Chapter 10
Ecological Determinants of Parasitism in Howler Monkeys

Rodolfo Martínez-Mota, Martín M. Kowalewski, and Thomas R. Gillespie

Abstract Infectious diseases caused by pathogens are now recognized as one of the most important threats to primate conservation. The fact that howler monkeys (*Alouatta* spp.) are widely distributed from Southern Mexico to Northern Argentina, inhabit a diverse array of habitats, and are considered "pioneers," particularly adapted to exploit marginal habitats, provides an opportunity to explore general trends of parasitism and evaluate the dynamics of infectious diseases in this genus. We take a meta-analysis approach to examine the effect of ecological and environmental variables on parasitic infection using data from 7 howler monkey species at more than 35 sites throughout their distribution. We found that different factors including precipitation, latitude, altitude, and human proximity may influence parasite infection depending on the parasite type. We also found that parasites infecting howler monkeys followed a right-skewed distribution, suggesting that only a few individuals harbor infections. This result highlights the importance of collecting large sample sizes when developing these kinds of studies. We suggest that future studies should focus on obtaining fine-grained measurements of ecological and microclimate changes to provide better insights into the proximate factors that promote parasitism.

Resumen Las enfermedades infecciosas causadas por patógenos son reconocidas en la actualidad como una de las principales amenazas para la conservación de primates. Los monos aulladores (*Alouatta* spp.) son los primates con mayor distribución en Las Américas, desde el sur de México hasta el noreste de la Argentina. Además, habitan una gran variedad de hábitats y son considerados "pioneros." al encontrarse frecuentemente en áreas marginales. Esto los convierte en modelos

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ideales para explorar tendencias generales de parasitismo y evaluar la dinámica de enfermedades infecciosas. Se realizó un meta-análisis para examinar los efectos de variables ecológicas y ambientales sobre infecciones por parásitos utilizando datos de siete especies de monos aulladores distribuidos en más de 35 sitios a lo largo de su distribución. Se encontró que factores tales como precipitación, latitud, altitud y la proximidad a asentamientos humanos afectan en diferentes grados a la infección parasitaria según el tipo de parásito considerado. También se encontró que los parásitos de monos aulladores siguen una distribución sesgada, indicando que pocos individuos dentro de una población muestran infecciones por parásitos. Esto sugiere la importancia de colectar un número de muestras apropiado. Se recomienda que los estudios futuros se enfoquen en obtener estimaciones detalladas de cambios ecológicos y microclimáticos. Esto permitirá identificar en forma más precisa cuáles son los factores próximos que promueven el parasitismo.

Keywords Disease ecology • Prevalence • Richness • Latitude • Precipitation • Habitat disturbance

10.1 Introduction

Infectious diseases caused by pathogens are now recognized as one of the most important threats for wildlife and primate conservation (Daszak et al. 2000; Leendertz et al. 2006; Gillespie et al. 2008). Several studies have documented that pathogens are capable of reducing wildlife populations (e.g., amphibians (Daszak et al. 1999); Ethiopians wolves (Laurenson et al. 1998)). In primates, the most dramatic cases come from studies of apes impacted by respiratory pathogens or the Ebola hemorrhagic fever (Bermejo et al. 2006; Köndgen et al. 2008; Palacios et al. 2011). Yellow fever outbreaks have impacted populations of mantled (*Alouatta palliata*), brown (*A. guariba*), and black-and-gold (*A. caraya*) howler monkeys (Rifakis et al. 2006; Milton et al. 2009; Holzmann et al. 2010; de Almeida et al. 2012). These studies have demonstrated the vulnerability of primates to infectious diseases and have highlighted the importance of health monitoring to detect primate populations at risk due to pathogenic infection (Leendertz et al. 2006).

Howler monkeys (genus *Alouatta*) have a wide distribution from Southern Mexico to Northern Argentina and inhabit diverse habitats including tropical rain forests, dry deciduous forests, mountain forests, lowland forests, and mangroves, due to their dietary flexibility and ability to exploit difficult-to-digest food items, such as mature leaves and unripe fruits (Di Fiore et al. 2011). Howlers have been studied extensively, including aspects of their behavior (e.g., male and female reproductive behavior (Van Belle et al. 2009; Kowalewski and Garber 2010)), demography (e.g., population change (Clarke et al. 2002; Rudran and Fernandez-Duque 2003)), ecology (e.g., feeding ecology (Milton 1980; Silver et al. 1998)), and parasitism (Table 10.1). More than 60 % of the studies reported in Table 10.1 have focused on gastrointestinal parasites voided in feces, given that fecal samples can be

Table 10.1 Studies of parasitic infection in wild howler monkeys (genus *Alouatta*)

Species	Study site	Latitude	Habitat type	Altitude (m)	Rainfall (mm/year)	Human proximity	Sample type	Sample size	# of individuals	# of groups	Source
A. arctoidea	Hato El Frio, Venezuela	7° 30′ N	MF	60	1,424	Rural	Collected specimens	Unk	38	6	1
A. belzebul	Rio Tocantins, Tucurui, Brazil	3° 40′ S	MF, C	75	2,740	Rural	Feces	212	Unk	50	2
A. caraya	Parana River, Parana, Brazil	22° 46′ S	MF	252	1,700	Rural	Blood	17	17	Unk	3
	Nova Querencia, Mato Grosso do Sul, Brazil	20° 43′ S	LF	450	1,379	Rural	Feces	59	6	1	4
	Tocantins River, Goias, Brazil	13° 49′ S	SF	460	1,750	Rural	Blood	42	42	Unk	5
	Porto Primavera, Sao Paulo-Mato Grosso do Sul, Brazil	21° 15′ S	SF	302	1,500	Rural	Blood	590	590	Unk	5
	Bella Vista, Corrientes, Argentina	28° 30′ S	F*	60	1,200	Remote	Collected specimens	302	302	Unk	6
	Parana River, Chaco, Argentina	27° 20′ S	SF	60	1,200	Remote	Feces	28	28	Unk	7
	Rio Riachuelo, Corrientes, Argentina	27° 30′ S	SF	55	1,200	Rural	Blood	30	30	Unk	8
		27° 30′ S	SF	55	1,200	Rural	Feces	256	16	2	9
		27° 30′ S	SF	55	1,200	Rural	Collected specimens	110	110	Unk	10
	Las Lomas, Corrientes, Argentina	27° 23′ S	MF	67	1,200	Remote	Feces	60	20	2	11
	Isla Brasilera, Corrientes, Argentina	27° 20′ S	MF	54	1,200	Remote	Blood/feces/fur	12	14	Unk	12
		27° 20′ S	MF	54	1,200	Remote	Feces	30	30	Unk	13
	Yaciretá, Corrientes, Argentina	27° 28′ S	SF	65	1,200	Rural	Blood/feces/fur	9	9	Unk	12
	Estación Biológica, Corrientes, Argentina	27° 30′ S	SF	59	1,200	Rural	Feces	30	30	Unk	13
	San Cayetano, Corrientes, Argentina	27° 34′ S	SF	60	1,200	Urban	Blood/feces/fur	21	21	Unk	12
		27° 34′ S	SF	60	1,200	Urban	Feces	30	30	Unk	13
A. guariba	Morro Sao Pedro, Porto Alegre, Brazil	30° 01′ S	F*	230	1,324	Rural	Feces	53	Unk	Unk	14
	Reserva Biológica Lami, Porto Alegre, Brazil	30° 15′ S	F*	200	1,324	Urban	Feces	114	Unk	Unk	14
	Mata de Ribeirão Cachoeira, Brazil	22° 50′ S	MF	650	1,049	Remote	Feces	112	Unk	Unk	15

(continued)

Table 10.1 (continued)

