictory terminology for both parasites and hosts. The organisms under review include ones traditionally considered parasites: the protozoa, cestodes and trematodes, nematodes, thorny-headed worms, and arthropods. Viruses, rickettsia, fungi, and bacteria are not included.

PROTOZOAN PARASITES

New World trypanosomes (*Trypanosoma* spp.) are flagellated blood and tissue parasites that utilize kissing bugs (order Hemiptera: family Reduviidae) as intermediate hosts and vectors. Identification is often difficult because of changes in appearance at different life cycle stages and because many morphologically indistinguishable forms are found naturally in different hosts. Trypanosomes have been reported from *Alouatta belzebul, A. caraya, A. palliata*, and *A. seniculus* (Dunn *et al.,* 1963). The validity of

Table I. Host–Parasite Citations for *Alouatta* spp.

	No. infected/ No. examined	Country	Reference(s)
Alouatta belzebul			
Plasmodium brasilianum	0/49	Brazil	Deane *et al.*, 1969; Ferreira *et al.*, 1970; Deane, 1971
Trypanosoma minasense		Brazil	Deane and Damasceno, 1961
Trypanosoma mycetae		Brazil	Deane and Damasceno, 1961; Deane, 1967b; Hoare, 1972
		Eastern Brazil	Dunn *et al.*, 1963
Mathevotaenia (= *Oochoristica*) *megastoma*		—	Dunn, 1963
		Brazil	Stiles *et al.*, 1929
Ascaris elongata (?)		Brazil	Stiles *et al.*, 1929
Cebidicola (= *Tricho-dectectes*) sp.		—	Stiles *et al.*, 1929
Alouattamyia baeri		Brazil	Guimaraes, 1971
A. caraya			
Plasmodium brasilianum		Brazil	Deane and Ferreira, 1973
Trypanosoma cruzi	1/30	Argentina	Travi *et al.*, 1986
	1/1	Brazil	Funayama and Baretto, 1970
Trypanosoma mycetae		Brazil	Hoare, 1972; Dunn *et al.*, 1963
		Argentina	Hoare, 1972; Dunn *et al.*, 1963
Balantidium aragãoi		Brazil	Stiles *et al.*, 1929
Chilomastix sp.			Stiles *et al.*, 1929
Retortamonas intestinalis			Stiles *et al.*, 1929
Giardia intestinalis			Stiles *et al.*, 1929
Entamoeba sp.		Brazil	Stiles *et al.*, 1929
Trichomonas sp.		Brazil	Stiles *et al.*, 1929
Bertiella mucronata	6/84	Argentina	Pope, 1966
	6/88	Argentina	Coppo *et al.*, 1979
		Paraguay	Stiles *et al.*, 1929; Dunn, 1963
Mathevotaenia megastoma		Brazil	Dunn, 1963; Stiles *et al.*, 1929
Moniezia rugosa			Dunn, 1963
Ancylostoma spp.			Stiles *et al.*, 1929
Ancylostoma quadridentata			Stiles *et al.*, 1929
Longistriata dubia		Brazil	Durette-Desset, 1963, 1969
Ascaris lumbricoides			Boero *et al.*, 1968
Trypanoxuryis minutus	19/88	Argentina	Pope, 1966
	3/88	Argentina	Coppo *et al.*, 1979
		Brazil	Inglis and Diaz-Ungria, 1959
Dipetalonema gracile			Stiles *et al.*, 1929
Filaria sp.		Brazil	Stiles *et al.*, 1929
Amblyomma sp. (larva)		Argentina	Moriena *et al.*, 1979
Amblyomma sp.	1/88	Argentina	Coppo *et al.*, 1979
Pediculus mjobergi			Boero and de Boehringer, 1963
	111/302	Argentina	Pope, 1966
	45/88	Argentina	Coppo *et al.*, 1979
Cebidicola semiarmatus		Brazil	Emerson and Price, 1975