Species	Study site	Latitude	Habitat type	Altitude (m)	Rainfall (mm/year)	Human proximity	Sample type	Sample size	# of individuals	# of groups	Source
A. macconnelli	Sinnamary River, Petit Saut Dam, French Guiana	5° 04′ N	C	45	3,000	Remote	Blood	117	117	Unk	16
		5° 04′ N	C	45	3,000	Remote	Blood	81	81	Unk	17
		5° 04′ N	C	45	3,000	Remote	Blood	50	50	Unk	18
	Biological Dynamics of Forest Fragments Project, Manaus, Brazil	2° 30′ S	C	38	2,606	Rural	Feces	35	24	3	19
	Balbina, Uatuma River, Amazonas State, BRA	1° 55′ S	C	34	2,262	Rural	Blood	31	31	Unk	20
A. palliata	Los Tuxtlas Biosphere Reserve, Mexico	18° 34′ N	C	300	4,900	Remote	Feces	38	Unk	Unk	21
	Los Tuxtlas Biosphere Reserve, Mexico	18° 34′ N	SF	300	4,900	Rural	Feces	63	Unk	Unk	21
		18° 34′ N	F*	100	4,900	Rural	Darted individuals[a]	6	6	5	22
		18° 38′ N	MF, SF	100	4,900	Rural	Feces	288	12	3	23
		18° 18′ N	SF	180	4,900	Rural	Feces	278	43	5	24
	Carlos Green, Mexico	17° 41′ N	F*	15	4,014	Rural	Blood	1	1	Unk	25
	Pochitocal, Mexico	18° 15′ N	F*	5	4,014	Rural	Blood	19	19	Unk	25
	Macuspana, Mexico	17° 38′ N	SF	15	3,186	Rural	Feces	Unk	27	2	26
	El Zapotal, Mexico	16° 43′ N	SF	700	950	Urban	Feces	67	15	1	27
	Barro Colorado Island, Panama	9° 10′ N	LF	120	2,612	Remote	Darted individuals[a]	Unk	Unk	Unk	28
	Chomes, Costa Rica	10° 02′ N	MF	9	1,950	Rural	Feces	9	Unk	Unk	29
	Parque Nacional Palo Verde, Costa Rica	10° 22′ N	LF	15	1,950	Remote	Feces	20	Unk	Unk	29
	Parque Nacional Cahuita, Costa Rica	9° 43′ N	LF	20	3,000	Remote	Feces	29	29	Unk	29
A. palliata	San Ramón, Costa Rica	10° 05′ N	SF	1,020	1,500	Urban	Feces	7	5	Unk	29
	Chira, Costa Rica	10° 06′ N	MF	8	2,000	Rural	Feces	5	5	Unk	29
	Gran Nicoya, Costa Rica	9° 59′ N	MF	100	1,950	Rural	Feces	18	Unk	Unk	29
	Playa Potrero, Costa Rica	10° 27′ N	SF	20	1,500	Urban	Feces	8	Unk	Unk	29
	Parque Nacional Manuel Antonio, Costa Rica	9° 24′ N	LF	45	4,000	Urban	Feces	6	Unk	Unk	29
	La Pacifica, Costa Rica	10° 28′ N	MF	45	1,553	Rural	Feces	200	108	13	30
	La Selva Biological Reserve, Costa Rica	10° 26′ N	LF	35	3,962	Rural	Feces	84	13	2	31

A. pigra	Reforma Agraria, Mexico	16° 15′ N	LF	181	3,000	Rural	Feces	17	Unk	Unk	21
	Calakmul Biosphere Reserve, Mexico	18° 06′ N	C	50	820	Remote	Feces	29	Unk	Unk	21
		18° 06′ N	C	50	820	Remote	Feces	Unk	4	2	32
	Palenque Biosphere Reserve, Mexico	17° 27′ N	LF	500	2,200	Remote	Feces	29	Unk	Unk	21
		17° 27′ N	LF	500	2,200	Remote	Feces	Unk	3	2	32
	Community Baboon Sanctuary, Belize	17° 33′ N	MF	28	1,995	Rural	Feces	Unk	13	3	32
	Cockscomb Basin Wildlife Sanctuary, Belize	16° 49′ N	C	200	2,700	Remote	Feces	Unk	5	2	32
	Montes Azules Biosphere Reserve, Mexico	16° 07′ N	C	181	3,000	Remote	Feces	23	Unk	Unk	21
		16° 07′ N	C	181	3,000	Remote	Feces	151	15	3	33
	El Tormento, Mexico	18° 36′ N	LF	90	1,380	Rural	Feces	39	Unk	Unk	21
		18° 36′ N	LF	90	1,380	Rural	Feces	81	69	17	34
		18° 36′ N	LF	90	1,380	Rural	Blood	12	12	3	25
	Carlos Green, Mexico	17° 41′ N	F*	15	4,014	Rural	Blood	2	2	Unk	25
	Pochitocal, Mexico	18° 15′ N	F*	5	4,014	Rural	Blood	6	6	Unk	25
	Lamanai Archaeological Reserve, Belize	17° 46′ N	MF	16	1,200	Rural	Feces	99	Unk	22	35
	Catazaja, Mexico	17° 35′ N	SF	20	1,400	Rural	Feces	218	43	6	36
	Punta Laguna, Mexico	20° 38′ N	MF	14	1,500	Remote	Feces	3	3	2	37
	Petcacab, Mexico	19° 17′ N	C	31	1,200	Remote	Feces	8	8	4	37
	Macuspana, Mexico	17° 38′ N	SF	15	3,186	Rural	Feces	Unk	7	2	26
	Monkey River, Belize	16° 21′ N	LF	12	2,500	Rural	Feces	315	18	4	38
A. sara	Tambopata National Reserve, Peru	13° 8′ S	C	250	2,400	Rural	Feces	16	16	4	39

Habitat type: *C* continuous forest, *SF* small-size fragments, *MF* medium-size fragments, *LF* large-size fragments, *F** indicates a fragmented forest but the size cannot be obtained from the literature. *Unk* unknown. We wrote "unknown" when ambiguous information regarding sample size, number of individuals, or number of groups was presented in the studies

Source: [1]Braza (1980), [2]Martins et al. (2008), [3] Garcia et al. (2005), [4]Godoy et al. (2004); [5]Duarte et al. (2006), [6]Pope (1966), [7]Venturini et al. (2003), [8]Travi et al. (1986), [9]Delgado (2006), [10]Coppo et al. (1979), [11]Milozzi et al. (2012), [12]Santa Cruz et al. (2000), [13]Kowalewski et al. (2011), [14]Cabral et al. (2005), [15]Santos et al. (2005), [16]Fandeur et al. (2000), [17]Volney et al. (2002), [18] Carme et al. (2002), [19]Gilbert (1994), [20]Lourenco de Oliveira and Deane (1995), [21]Trejo-Macías et al. (2007), [22]Cristóbal-Azkarate et al. (2012), [23]Cristóbal-Azkarate et al. (2010), [24]Valdespino et al. (2010), [25] Rovirosa-Hernández et al. (2013), [26]González-Hernández et al. (2011), [27]Castillejos (1993), [28]Milton (1996), [29]Chinchilla Carmona et al. (2005), [30]Stuart et al. (1990), [31]Stoner (1996), [32]Vitazkova and Wade (2007), [33]Stoner and González Di Pierro (2006), [34]Martínez-Mota unpublished data, [35]Eckert et al. (2006), [36]Alvarado-Villalobos (2010), [37]Bonilla-Moheno (2002), [38]Kowalzik et al. (2010), [39]Phillips et al. (2004)

[a]Individuals were darted for clinical evaluation and collection of botfly parasites

collected noninvasively without disturbing individuals (Gillespie 2006). The content of these papers ranges from descriptions (e.g., reports of parasites infecting *A. pigra* (Vitazkova and Wade 2006)) to studies relating parasitic infection to demographic (e.g., group size (Stoner and González Di Pierro 2006)) or ecological variables (e.g., forest fragmentation (Valdespino et al. 2010); contact with domesticated animals (Kowalewski et al. 2011)). In this chapter, we take a meta-analysis approach to examine the effect of ecological and environmental variables on parasitic infection of howler monkeys. First, we review variables that affect patterns of parasite infection, and second, we test whether different predictors such as forest fragmentation, human proximity, and climatic factors influence parasitism in howler monkeys.

10.2 Background

10.2.1 Habitat Disturbance, Forest Fragmentation, and Parasitic Infection

Habitat disturbance associated with anthropogenic activities, such as extensive logging, agriculture, cattle ranching, and ecotourism, has been added to the set of factors that promote the spread of parasites and increase the probability of pathogen exchange (Patz et al. 2000; Smith et al. 2009). These environmental changes favor the dispersal, establishment, and abundance of parasites that were previously rare (Wilcox and Ellis 2006). Evidence suggests that transformation of primate habitats alters parasite–host dynamics, affecting the potential for parasite transmission among primate hosts. For example, Gillespie et al. (2005) found that redtail guenons (*Cercopithecus ascanius*) inhabiting logged forest showed an approximate 85 % increased prevalence of the gastrointestinal parasite *Oesophagostomum* spp., compared to individuals living in an undisturbed forest. Similarly, Goldberg et al. (2008) found that humans harbored bacteria that were genetically more similar to those hosted by redtail guenons that inhabited fragments located near their settlements, compared to bacteria from guenons living in an undisturbed forest, suggesting that bacterial transmission between humans and primates had occurred. Primates inhabiting fragmented forests may be at greater risk of infectious diseases, in particular those living in proximity to human populations, due to increased exposure to pathogens that proliferate in anthropogenically disturbed habitats (Gillespie and Chapman 2006, 2008). Other studies, however, have not found clear differences in measures of parasitic infection when comparing populations of primates inhabiting forests with different degrees of disturbance (sifakas, *P. edwardsi* (Wright et al. 2009); mangabeys, *Cercocebus galeritus galeritus* (Mbora and McPeek 2009)). Clearly teasing out generalities and site-specific variation in how habitat disturbance affects the transmission of parasites in different primate species will be a major area of research in coming years.

10.2.2 Effects of Climate on Parasites

Studies of parasites hosted by wild primates should also take into consideration other factors that may play an interactive role in parasite–host dynamics. For example, climatic conditions, such as the amount of rainfall or moisture, have been identified as important variables for the proliferation of parasite vectors (Altizer et al. 2006; Vittor et al. 2006). In the case of malaria, a vector-borne disease caused by the protozoan *Plasmodium* spp., changes in patterns of precipitation were followed by malaria outbreaks in several African human populations (Zhou et al. 2004; Pascual et al. 2008). In this regard, Odongo-Aginya et al. (2005) reported that density of malaria parasites found in blood samples of human patients fluctuated with mean monthly rainfall during a year in the Entebbe Municipality, Uganda. Parasite vectors, such as mosquitos (e.g., *Anopheles* spp.), benefit from changes in rainfall patterns, given that these conditions increase humidity and availability of water sources, which provide more breeding sites, speed vector development, and increase vector abundance, potentially spreading a disease more efficiently (Patz et al. 2000; Vittor et al. 2006).

Rainfall also has been associated with an increase in protozoan infections such as cryptosporidiosis and giardiasis in human populations (Jagai et al. 2009) as well as in nonhuman primates (chimpanzees (Gonzalez-Moreno et al. 2013); black howler monkeys (Vitazkova and Wade 2006)). This might be the result of a high concentration of oocytes and cysts in water sources that tend to accumulate after heavy rainfall (Muchiri et al. 2009). In addition, precipitation plays an important role in the survival, development, and transmission of soil-transmitted helminths including hookworms (e.g., *Necator americanus*), whipworms (e.g., *Trichuris trichiura*), pinworms (e.g., *Enterobius vermicularis*), or roundworms (e.g., *Ascaris lumbricoides*) which are gastrointestinal parasites of public health concern (Bethony et al. 2006) reported to infect several nonhuman primates such as howler monkeys, orangutans, red langurs, gibbons, and chimpanzees (Vitazkova 2009; Gillespie et al. 2010, 2013; Hilser 2011). Moisture favors the survival and development of different parasite stages that are otherwise compromised by desiccation during dry periods (Gillespie 2006). Thus, we would expect that precipitation also affects patterns of parasite infection in howler monkeys.

Temperature is one of the critical climate factors affecting pathogen survival, distribution, and transmission (Harvell et al. 2002; Poulin 2006). For example, climate variability (e.g., short-term fluctuations around mean temperature) has been found to be a driver of malaria epidemics in African human populations (Lindblade et al. 2000; Zhou et al. 2004). This is most likely due to changes in land use and habitat modification that have led to an increase in temperature that in turn has altered vector distribution and parasite infection patterns (Lindblade et al. 2000; Harvell et al. 2002; Zamora-Vilchis et al. 2012). In parasite studies, altitude has been used as a proxy of temperature, implying that temperature decreases as elevation increases. In fact, a negative relationship between blood parasite prevalence and altitude has been described in birds (Zamora-Vilchis et al. 2012). Patterns of parasitism in primates also may vary according to an altitudinal gradient; for instance, Appleton and Henzi (1993) found that diversity of gastrointestinal parasites was lower in chacma baboons (*Papio cynocephalus ursinus*) that ranged at a high altitude (1,835–2,250 m), where temperature changes can be extreme representing a hostile environment for parasites, than in baboons ranging at 100–200 m altitude in Natal, South Africa. Given that parasites can be sensitive to temperature and be affected by an altitudinal gradient, it may be expected that at higher altitudes howler hosts present lower parasitic infection compared to howlers ranging at a low altitude. Since howler monkeys may inhabit forests both at sea level and at high altitude, this feature allows us to explore whether parasitic infection in howler monkeys follows an altitudinal gradient.

10.2.3 Host Distribution

A latitudinal gradient may affect patterns of parasitic infection, given that abundance and diversity of species increase in tropical areas at lower latitudes (Guernier et al. 2004; Hillebrand 2004). In general, it is acknowledged that geographic zones close to the equator may encompass a large variety of habitats and are characterized by high-energy productivity and favorable climatic conditions (Pianka 1966; Rohde 1992; Luo et al. 2012), which, in turn, may allow the establishment and proliferation of a diverse array of vertebrate hosts compared to temperate zones (Hawkins et al. 2003). This availability and diversity of hosts might favor transmission rates among generalist parasites (Nunn et al. 2005). Parasite species also may follow this latitudinal gradient; for example, species richness of pathogens responsible for infectious diseases in humans was found to be higher in tropical areas at lower latitudes (Guernier et al. 2004). In a meta-analysis of 119 primate host species, Nunn et al. (2005) found that species richness of protozoan parasites, but not helminths and viruses, increased towards the equator. According to this, howler monkeys that range in tropical areas close to the equator are expected to harbor more parasite species compared to howlers found at higher latitudes.

10.3 Goals and Expectations

Existing published data on parasites harbored by different species of howlers creates an opportunity to explore general trends of parasitism in these New World primates. Therefore, the main goal of this chapter is to examine the effect of multiple variables on measures of parasitic infection reported for several species of howler monkeys. We predict that:

1. Howler geographic distribution will have an effect on parasitic infection. We expect that parasite prevalence and species richness as measures of parasitic infection will be higher in howlers living close to the equator compared to howlers living at higher latitudes.

2. Given that humidity and rainfall may favor the development of parasites at different stages, we expect that measures of parasitic infections will be positively correlated with precipitation in howler monkeys. Furthermore, we expect that howlers living at lower altitudes show higher parasitic infection than howlers living at higher altitudes.
3. Habitat disturbance and forest fragmentation have been recognized as factors that modify parasitic infection dynamics; in this regard, we expect that howlers living in fragmented/disturbed habitats show higher parasite prevalence and richness than howlers inhabiting undisturbed forests. In addition, in anthropogenically disturbed habitats, the likelihood of contact between human and nonhuman primates is higher compared to remote areas, increasing the probabilities of pathogen exchange (Gillespie et al. 2008; Rwego et al. 2008). Thus, we expect that howlers inhabiting areas close to human settlements show an increase in measures of parasitic infection.

10.4 Methods

10.4.1 Data Collection

We conducted a literature review and analyzed published material including scientific articles, brief reports, and dissertation theses that reported parasitic infection in howler monkeys including mantled howlers (*Alouatta palliata*), black howlers (*A. pigra*), red howlers (*A. macconnelli* and *A. sara*), red-handed howlers (*A. belzebul*), brown howlers (*A. guariba*), and black-and-gold howler monkeys (*A. caraya*). We also searched any record of published material in the Global Mammal Parasite Database (www.mammalparasites.org, Nunn and Altizer 2005). We obtained parasite prevalence data reported for each species of parasite and recorded the number of parasite species reported in each study case. For each study site, we obtained ecological/environmental data including latitude, altitude (meters), and annual precipitation (millimeters) from primary literature (i.e., when reported in the study) or from websites such as WorldClim and Google Earth.

We categorized the howler monkey habitats as fragmented or continuous based on forest size (Marsh 2003; Kowalewski and Gillespie 2009). We assigned the category of small forest fragments to those with 1–100 ha forest cover. Fragments ranging in size from 100 to 1,000 ha were considered medium-size fragments, and those ranging from 1,000 to 10,000 ha of forest cover were assigned to the large-fragment category. Continuous habitats were those characterized by having ≥10,000 ha of forest area. Moreover, howler habitats were divided in three categories according to their proximity of human settlements, following Kowalewski and Gillespie (2009): (1) we considered an area as "remote" when the site was almost or totally isolated from human settlements. (2) We assigned the category of "rural" area to howler habitats that were close to rural populations, fishing camps, and/or were regularly visited by people. This applies mostly to forest fragments located nearby human settlements, where locals possibly carry out activities such as selective logging, cattle ranching, or hunting, showing a constant presence in howler habitats. (3) An "urban" site was considered when howler habitats were in close proximity to or immersed within human settlements characterized by dense human populations.