Table I. Continued

	No. infected/ No. examined	Country	Reference(s)
A. fusca			
Plasmodium sp.			
(*P. brasilianum* and		Brazil	Deane, 1971
simium combined)	235/446	Brazil	Deane *et al.*, 1969
Plasmodium brasilianum		Brazil	Deane, 1967; Deane *et al.*, 1968
		Brazil	Deane and Ferreira, 1969
Plasmodium simium		Brazil	da Fonesca, 1951
		Brazil	Deane, 1967
		Brazil	Deane and Almeida, 1967
Trypanosoma mycetae		Brazil	Deane and Damasceno, 1961
Trypanosoma hippicum			Stiles *et al.*, 1929
Trypanosoma venezuelense			Stiles *et al.*, 1929
Moniezia rugosa			Dunn, 1963
Trichuris dispar			Stiles *et al.*, 1929
Trypanoxuryis minutus		Venezuela	Inglis and Diaz-Ungria, 1959
		Venezuela	Diaz-Ungria, 1965
Parabronema bonnei		Venezuela	Diaz-Ungria, 1963, 1965
Dipetalonema gracile		Venezuela	Diaz-Ungria, 1965
Microfilaria sp.		Brazil	Stiles *et al.*, 1929
Cebidicola (= *Trichodectectes*) *semiarmatus*		Brazil	Stiles *et al.*, 1929; Emerson and Price, 1975
A. palliata (combined with reports on *A. villosa* from Panama)			
Plasmodium brasilianum	2/8	Panama	Clark, 1931
Plasmodium brasilianum	1/66	Panama	Dunn and Lambrecht, 1963
Plasmodium simium (expert)			Rossan *et al.*, 1975
Plasmodium falciparum (exper)			Baerg and Young, 1970; Rossan and Baerg, 1975
Trypanosoma mycetae		Guatemala	Hoare, 1972; Dunn *et al.*, 1963
	2/117	Panama	Sousa *et al.*, 1974
trypanosomes	5/8	Panama	Clark, 1931
Trichomonas sp.	6/8	Panama	Hegner, 1935
Giardia sp.	4/8	Panama	Hegner, 1935
Entamoeba (= *Endamoeba*) sp.	1/8	Panama	Hegner, 1935
Chilomastix sp.	1/8	Panama	Hegner, 1935
Retortamonas sp.	1/8	Panama	Hegner, 1935
Isospora arctopitheci (exper)		Panama	Hendricks, 1977
Toxoplasma sp.	0/8	Panama	Frenkel and Sousa, 1983
Controrchis biliophilus	50/155	Costa Rica	Stuart *et al.*, 1988
		Mexico	Gonzalez *et al.*, 1983
	5/5	Costa Rica	Jiménez-Quirós and Brenes, 1957

Table I. Continued

	No. infected/ No. examined	Country	Reference(s)
Raillietina demerariensis	1/54	Panama	Thatcher and Porter, 1968
unid. strongylid	22/155	Costa Rica	Stuart *et al.*, 1988
Trypanoxyuris minutus	152/155	Costa Rica	Stuart *et al.*, 1988
	14/84	Panama	Thatcher and Porter, 1968
Parabronema bonnei	1/84	Panama	Thatcher and Porter, 1968
Dipetalonema (= *Tetrapetalonema*) *marmosetae*	4/106	Panama	Sousa *et al.*, 1974
Prosthenorchis elegans	1/84	Panama	Thatcher and Porter, 1968
Alouattamyia baeri		Costa Rica	Zeledon *et al.*, 1957
		Guyana and Panama	Shannon and Greene, 1926
		Panama	Dunn, 1934; Goldman, 1920
A. pigra			
No parasites reported			
A. seniculus			
Plasmodium brasilianum	2/18	Brazil	Deane and de Almeida, 1967
		Brazil	Deane and Ferreira, 1969
		Brazil	Deane *et al.*, 1968
		Brazil	Deane *et al.*, 1970
	0/2	Colombia	Dunn and Lambrecht, 1963
Trypanosoma cruzi		Venezuela	Hoare, 1972
Tyrpanosoma hippicum			Stiles *et al.*, 1929
Trypanosoma lambrechti		Brazil	Deane *et al.*, 1970
Trypanosoma mycetae		French Guiana	Hoare, 1972; Dunn *et al.*, 1963; Stiles *et al.*, 1929
Trypanosoma venezuelense			Stiles *et al.*, 1929
Trypanosoma sp.		Fr. Guiana	Stiles *et al.*, 1929
Balantiium sp.			Stiles *et al.*, 1929
Toxoplasma sp.			Stiles *et al.*, 1929
Controrchis biliophilus		Brazil	Gomes and Pinto, 1978
Raillietina alouattae	2/?	Surinam	Baylis, 1947
	1/1	Br. Guyana	Dunn, 1963; Perkins, 1950
Raillietina demerariensis		Surinam	Dunn, 1963; Joyeux and Baer, 1948
Trichuris dispar			Stiles *et al.*, 1929
Trypanoxyuris minutus	1/1	Colombia	Hugghins, 1963
		Brazil	Stiles *et al.*, 1929; Inglis and Diaz-Ungria, 1959
	1/1	Surinam	Van Thiel, 1925
Ascaris lumbricoides			Canavan, 1929, 1931
Parabronema bonnei		Surinam	Van Thiel, 1925
Physaloptera dilatata	1/1	Colombia	Hugghins, 1963
Filariopsis asper		Surinam	Stiles *et al.*, 1929
Amblyomma cajennense		Venezuela	Jones *et al.*, 1972
Amblyomma spp.		Venezuela	Jones *et al.*, 1972
Cebidicola extrarius		Venezuela	Emerson and Price, 1975