10.4.2 Data Analysis

We divided prevalence data into two broad categories, helminth and protozoan parasites: (1) We divided the helminth parasite data set into nematodes (82 records), trematodes (38 records), and cestodes (13 records) and also analyzed the effect of predictor variables on prevalence of *Trypanoxyuris* parasites, given that this was a well-represented genus in 4 out of 7 howler species (exception were *A. guariba*, *A. macconnelli*, and *A. sara*). (2) We separately analyzed prevalence data of protozoan parasites: we first divided this data set in a general category named amoebae parasites (34 records), which included the genera *Entamoeba*, *Endolimax*, *Iodamoeba*, and unknown reported amoebae. Thereafter, we analyzed *Giardia* prevalence (21 records) separately since these parasites were represented in 5 of 7 howler species (*A. belzebul*, *A. caraya*, *A. guariba*, *A. palliata*, and *A. pigra*) in our database. Finally, we analyzed data on *Plasmodium* prevalence (17 records). *Plasmodium* data were only available for 2 South American howler species (*A. caraya* and *A. macconnelli*); however, given that malaria infection is frequently associated with ecological changes (Zhou et al. 2004), we decided to explore the effect of ecological/environmental variables on the prevalence of this genus.

Parasite prevalence usually follows an aggregated distribution (e.g., negative binomial (Wilson et al. 2002)), thus we log-transformed helminth and protozoan prevalence and analyzed these data using generalized linear models with an identity link function in the R software (MASS library, version 2.15.1) (Crawley 2007). We considered the following predictor variables: forest type as a categorical variable, which includes fragments of different size and continuous forests. Similarly, human proximity was included as a categorical variable with three levels (1 = remote, 2 = rural, 3 = urban). Latitude, annual precipitation (millimeters), and altitude (meters) were included as continuous variables. We ran each model taking into account all predictor variables and selected the best model using the Akaike information criterion. Thereafter we ran a deviance test to assess model adequacy.

We also tested the effects of forest type, latitude, altitude, and precipitation and the effect of human proximity on parasite species richness (i.e., number of parasite species reported per howler population). We analyzed these data with a generalized linear model with a negative binomial link function (Wilson and Grenfell 1997; Crawley 2007) using the glm.nb procedure of the MASS library in the R software (version 2.15.1).

10.5 Results

10.5.1 Helminth Analysis

Nematodes: We found that precipitation was a predictor of nematode prevalence ($\chi^2 = 13.53$, $p = 0.003$) in howler monkeys. Figure 10.1 shows that nematode prevalence increases with precipitation. Other terms included in the model, such as forest type, latitude, or altitude, did not have an effect on the response variable. Similarly, human proximity did not have any effect on nematode prevalence.

Trematodes and Cestodes: We did not find any significant effect of forest type, latitude, precipitation, altitude, or human proximity on the prevalence of trematodes and cestodes hosted by howler monkeys. However, we found a trend of cestode prevalence being higher in howlers from remote forests compared to howlers inhabiting rural areas (Fig. 10.2). We did not find any record of cestode parasites at the "urban" level in the "human proximity" categorical variable in our data set; thus, this level was not considered in the analysis.

Trypanoxyuris: Prevalence of *Trypanoxyuris* parasites was not predicted by any of our predictor variables; however, we found a trend in which prevalence was higher at lower altitudes and decreased at higher altitudes (Fig. 10.3).

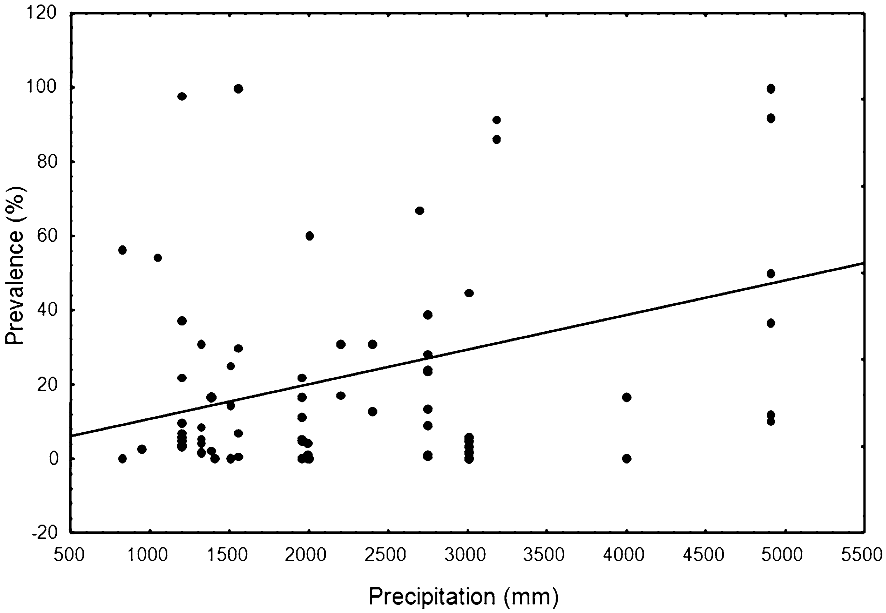

Fig. 10.1 Relationship between nematode prevalence hosted by howler monkeys and precipitation

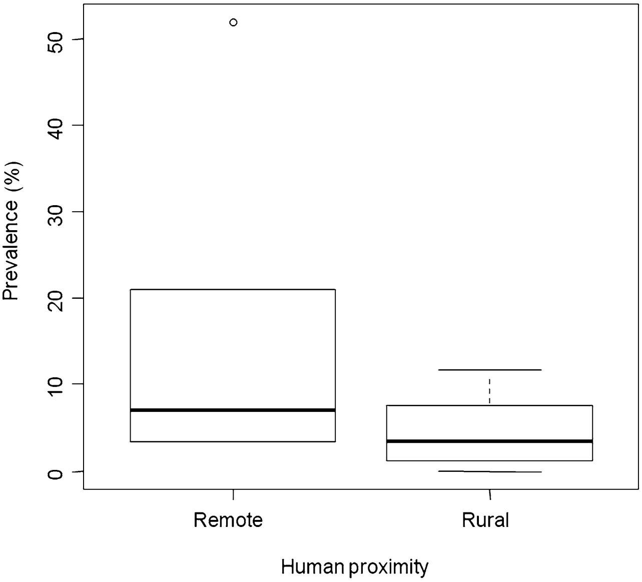

Fig. 10.2 Effects of human proximity on cestode prevalence (%) hosted by howler monkeys. Human proximity categories included in the analysis were remote and rural (see methods for description). Box and whisker plot shows the median, percentiles (25 and 75 %), and the minimum and maximum value

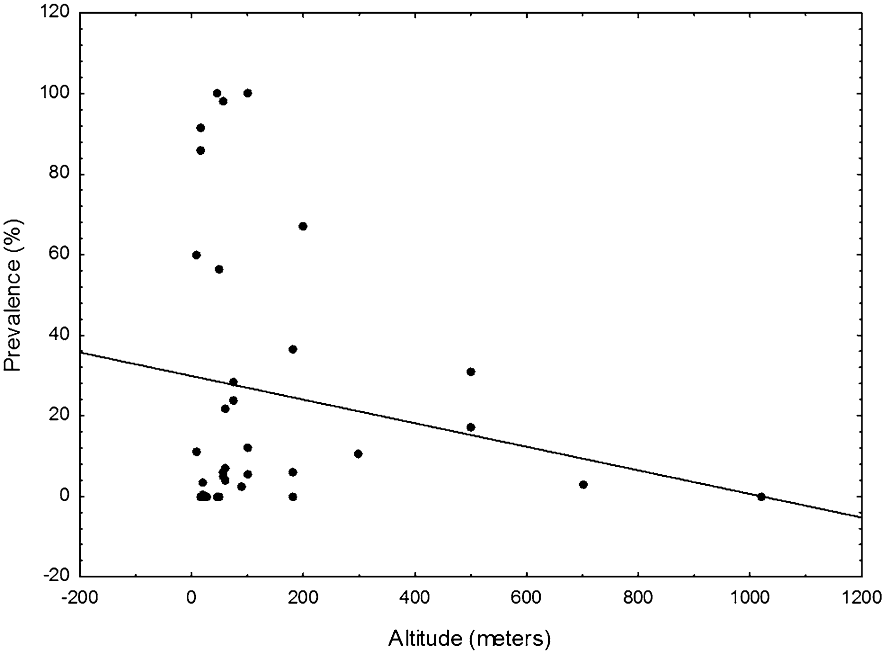

Fig. 10.3 Scatterplot showing a negative relationship between altitude (m) and prevalence (%) of *Trypanoxyuris* spp. reported to infect different howler monkeys

10.5.2 Protozoan Analysis

Amoebae Parasites: We found that the interaction between latitude and precipitation had an effect on the prevalence of amoeba parasites ($\chi^2 = 9.08$, $p < 0.001$). Amoebae prevalence increased close to the equator and at sites where precipitation was high (Fig. 10.4). Other predictors, such as forest type, altitude, or human proximity had no affect on overall amoebae prevalence.

Giardia: Precipitation predicted *Giardia* prevalence ($\chi^2 = 8.6$, $p < 0.05$), producing a negative (exponential) relationship between precipitation and *Giardia* prevalence (Fig. 10.5). Other predictors were not significant.

Plasmodium: *Plasmodium* prevalence was not predicted by any of our independent variables.

10.5.3 Parasite Richness Analysis

We did not find any effect of forest type, latitude, altitude, precipitation, or the degree of human proximity on parasite species richness.

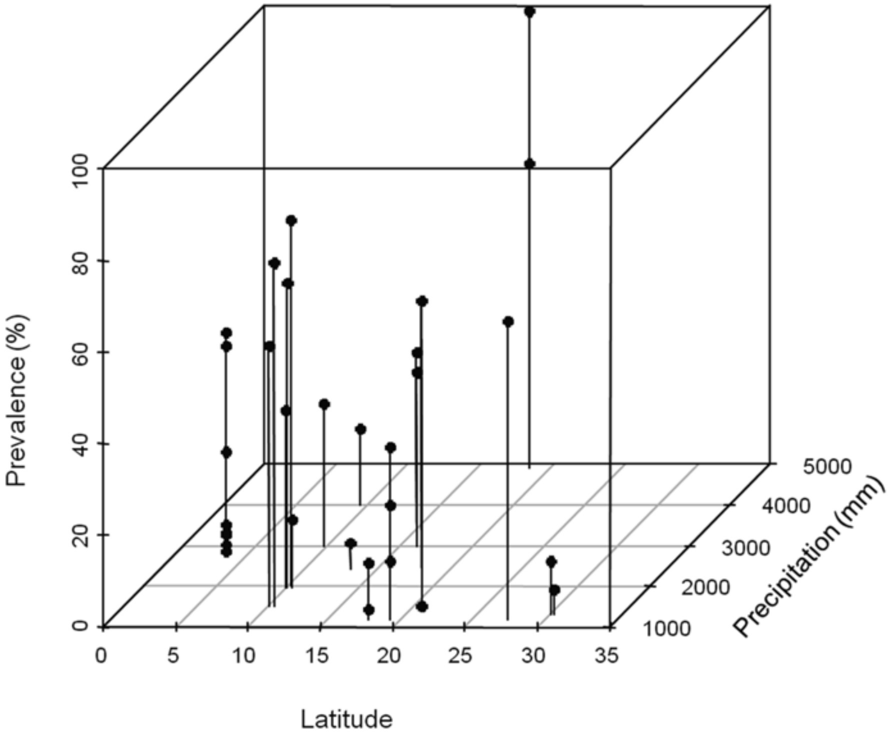

Fig. 10.4 Relationship among amoebae prevalence (%), latitude, and precipitation (mm) in howler monkeys (Genus *Alouatta*)

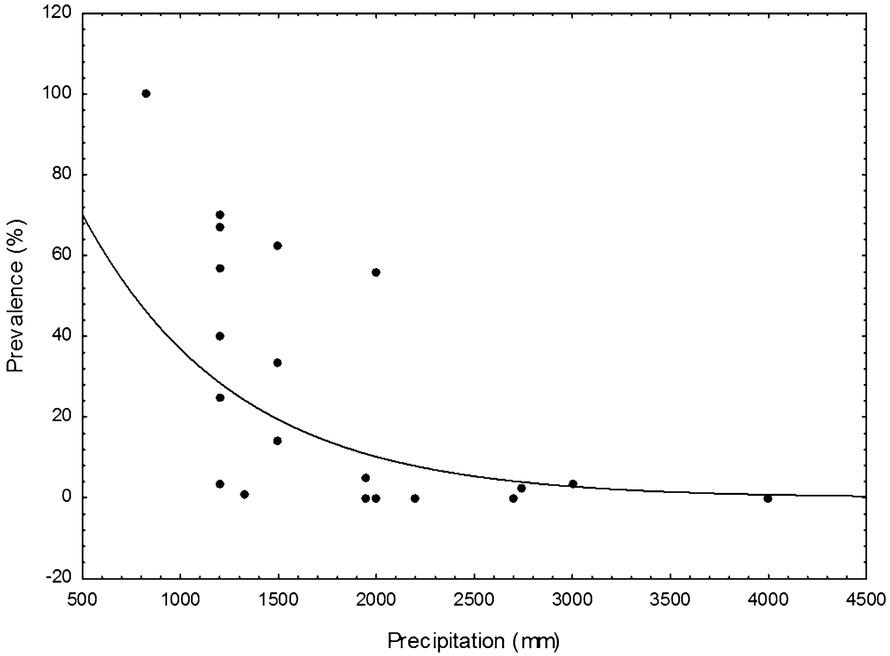

Fig. 10.5 Negative relationship between prevalence (%) of *Giardia* spp. reported for different species of howler monkeys and precipitation (mm)

10.6 Discussion

10.6.1 Effects of Climatic Factors

In this review, we found that different factors including precipitation, latitude, altitude, and human proximity may influence parasite infection in howler monkeys. However, the effect of each of these predictor variables varies depending on the parasite category (Table 10.2). Table 10.2 summarizes general trends found in our analysis. For example, in the case of helminth parasites, precipitation positively predicted nematode, but not trematode and cestode prevalence. Moreover, altitude only affected prevalence of the nematode *Trypanoxyuris*. Humidity and rainfall are critical climatic factors for the survival and spread of parasites, especially soil-transmitted helminths (e.g., *Ascaris* spp.) that are sensitive to desiccation (Patz et al. 2000). It is possible that the encounter rate with nematodes that proliferate in forests characterized by high precipitation is higher for howlers inhabiting these sites than for howlers living in drier environments. To our surprise, trematode prevalence was not predicted by precipitation, despite the majority of these parasites requiring intermediate hosts dependent on water sources (e.g., mollusks such as snails) during

Table 10.2 Effects of precipitation, latitude, and altitude on parasite prevalence and richness in howler monkeys (genus *Alouatta*)

	Nematodes	Trematodes	Cestodes	*Trypanoxyiuris*[a]	Amoeba	*Giardia*	*Plasmodium*	Parasite richness
Precipitation	+	0	0	0	+	–	0	0
Latitude	0	0	0	0	–	0	0	0
Altitude	0	0	0	–	0	0	0	0

+ = positive relationship; − = negative relationship; 0 = no significant effect

[a] Indicates that although not significant there exists a trend

their life cycles. The lack of connection between precipitation and trematode prevalence in howlers may be the result of spatial variability in the intermediate host distribution (Wilson et al. 2002), which may limit the probability of contact between trematode-infective stages and howler monkeys as definitive hosts. Alternately, trematodes that proliferate in howler habitats may be using vertebrates other than howlers as definitive hosts. It is also possible that lower trematode prevalence and richness at some sites simply are the result of using different procedures varying in efficiency to isolate trematode eggs from feces (e.g., flotation and sedimentation techniques), which makes comparing the results of studies difficult (Gillespie 2006).

On the other hand, prevalence of protozoan parasites such as amoebae was affected by the interaction between rainfall and latitude. Howler monkeys living in sites characterized by high amount of annual precipitation and close to the equator have higher prevalence of amoeba parasites compared to howler hosts at higher latitudes living in areas with lower rainfall. Amoebae are waterborne protozoan parasites transmitted via fecal–oral route, and while some species like *Entamoeba coli* are not pathogenic, others, such as *E. histolytica* and *Endolimax nana*, may cause dysentery and diarrheic events, respectively, in human populations (Graczyk et al. 2005). Howler monkeys inhabiting tropical areas characterized by heavy rainfall may be infected by amoebae while drinking water accumulated in tree holes following rainfall events (*A. caraya* (Giudice and Mudry 2000); *A. pigra* (Martinez-Mota, unpubl. data)). However, in our experience, howler monkeys rarely show diarrheic episodes or clinical signs of enteric disease. In fact, in this review, only 11.7 % of our amoebae records were of the diarrheic-causing protozoa *E. nana*, while the majority were *Entamoeba* spp. (20.6 %) and unknown amoebae (29.4 %). Further studies using molecular tools (e.g., PCR) should be used to determine whether amoebae parasites infecting howlers are of pathogenic potential.