Table I. Continued

	No. infected/ No. examined	Country	Reference(s)
Cebidicola semiarmatus		Brazil	Emerson and Price, 1975
Alouattamyia baeri		Br. Guiana	Stiles *et al.*, 1929
Alouatta sp.			
Trypanosoma brimonti (from A. *pigra*?)		Guatemala	Dunn *et al.*, 1963
Tetrapetalonema sp.			Dunn, 1968
Amblyomma cajennense		Brazil	Aragão, 1936

Table II. Taxonomic List of Parasites Reported from *Alouatta* spp.

Phylum Sarcomasticophora
- Subphylum Mastigophora
  - Class Zoomastigophora
    - Order Kinetoplastida
      - Family Trypanosomatidae
        - *Trypanosoma cruzi* (Chagas, 1909)
        - *T. brimonti* Giaquinto, 1933
        - *T. florestali* Romaña, 1932
        - *T. hippicum* Darling, 1910
        - *T. lambrechti* Marinkelle, 1968
        - *T. manguinhense* Qrantes and da Fonseca, 1932
        - *T. minasense* Chagas, 1909
        - *T. mycetae* Brumpt, 1913
        - *T. venezuelense* Mesnil, 1910
    - Order Retortamonadida
      - Family Retortamonadidae
        - *Chilomastix* sp.
        - *Retortamonas intestinalis* (Wenyon and O'Connor, 1917) Wenrich, 1932
    - Order Diplomonadida
      - Family Hexamitidae
        - *Giardia lamblia* Stiles, 1915
    - Order Trichomonadida
      - Family Trichomonadidae
        - *Trichomonas* sp.
- Subphylum Sarcodina
  - Class Rhizopodea
    - Order Amoebida
      - Family Endamoebidae
        - *Entamoeba* (=*Endamoeba*) sp.
        - *Entamoeba histolytica* (exper.)

Phylum Apicomplexa
- Class Sporozoa
  - Order Eucoccida
    - Family Eimeriidae
      - *Isospora arctopitheci* (exper.)

Table II. Continued

Family Sarcocystidae
Toxoplasma gondii Nicole and Manceaux, 1908
Family Plasmodiidae
Plasmodium brasilianum Gonder and von Berenberg-Gossler, 1908
P. simium da Fonseca, 1951
P. falciparum (exper.)

Phylum Ciliophora
Class Ciliata
Order Prostomatida
Family Balantidiidae
Balantidium sp. (prob *B. coli*)
B. aragãoi Da Cunha and Muniz, 1927

Phylum Platyhelminthes
Class Trematoda
Order Digenea
Family Dicrocoelidae
Controrchis biliophilus Price, 1928
Class Cestoda
Order Cyclophyllidea
Family Anoplocephalidae
Mathevotaenia (=*Oochoristica*) *megastoma* (Diesing, 1850) Spasski, 1951
Bertiella mucronata (Meyner, 1895) Stiles and Hassall, 1902
Moniezia rugosa (Diesing, 1850) Luhe, 1895
Family Davaineidae
Raillietina alouattae Baylis, 1947
R. demerariensis (Daniels, 1895) Lopez-Neyra, 1931

Phylum Nematoda
Class Aphasmidea
Order Trichurata
Family Trichuridae
Trichuris sp.
Trichuris dispar Rudophi, 1802
Class Phasmidea
Order Strongylata
Unid. strongylid
Superfamily Ancylostomatoidea
Family Ancylostomatidae
Ancylostoma spp.
A. quadridenata Molin, 1861
Superfamily Metastrongyloidea
Family Filariodidae
Filariopsis (=*Filariodes*) *asper*
Superfamily Trichostrongyloidea
Family Viannaiidae
Vianella (=*Longistriata*) *dubia* Durette-Desset, 1963
Order Ascaridata
Family Ascarididae
Ascaris lumbricoides Linnaeus, 1758
Ascaris elongata (?) Rudophi, 1802
Order Oxyurata

Table II. Continued

	Family Oxyuridae
	Trypanoxyuris minutus (Schneider, 1866)
	Order Spirurida
	Family Physalopteridae
	Physaloptera dilatata Rudophi, 1802
	Family Habronematidae
	Parabronema (= *Squamanema*) *bonnei* (van Thiel, 1925) Diaz-Ungria, 1965
	Order Filariata
	Family Onchocercidae
	Dipetalonema gracile (Ruldolphi, 1809)
	D. marmosetae (Faust, 1935)
	Tetrapetalonema sp.
	Family Filariidae
	Filaria sp.
Phylum Acanthocephala	
Class Archiacanthorhynchida	
	Order Oligacanthorhychida
	Family Oligacanthorhynchidae
	Prosthenorchis elegans (Diesing, 1851)
Phylum Arthropoda	
Class Arachnida	
	Order Acari
	Family Ixodidae
	Amblyomma sp.
	A. cajennense (Fabricius, 1787)
Subphylum Uniramia	
Class Insecta	
	Order Anoplura
	Family Pediculidae
	Pediculus mjobergi Ferris, 1916
	Order Mallophaga
	Family Trichodecctidae
	Cebidicola (=*Trichodectes*) *extrarius* (Neumann, 1913)
	C. semiarmatus (Neumann, 1913)
	Order Diptera
	Family Cuterebridae
	Alouattamyia baeri (Shannon and Greene, 1925)

many species of *Trypanosoma* and the relationship between the various named species are unclear and controversial. Many are simply lumped as *T. rangeli*-like. The trypanosome species reported from *Alouatta* spp. are listed in Tables I and II without any attempt on our part to evaluate critically the validity of each species. One of the Central and South American trypanosomes, *Trypanosoma cruzi*, is a significant and dangerous disease of humans. However, only Funayama and Baretto (1970) and Travi *et al.* (1986) have reported naturally occurring *Trypanosoma cruzi* infections in howlers. Marinkelle (1982) surveyed primates in Colombia and reported

Trypanosoma cruzi from 15 of the 18 primate species examined. No *Alouatta seniculus* was infected, but Marinkelle (1982) examined only three individuals. Considering the range of primate hosts that can be infected, howlers must still be considered potential reservoir hosts for *Trypanosoma cruzi*.

Most of the other flagellates (*Chilomastix, Retortamonas, Giardia*, and *Trichomonas*) are intestinal commensals or parasites of humans, causing relatively little pathogenesis. Many reports probably reflect contact with humans rather than the normal parasitic fauna of howlers. However, *Retortamonas* (= *Embadomonas*) *intestinalis* may occur naturally through accidental ingestion of an insect host (Cheng, 1964).