In contrast with the pattern found in the amoebae analysis, we found that howlers inhabiting areas with lower annual precipitation have higher *Giardia* prevalence. Giardiasis is a waterborne reemerging infectious disease widely distributed in the tropics. Transmission of *Giardia* occurs by the fecal–oral route, usually when a host ingests cyst-contaminated water and food. Typical symptoms may involve diarrhea, abdominal pain, and weight loss (Thompson 2000; Fayer et al. 2004). Given the zoonotic potential of these protozoa found infecting wildlife, livestock, and humans, giardiasis has become a disease of human health concern (Thompson 2000; Volotao et al. 2008). We found in our meta-analysis that *Giardia* spp. was reported to infect *A. belzebul*, *A. caraya*, *A. guariba*, *A. palliata*, and *A. pigra*. Although prevalence of this parasite has been associated with heavy rainfall and water sources (Hunter 2003; Fayer et al. 2004), our results indicate the opposite trend. Kowalewski et al. (2011) suggested that due to the interplay of additional factors associated with anthropogenic disturbance, such as presence of infected cattle and the common use of small water reservoirs, howler habitat use and stress levels, together with human presence may drive *Giardia* infection patterns in howler monkeys.

In human patients, *Plasmodium* infection correlates negatively with altitude and increases in parallel with precipitation (Drakeley et al. 2005; Odongo-Aginya et al. 2005); however, in our study, none of our predictor variables had a significant effect on *Plasmodium* prevalence. New World primates are potential hosts for *Plasmodium*, and prevalence of this pathogen increases with primate group size (Nunn and Heymann 2005). The fact that we failed to detect any trend in *Plasmodium* infection may be associated to the small number of reported cases in our data base ($n=17$). The small number of reports of *Plasmodium* infection in howlers probably reflects that only few studies have carried out health monitoring initiatives. We suggest that as part of complete health monitoring (or during translocation and/or capture procedures for marking purposes), howlers should be tested for *Plasmodium*. With this new information we will be able to determine if howlers have been exposed to this parasite along their entire distribution.

10.6.2 Parasite Species Richness

Although parasite species richness in primates increases towards the equator (Nunn et al. 2005), we failed to find this relationship in howler monkeys. Our results differ from those of Nunn et al. (2005), who found that latitude negatively predicts protozoan parasite diversity in primates. Nunn et al. used a large database (119 primate taxa) including species with distinct life histories and ecological features (e.g., arboreal and terrestrial, insectivores, folivores, and frugivores), which may explain variation in diversity of parasites hosted by primates. Despite the fact that the genus *Alouatta* is widely distributed from Mexico to South America, with species inhabiting different forest types and ecosystems, all howler species share similar life histories and behavioral ecology, and this might be the reason for the lack of variation in parasite species richness along a latitudinal gradient. Our results suggest that other factors, which in some instances covary with latitude, must be responsible for changes in parasite species diversity within primate hosts.

Parasite species richness has been considered an important disease risk indicator (Nunn and Altizer 2006). Poulin and Morand (2000) suggest that the observed parasite diversity within a host is the result of coevolutionary processes between parasites and host and may reflect the susceptibility of hosts to be colonized by parasites. Furthermore, parasite colonization process and diversity are driven to some extent by host ecological traits (Poulin and Morand 2000). In our analysis, we found that the number of parasite species reported to infect howler monkeys is rather low (average: 5.2 ± 2.3 per population, range: 2–12). This might be the result of howler monkey ecological traits such as arboreality, which may prevent monkeys from contacting infective stages of some parasite species that are more commonly found on the ground. Gillespie et al. (2005) reported that in logged forests the arboreal black-and-white colobus (*Colobus guereza*) showed lower parasite diversity compared to redtail guenons (*Cercopithecus ascanius*), which frequently feed on insects in the lower strata of the canopy (Rode et al. 2006). Such feeding habits may expose primates to parasites that use invertebrates as intermediate hosts. Howler monkeys do not actively feed on insects; moreover, the ingestion of substantial amounts of leaves during certain seasons may contribute to their resistance to parasites, since leaves of species such as *Ficus* spp. may act as natural antiparasitic agents due to their secondary compound content (Huffman 1997; Stoner and González Di Pierro 2006).

We cannot discard the possibility that howler monkeys are intrinsically prone to host few parasite species. Due to their high dispersal and colonizing ability (Ford 2006), and their ecological flexibility, howlers are considered “pioneers,” specially adapted to exploit marginal habitats (Rosenberger et al. 2011). The latter probably contributed to their higher resistance to pathogen infections. Studies examining the immune function in howlers may shed light on this possibility.

10.6.3 Human Proximity and Habitat Disturbance

Although we did not find any significant effect of human proximity on parasite prevalence (nematodes, trematodes, amoebae parasites, and the specific genera *Trypanoxyuris*, *Giardia*, and *Plasmodium*), we found a trend in which cestode prevalence was slightly higher in howlers inhabiting remote and less disturbed areas compared to howlers from rural sites that are characterized by a constant presence of people. Surprisingly, we did not find any effect of human proximity on species richness. Howler monkeys inhabiting more conserved and remote areas may interact with a diverse array of fauna, which could increase the probability of parasite transmission, especially generalist parasites that infect different host species. In contrast, it is possible that howlers that inhabit forests located in rural areas do not come into close contact with other vertebrates such as small mammals. In rural areas, hunting is a common activity practiced by local people and decreases the abundance of vertebrates (Peres 2001) serving as potential hosts. In addition, howler habitats located near rural areas are often characterized by anthropogenic impact, such as slash-and-burn agriculture, which involves burning a piece of land before cultivation. Bloemers et al. (1997) found that forest fragments that have been impacted by slash-and-burn agriculture had lower nematode diversity. It is possible that fire associated with this practice, as well as changes in microclimatic conditions, such as decreased humidity and increased desiccation associated with edge effects in forest fragments (Laurance 2000), negatively affect the survival of infective stages of parasites.

Although habitat disturbance has been related to increases in parasitic infection and clearly modifies parasite–host dynamics in primates (Gillespie et al. 2005; Gillespie and Chapman 2006, 2008), mechanisms for such change may be highly influenced by the nature and magnitude of the disturbance experienced. Our analysis failed to detect an effect of the habitat type on parasite prevalence and richness of howler monkeys. Our results paralleled those of Kowalewski and Gillespie (2009) who found that habitat disturbance did not predict parasitism in South American howler monkeys and agree with recent findings which show that primates inhabiting disturbed forests do not have higher parasitic infections than primates living in conserved habitats (Young et al. 2013). This lack of effect of forest type on parasitism may be related to our classification scheme of continuous or fragmented forest (e.g., small, medium, and large fragments). These are artificial categories that do not take into consideration other interacting variables affecting parasitism. Consequently, we suggest that future parasite studies in howler monkeys and other primates avoid the continuous-fragmented forest dichotomy since this categorical variable does not add any explanation power to results. Instead, we encourage primatologists to collect and quantify ecological and environmental data in order to provide better explanations of parasitic infection patterns. We believe that including a general quantitative assessment of habitat disturbance such as an index of logging extraction (Gillespie and Chapman 2006, 2008), size and shape of howler habitats (Valdespino et al. 2010), exposure rates of individuals to a matrix of human-transformed habitat (Zommers et al. 2012), human and domestic animal proximity (Rwego et al. 2008), together with quantitative data of microclimatic variation (e.g., humidity, temperature, rainfall) will improve the quality of explanatory variables and give us better insights into the proximate factors that affect parasitism in howler monkeys.

10.7 Final Remarks

One characteristic of parasites is that they are not evenly distributed in a host population (Wilson et al. 2002). According to the data we analyzed from 31 studies, parasites infecting howler monkeys followed an aggregated (right-skewed) distribution (Fig. 10.6a, b) in which only few individuals in the population harbor parasites. For example, Fig. 10.6 shows that the proportion of infected howlers (i.e., prevalence) with helminth (A) and protozoan (B) parasites is rather low, suggesting that only few sampled individuals per study presented evidence of parasitic infection. This characteristic has significant implications for detecting parasitic infection in a specific population and calls attention to the importance of gathering a large sample size (number of individuals sampled and number of samples collected per individual; Gillespie 2006). This is particularly important given that many studies reporting parasites in howlers are based only on brief surveys and small sample sizes.