Two species of malarial parasites, *Plasmodium brasilianum* and *P. simium*, have been reported from Neotropical primates. Clark (1931) reported *Plasmodium* sp. in several Panamanian primates. The species was later identified as *Plasmodium brasilianum* by Taliaferro (1932). Dunn and Lambrecht (1963) stated that while *Plasmodium brasilianum* had been found in almost all cebid genera, *P. simium* was found only in *Alouatta fusca* from Brazil. They listed *Plasmodium brasilianum* in 3 of 74 howlers from Panama, neither of 2 red howlers from Colombia, and none of 34 black howlers from Brazil. Their other records suggest that spider monkeys (*Ateles geoffroyi*) are more significant hosts (62/387) than howlers, at least in Central America. Deane (1967a) and Deane *et al.* (1969) summarized many years of investigation into primate malarial hosts in Brazil and reported that 235 of 446 *Alouatta fusca* and 5 of 39 *A. seniculus* were infected with *Plasmodium*. One *Alouatta nigerrima* (?), 49 *A. belzebul*, and 3 *A. caraya* were uninfected. *Ateles paniscua* and *Lagothrix lagotricha* were also common hosts, with infection rates varying from 25 to 42%. Deane (1967a) clarified the distribution of the 2 species of *Plasmodium* in Brazil by determining that *P. simium* occurs only in the coastal mountain forests of the southern states, So Paulo and Santa Catarina. *Plasmodium brasilianum* occurs both in the southern states and in the Amazon.

Dunn (1965) believed that *Plasmodium brasilianum* was virtually identical to *P. malariae* of humans, and *P. simium* corresponded to *P. vivax*. Dunn (1965) commented that both *Plasmodium brasilianum* and *P. simium* probably reflect a post-1492 introduction of malaria by humans from the Old World and subsequent adaptation to Neotropical primates. Deane (1967a) reported that a forest guard contracted *Plasmodium simium* while using himself as bait in a canopy collecting station. Both species of *Plasmodium* must be considered as actual or potential zoonotic diseases, though relatively little cross-infection has been demonstrated. Additional fieldwork is needed to clarify the ecology of these two species of primate malaria.

TREMATODA (FLUKES)

Dicrocoelid trematodes occur widely in both New and Old World monkeys (Goldberger and Crane, 1911; Stunkard and Goss, 1950; Kingston and Cosgrove, 1967; Thatcher and Porter, 1968), usually species that use insects as a larger dietary component than is characteristic of howlers. However, Sandground (1929) described *Dicrocoelium colobusicola* from folivorous *Colobus* sp. in Africa. Typically dicrocoelids utilize two intermediate hosts; the first is a snail that consumes the eggs in feces. The second intermediate host, often an ant, eats slime balls passed by the snail. The slime balls contain larval trematodes. Final transmission occurs when the definitive host consumes the ant or other arthropodan host. An important dicrocoelid in howler monkeys is *Controrchis biliophilus*, which Price (1928) originally described from a spider monkey (*Ateles geoffroyi*) that had died in the U.S. National Zoo. The origin of the monkey was not given by Price, but the species suggests Central America. Jiménez-Quirós and Brenes (1957) described *Controrchis caballeroi* from mantled howlers in the Cañas area of Costa Rica but it differed only in size from Price's description of the nominate species. Since howlers and spider monkeys were historically sympatric around Cañas, this size difference probably reflects differences in host rather than different parasitic species. The life cycle of the species and the mode of host infection are unknown.

CESTOIDEA

Cestodes (tapeworms) generally cause little pathogenesis or problems in the definitive host other than utilizing a portion of the hosts' food and vitamins. There is no suggestion that natural infections pose a serious health hazard for wild howlers though some of the species infecting them occasionally infect humans (Joyeux and Baer, 1929). *Bertiella* sp. and *Moniezia* sp. are probably transmitted through consumption of oribatid mites (Dunn, 1963).

Raillietina spp. from howlers are normally found in histricomorph rodents (Dunn, 1962). Dunn (1962, 1963) suggested that *Raillietina alouattae* and *R. demerariensis* could be accidental in howlers and stated that the taxonomic status of these two species as well as that of *R. trinitatae* is unclear. The status of *Railietina multitesticulata*, which Dunn (1963) believed to be synonymous with *R. alouattae*, is also unclear. We follow Dunn (1963) and identify Perkins' (1950) drawing as *Railietina alouattae*. Other reports (Fiennes, 1967) suggest that *Railietina alouattae* is synonymous with *R. demerariensis*.

Mathevotaenia megastoma has several synonyms (*Taenia metastoma, Oochoristica megastoma, Atriotaenia megasttoma,* and *Bertiella fallax*. We follow Schmidt (1986) in placing the species in *Mathevotaenia* based on a simple genital atrium. Dunn (1963) suggested that beetles, moths, or butterflies could serve as intermediate hosts. Presumably the intermediate hosts would be accidentally consumed when howlers ate flowers or fruits.

NEMATODA

Roundworms (nematodes) occur more frequently than either trematodes or cestodes in howlers. Several of the genera—(*Trichuris, Ancylostoma, Ascaris*)—are common parasites of humans. In the case of all three nematodes, reports usually contain little information other than listing presence of the parasites (Stiles *et al.,* 1929; Canavan, 1929, 1931; Dunn, 1968). It is unclear whether they represent natural infections, captive infections, or zoonotic infections from howler/human interactions.

The roundworms most commonly reported from howlers are *Trypanoxyuris minutus, Squamanema* (=*Parabronema*) *bonnei*, and *Dipetalonema gracile*. *Trypanoxyuris* is the howler equivalent of the ubiquitous pinworm of humans. These nematodes probably have a direct life cycle maintained by fecal contamination and egg ingestion. Inglis and Diaz-Ungria (1959) described 6 species of *Trypanoxyuris* in Neotropical primates, including *T. minutus* in *Alouatta seniculus, A. caraya*, and *A. fusca*. Host specificity in oxyurid pinworms are well-known (Brooks and Glen, 1982) but the exact relationship of *Trypanoxyuris* spp. to each other and to their primate hosts outside of Venezuela remains uncertain.

Parabronema is usually described as a spirurid parasite of elephants (Cheng, 1964), but there are several reports of *Squamanema* (= *Parabronema*) *bonnei* in howlers (Table I). As with most other spirurids, transmission presumably occurs via ingestion of an insect host but the actual life cycle is unknown.

Dipetalonema gracile is a filarial worm found in the body cavity of many cebids. Transmission of the microfilaria into the primate host is presumed to be through the feeding of a mosquito but virtually nothing is known of its life history or ecology. Dunn (1968) listed a related genus, *Tetrapetalonema*, from howlers and other Neotropical primates. However, Sousa *et al.* (1974) reported 4 of 106 howlers from Panama parasitized by *Dipetalonema marmosetae*, a species originally described by Faust (1935) as *Tetrapetalonema marmosetae*. Anderson *et al.* (1974) list *Tetrapetalonema* as a valid genus but only of humans, apes and Asian primates. Taxonomic

disagreements over filarial worm classification confound the identity of this parasite.

ACANTHOCEPHALA

Thorny-headed worms are common and important parasites of many Neotropical primates, particularly marmosets. They damage the gut of the host and open a pathway for secondary bacterial infection. Cockroaches often serve as intermediate hosts in captivity. Only Thatcher and Porter (1968) have reported a thorny-headed worm (*Prosthenorchis elegans*) in *Alouatta* sp: the monkey was held at an animal dealer's shop for over a month and infection was probably accidental.

ARTHROPODA

Some forms of maturing dipteran (fly) larvae develop subcutaneously on warm-blooded vertebrates. *Alouattamyia baeri* infested an owl monkey (*Aotus trivirgatus*) and *Alouatta belzebul* in Brazil (Guimares, 1971). Shannon and Greene (1926) described this bot fly species from *Alouatta palliata* in Guyana and Panama, while Zeledon *et al.* (1957) reported it from *A. palliata* in Costa Rica. Goldman (1920) described all of the howlers collected in the Panama Canal Zone with numerous larvae, primarily in the skin of the throat. Shannon and Greene (1926) thought that the eggs of *Alouattamyia* sp. might be consumed along with leaves by the monkey and then burrow to the region of the throat. However, rodent and cattle experiments suggest that the location of the bot is species specific and not determined by entry location (Catts, 1965). Other arthropodan parasites include the sucking louse, *Pediculus mjobergi*, and the biting lice, *Cebidicola extarius* and *C. semiarmatus*, though their prevalence is not as great as expected given that howlers do not usually groom each other.