More than 60 % of the studies analyzed in this chapter (Table 10.1) used fecal material to recover gastrointestinal parasite eggs, cysts, oocysts, and larvae. Egg counts have been used as a proxy of parasite intensity or load in many studies in nonhuman primates including red colobus monkeys (*Procolobus rufomitratus* (Chapman et al. 2009)), olive baboons (*Papio anubis* (Weyher et al. 2006)), and howler monkeys (mantled howlers, *A. palliata* (Stoner 1996); black howlers, *A. pigra* (Stoner and González Di Pierro 2006; González-Hernández et al. 2011)). Intensity is defined as the number of adult individuals of a specific parasite species within a host (Bush et al. 1997). Because intensity of adult individuals can induce morbidity, this measure provides an important index of disease risk (Bethony et al. 2006); however, helminth parasite egg production does not correlate with the number of adult parasites infecting a single host (Anderson and Schad 1985), which makes egg counts a limited measure of parasite intensity. Despite this being reiterated in the primate literature (Gillespie 2006), primatologists continue using this measure as an index of intensity. This is an incorrect procedure that should be avoided in howler parasite studies. First of all, egg output rate is characterized by day-to-day variability

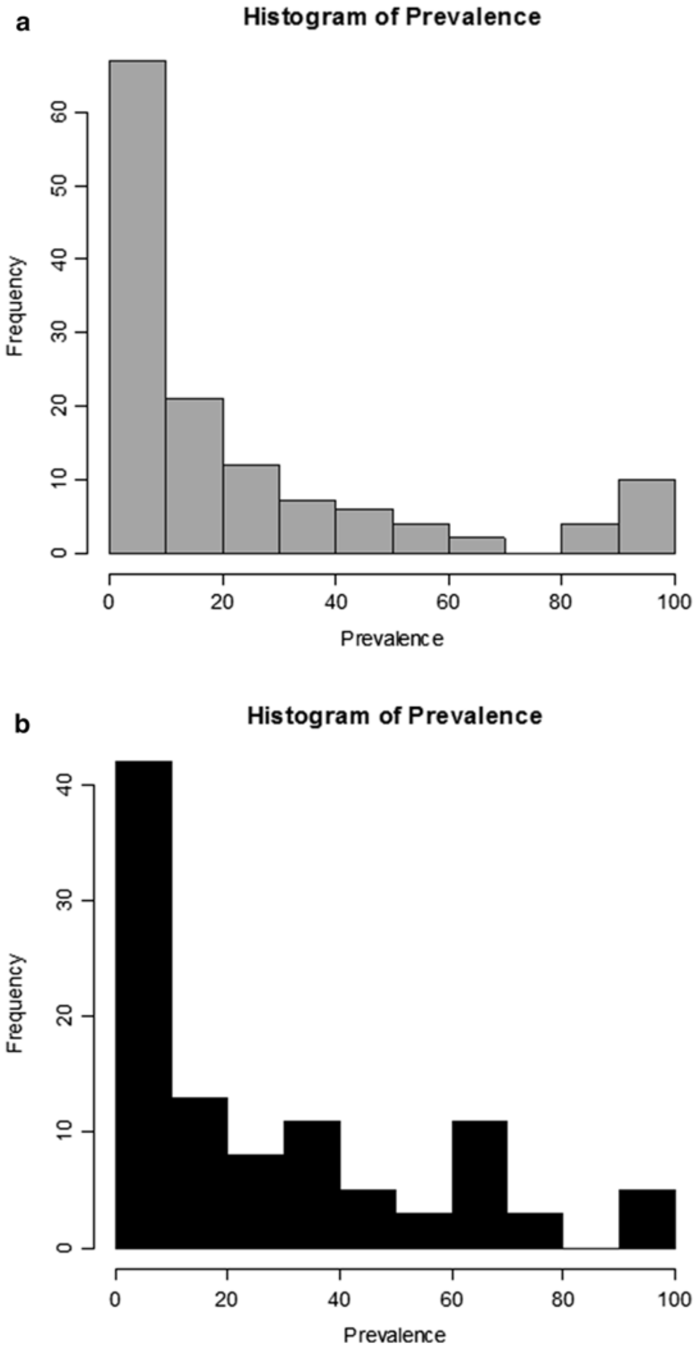

Fig. 10.6 Frequency of helminth (**a**) and protozoan (**b**) prevalence reported in howler monkey studies

within and between individual hosts (Anderson and Schad 1985; Wilson et al. 2002), which may lead to incorrect conclusions, based on false-negative results, such as claiming that a howler monkey population is not infected by certain parasite species. Second, number of eggs shed in feces is not constant over time and does not indicate degree of infection (Ezenwa 2003). Actually, parasite egg output in humans has been found to decrease when worm burden increases due to a density-dependent effect on parasite fecundity (Anderson and Schad 1985). Because of this, helminth egg counts do not provide an accurate measure of parasite intensity.

Our goal is not to minimize the damaging effects that pathogens may have on howler monkeys, but rather to draw attention to the fact that parasitic infection in howler monkeys is driven by complex interactions among environmental and ecological factors, which vary according to parasite type. There is strong evidence that infectious diseases have the potential to increase mortality in howler populations (Holzmann et al. 2010; de Almeida et al. 2012). Unfortunately, there is a disconnection between such sporadic evidence of pathogenic threats to howlers and the ubiquitous data typically collected in the study of howler parasites. Howler parasite studies are generally focused on relating parasitic infections to seasonal periods (e.g., wet vs. dry), forest type (e.g., disturbed vs. undisturbed), or sex (e.g., male vs. female), and although these are important variables to be taken into account, fine-grained estimations of ecological and microclimate change will provide better insights into the proximate factors that promote parasitism in howler monkeys. Finally, we want to point out that there is a gap in primate gastrointestinal parasite taxonomy, which highlights the need to collaborate with molecular parasitologists to correctly identify parasite taxa hosted by howler monkeys. In this way, we will be able to accurately determine parasites with pathogenic potential and then assess disease risk.

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References

Altizer S, Dobson A, Hosseini P, Hudson P, Pascual M, Rohani P (2006) Seasonality and the dynamics of infectious diseases. Ecol Lett 9:467–484

Alvarado-Villalobos MA (2010) Prevalencia e intensidad de parásitos intestinales de *Alouatta pigra* en fragmentos de selva en Playas de Catazajá. Chiapas. Bachelors thesis, Universidad Autónoma de Ciudad Juárez, Chihuahua, México

Anderson RM, Schad GA (1985) Hookworm burdens and faecal egg counts: an analysis of the biological basis of variation. Trans R Soc Trop Med Hyg 79:812–825

Appleton CC, Henzi SP (1993) Environmental correlates of gastrointestinal parasitism in montane and lowland baboons in Natal, South Africa. Int J Primatol 14:623–635

Bermejo M, Rodríguez-Teijeiro JD, Illera G, Barroso A, Vilà C, Walsh PD (2006) Ebola outbreak killed 5000 gorillas. Science 314:1564

Bethony J, Brooker S, Albonico M, Geiger SM, Loukas A, Diemert D, Hotez PJ (2006) Soil-transmitted helminth infections: ascariasis, trichuriasis, and hookworms. Lancet 367:1521–1532

Bloemers GF, Hodda M, Lambshead PJD, Lawton JH, Wanless FR (1997) The effects of forest disturbance on diversity of tropical soil nematodes. Oecologia 111:575–582

Bonilla-Moheno M (2002) Prevalencia de parásitos gastroentéricos en primates (*Alouatta pigra* y *Ateles geoffroyi yucatanensis*) localizados en hábitat conservado y fragmentado de Quintana Roo, México. Bachelors thesis, Universidad Nacional Autónoma de México, México DF

Braza F (1980) El araguato rojo (*Alouatta seniculus*). Doñana Acta Vertebr 75:1–175

Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. J Parasitol 83:575–583

Cabral JNH, Rossato RS, de M Gomes MJT, Araujo FAP, Oliveira F, Praetzel K (2005) Gastrointestinais de bugios-ruivos (*Alouatta guariba clamitans* Cabrera 1940) da regiao extremo-sul de Porto Alegre/RS- Brasil, diagnosticados atraves da coproscopia: implicacoes para a conservacao da especie e seus ha. Congresso Brasileiro de Parasitologia, Porto Alegre, RS, Brasil

Carme B, Aznar C, Motard A, Demar M, De Thoisy B (2002) Serologic survey of *Toxoplasma gondii* in noncarnivorous free-ranging neotropical mammals in French Guiana. Vector Borne Zoonotic Dis 2:11–17

Castillejos M (1993) Identificación de parásitos gastrointestinales en monos aulladores (*Alouatta palliata*), en la reserva "El Zapotal" Chiapas, México. Bachelors thesis, Facultad de Medicina Veterinaria y Zootecnia, Universidad Veracruzana, México