COPROLOGICAL EXAMINATION OF MANTLED HOWLERS IN COSTA RICA

Mantled howlers at Hacienda La Pacifica have been part of long-term ecological and behavioral studies since 1972 (Glander, 1975, 1980, 1981, 1992; Clarke and Glander, 1984; Clarke *et al.*, 1986; Stuart *et al.*, 1990; Moreno *et al.*, 1991; Teaford and Glander, 1991). Hacienda La Pacifica is a privately owned cattle ranch covering 1980 ha at the base of the Cordil-

lera de Tiliran, 5 km northwest of Cañas, Guanacaste Province, Costa Rica, at latitude 10°28'N and longitude 85°07'W. The ranch is 45 m above sea level within the lowland tropical dry forest life zone. Approximately 600 ha of semideciduous forest remains on the ranch in several large tracts as well as wind-break strips and riparian forests. As part of the long-term studies, as many howlers as possible are captured once per year for measuring, marking, and sexing of newborns.

Stuart *et al.* (1990) reported the initial results of our parasite survey. Further collection allowed longitudinal monitoring of the same individuals across several years and provide insight into the changing dynamics of the parasite–host relationship. Other samples were collected and examined from 15 howlers and 1 capuchin from Curu at the tip of the Nicoya Peninsula, 4 howlers in Guanacaste National Park, 34 howlers and 19 spider monkeys from Santa Rosa National Park, 2 howlers from La Selva, 15 howlers and 25 spider monkeys from Los Inocentes, and 1 howler and 8 capuchins at Lomas Barbudal National Park. Our objectives were to contrast parasitic infections in the same individuals across several years, to contrast infections in both wet and dry seasons, and to contrast the infection picture at La Pacifica with that of howler groups in other localities, particularly those where other nonhuman primate species occur sympatrically with them.

At La Pacifica there is no statistical difference in total parasite prevalence between males and females ($\chi^2 = 0.31$, $P = 0.577$) or between age groups (0–1, 1–3, 3–15, and >15 yr). However, when the prevalence of each parasite species is analyzed separately, *Controrchis biliophilus* presented a distinctive pattern, with infected levels of 4, 17, 25, and 33% for the respective age groups. We also found significantly more ($\chi^2 = 7.9$, $P = 0.005$) howlers parasitized with *Controrchis biliophilus* in dry forest (30%) than in riverine forests (13%). We compared 12 social groups with ≥10 individuals sampled. They exhibit significant differences ($\chi^2 = 20.1$, $P = 0.043$) in parasitic distribution among the groups. This agrees well with the results of Freeland (1979), who suggested that parasitic prevalence will be more similar within a social group than between separate groups.

A slight shift was seen in the parasitic species or infection rates of the La Pacifica subjects over ≥2 consecutive years. Of those samples collected at the same time of year but during different years, 5 subjects showed a change in parasitic species. Fourteen howlers had ≥1 samples collected during both the wet and the dry seasons, and they showed major shifts in the parasitic fauna between the two seasons. Seven of the individuals showed ≥1 species of *Entamoeba*. Based on size, nuclear number, and nuclear morphology, we identified *Entamoeba coli*, *E. hartmanii*, and *E. histolytica*. Three howlers were infected with *Giardia intestinalis*. They are all common

commensals or parasites of humans and suggest a human/primate/parasite connection at this site and a greater likelihood of the monkeys becoming infected during the wet season.

Samples from other Costa Rican sites show essentially the same suite of common parasites; *Entamoeba* spp., *Giardia intestinalis*, *Isopora arctopitheci*, *Controrchis biliophilus*, *Trypanoxyuris minutus*, *Strongyloides cebus*, an unidentified spirurid nematode, and several types of unidentified nematode larvae). However, the difference in relative prevalence of parasitic species in the same monkey species at the different sites is significant ($\chi^2 = 14.8$, $P = 0.000$). *Controtchis biliophilus* occurred in 67% of the Curu howlers, 47% of the Los Inocentes howlers, 24% of the La Pacifica howlers, and 9% of the Santa Rosa howlers. Similar differences characterize the prevalence of *Strongyloides cebus* (73, 13, 12, and 9%) from the same sites, respectively. Sample sizes from Guanacaste National Park, Lomas Barbudal, and La Selva are too small to test the data. Comparison among primate species also demonstrates differences, with 49% of *Ateles*, 51% of *Alouatta*, and 91% of *Cebus* being parasitized ($\chi^2 = 6.9$, $P = 0.032$). The pattern of infection changed, depending on the particular parasitic species. The prevalence of *Controrchis biliophilus* infections was 2, 26, and 9% in *Ateles*, *Alouatta*, and *Cebus* respectively ($\chi^2 = 13.5$, $P = 0.001$), but the prevalence of *Strongyloides cebus* was only 7, 15, and 0% ($\chi^2 = 4.0$, $P = 0.134$) in them. Comparisons between *Ateles* and *Alouatta* at Los Inocentes and at Santa Rosa indicate no overall difference in parasitic burden. However, the prevalence of *Controrchis biliophilus* is different at Los Inocentes ($\chi^2 = 10.2$, $P = 0.001$) but not at Santa Rosa ($\chi^2 = 1.7$, $P = 0.183$).

As incidental oddities, *Blastocystis hominis* occurred in 1 howler at Santa Rosa and 1 at Curu. *Isospora arctopitheci* occurred in 2 howlers from Curu, 2 from Santa Rosa, and 1 from Los Inocentes. Another oocyst type occurred in 3 howlers from La Pacifica, 2 from Guanacaste N.P., 4 from Curu, and 1 from Santa Rosa. Based upon size and appearance, the oocyst was tentatively identified as *Cryptosporidium parvum*. However, this could not be confirmed by modified acid fast strain or by immunofluorescent assay. Recent reports suggest that it may represent an infection by *Cyclospora cayetanensis* (Visvesvara *et al.,* 1997). Capuchin samples from Lomas Barbudal and from Curu contain several types of nematode larvae which we have not been able to identify. They do not appear to be shared with howlers from any of the sites, suggesting either different host feeding habits or different parasitic life cycles.

The overall patterns are consistent with the concept that moist conditions are generally more conducive to higher parasite prevalence (Stuart and Strier, 1995). The increase in prevalence of waterborne parasites during

the wet season indicates fecally contaminated water or food and possibly an exchange of parasites with local human populations.

Controrchis biliophilus showed more differences among age cohorts, groups, forest habitats, seasons, primate species, and localities than any other helminth parasite did. This dicrocoelid trematode is therefore likely to be the most useful in providing clues about the ecology and behavior of different primate species. Unfortunately, virtually nothing is known of its life cycle. The presumptive cycle would involve passage first through a snail and then through an anthropod. Repeated searches have failed to verify this cycle. Howler fecal material is quickly consumed by ants and beetles. Even postulating ants as the second intermediate host, it is difficult to imagine an infective ant picking one of the scattered trees from which howlers may safely feed, climbing >40 ft up, and then picking a particular developmental stage of a leaf or flower to attach (Glander, 1978). Determining the life cycle of *Controrchis biliophilus* is essential so that information may be applied to understand the hosts' behavior and habitat preferences.

It should be clear from this review of parasitism both as reported in the literature and as seen at a specific locality, that a definitive evaluation of the parasitic fauna of *Alouatta* spp. is needed. Most of the information available is fragmented, isolated and incomplete. The life histories and transmission patterns of many parasites are unknown and to a large extent unstudied. Even at a single site, the patterns of parasitism appear to be changing, reflecting differences in ease of parasitic transmission, host dietary preferences, and habitat utilization. Most parasite surveys of wild primates represent isolated snapshots in time and not the actual dynamics of parasite–host interactions. The changing patterns in parasitic prevalence are further complicated by the isolation of primate populations at different sites and the presence or absence of other primate species, including humans. These patterns can be clarified only by long-term or longitudinal studies of wild primate groups. The overall status of parasitism in Neotropical primates is in serious need of a comprehensive survey of parasitic patterns that can be correlated with host habits and habitats. A tremendous amount of work remains to be done in the areas of simple descriptive life history analysis and prevalence surveys.

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