Chapman CA, Rothman JM, Hodder SAM (2009) Can parasite infections be a selective force influencing primate group size? A test with red colobus. In: Huffman MA, Chapman CA (eds) Primate parasite ecology. The dynamics and study of host-parasite relationships. Cambridge University, Cambridge

Chinchilla Carmona M, Guerrero Bermúdez O, Gutiérrez-Espeleta GA, Sánchez Porras R, Rodríguez Ortiz B (2005) Parásitos intestinales en monos congo *Alouatta palliata* (Primates: Cebidae) de Costa Rica. Rev Biol Trop 53:437–445

Clarke MR, Crockett CM, Zucker EL, Zaldivar M (2002) Mantled howler population of Hacienda La Pacifica, Costa Rica, between 1991 and 1998: effects of deforestation. Am J Primatol 56:155–163

Coppo JA, Moreira RA, Lombardero OJ (1979) El parasitismo en los primates del CAPRIM. Acta Zool Lilloana 35:9–12

Crawley MJ (2007) The R book. Wiley, Sussex

Cristóbal-Azkarate J, Hervier B, Vegas-Carrillo S, Osorio-Sarabia D, Rodríguez-Luna E, Veà JJ (2010) Parasitic infections of three Mexican howler monkey groups (*Alouatta palliata mexicana*) living in forest fragments in Mexico. Primates 51:231–239

Cristóbal-Azkarate J, Colwell DD, Kenny D, Solórzano B, Shedden A, Cassaigne I, Rodríguez-Luna E (2012) First report of bot fly (*Cuterebra baeri*) infestation in howler monkeys (*Alouatta palliata*) from Mexico. J Wildl Dis 48:822–825

Daszak P, Berger L, Cunningham AA, Hyatt AD, Green DE, Speare R (1999) Emerging infectious diseases and amphibian population declines. Emerg Infect Dis 5:735–748

Daszak P, Cunningham AA, Hyatt AD (2000) Emerging infectious diseases of wildlife- threats to biodiversity and human health. Science 287:443–449

de Almeida MA, Dos Santos E, da Cruz CJ, da Fonseca DF, Noll CA, Silveira VR, Maeda AY, de Souza RP, Kanamura C, Brasil RA (2012) Yellow fever outbreak affecting *Alouatta* populations in southern Brazil (Rio Grande do Sul State), 2008–2009. Am J Primatol 74:68–76

Delgado A (2006) Estudio de patrones de uso de sitios de defecación y su posible relación con infestaciones parasitarias en dos grupos de monos aulladores negros y dorados (*Alouatta caraya*) en el nordeste argentino. Bachelors thesis, Universidad Nacional de Córdoba, Argentina

Di Fiore A, Link A, Campbell CJ (2011) The Atelines. Behavioral and socioecological diversity in a New World monkey radiation. In: Campbell CJ, Fuentes AF, MacKinnon KC, Bearder SK, Stumpf RM (eds) Primates in perspective, 2nd edn. Oxford University, New York

Drakeley CJ, Carneiro I, Reyburn H, Malima R, Lusingu JPA, Cox J, Theander TG, Nkya WMMM, Lemnge MM, Riley EM (2005) Altitude-dependent and -independent variations in *Plasmodium falciparum* prevalence in northeastern Tanzania. J Infect Dis 191:1589–1598

Duarte AMRC, Porto MAL, Curado I, Malafronte RS, Hoffmann EHE, de Oliveira SG, da Silva AMJ, Kloetzel JK, Gomes AC (2006) Widespread occurrence of antibodies against circumsporozoite protein and against blood forms of *Plasmodium vivax, P falciparum* and *P malariae* in Brazilian wild monkeys. J Med Primatol 35:87–96

Eckert KA, Hahn NE, Genz A, Kitchen DM, Stuart MD, Averbeck GA, Stromberg BE, Markowitz H (2006) Coprological surveys of Alouatta pigra at two sites in Belize. Int J Primatol 27:227–238

Ezenwa VO (2003) Thee effect of time of day on the prevalence of coccidian oocysts in antelope faecal samples. Afr J Ecol 41:192–193

Fandeur T, Volney B, Peneau C, De Thoisy B (2000) Monkeys of the rainforest in French Guiana are natural reservoirs for *P. brasilianum*/*P. malariae* malaria. Parasitology 120:11–21

Fayer R, Dubey JP, Lindsay DS (2004) Zoonotic protozoa: from land to sea. Trends Parasitol 20:531–536

Ford SM (2006) The biogeographic history of Mesoamerican primates. In: Estrada A, Garber PA, Pavelka MSM, Luecke L (eds) New perspectives in the study of Mesoamerican primates: distribution, ecology, behavior, and conservation. Springer, New York

Garcia JL, Svoboda WK, Chryssafidis AL, de Souza Malanski L, Shiozawa MM, de Moraes Aguiar L, Teixeira GM, Ludwig G, da Silva LR, Hilst C, Navarro IT (2005) Sero-epidemiological survey for toxoplasmosis in wild New World monkeys (*Cebus* spp.; *Alouatta caraya*) at the Paraná river basin, Paraná State, Brazil. Vet Parasitol 133:307–311

Gilbert KA (1994) Endoparasitic infection in red howling monkeys (*Alouatta seniculus*) in the Central Amazonian basis: a cost of sociality? PhD dissertation, The State University of New Jersey at New Brunswick Rutgers

Gillespie TR (2006) Noninvasive assessment of gastrointestinal parasite infections in free-ranging primates. Int J Primatol 27:1129–1143

Gillespie TR, Chapman CA (2006) Prediction of parasite infection dynamics in primate metapopulations based on attributes of forest fragmentation. Conserv Biol 20:441–448

Gillespie TR, Chapman CA (2008) Forest fragmentation, the decline of an endangered primate, and changes in host-parasite interactions relative to an unfragmented forest. Am J Primatol 70:222–230

Gillespie TR, Chapman CA, Granier EC (2005) Effects of logging on gastrointestinal parasite infections and infection risk in African primates. J Appl Ecol 42:699–707

Gillespie TR, Nunn CL, Leendertz FH (2008) Integrative approaches to the study of primate infectious disease: implications for biodiversity conservation and global health. Am J Phys Anthropol 51:53–69

Gillespie TR, Lonsdorf EV, Canfield EP, Meyer DJ, Nadler Y, Raphael J, Pusey AE, Pond J, Pauley J, Mlengeya T, Travis DA (2010) Demographic and ecological effects on patterns of parasitism in eastern chimpanzees (*Pan troglodytes schweinfurthii*) in Gombe National Park, Tanzania. Am J Phys Anthropol 143:534–544

Gillespie TR, Barelli C, Heistermann M (2013) Effects of social status and stress on patterns of gastrointestinal parasitism in wild white-handed gibbons (*Hylobates lar*). Am J Phys Anthropol 150:602–608

Giudice AM, Mudry MD (2000) Drinking behavior in the black howler monkey (*Alouatta caraya*). Zoocriaderos 3:11–19

Godoy KCI, Odalia-Rimoli A, Rimoli J (2004) Infeccao por endoparasitos em um grupo de bugios-pretos (*Alouatta caraya*), em um fragmento florestal no Estado de Mato Grosso do Sul. Neotrop Primates 12:63–68

Goldberg TL, Gillespie TR, Rwego IB, Estoff EL, Chapman CA (2008) Forest fragmentation as cause of bacterial transmission among non-human primates, humans, and livestock, Uganda. Emerg Infect Dis 14:1375–1382

González-Hernández M, Dias PAD, Romero-Salas D, Canales-Espinosa D (2011) Does home range use explain the relationship between group size and parasitism? A test with two sympatric species of howler monkeys. Primates 52:211–216

Gonzalez-Moreno O, Hernandez-Aguilar RA, Piel AK, Stewart FA, Gracenea M, Moore J (2013) Prevalence and climatic associated factors of *Cryptosporidium* sp. infection in savanna chimpanzees from Ugalla, Western Tanzania. Parasitol Res 112:393–399

Graczyk TK, Shiff CK, Tamang L, Munsaka F, Beitin AM, Moss WJ (2005) The association of *Blastocystis hominis* and *Endolimax nana* with diarrheal stools in Zambia school-age children. Parasitol Res 98:38–43

Guernier V, Hochberg ME, Guégan JF (2004) Ecology drives the worldwide distribution of human diseases. PLoS Biol 2:740–746

Harvell CD, Mitchell CE, Ward JR, Altizer S, Dobson AP, Ostfeld RS, Samuel MD (2002) Climate warming and disease risks for terrestrial and marine biota. Science 296:2158–2162

Hawkins BA, Porter EE, Dinis-Filho JAF (2003) Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. Ecology 84:1608–1623

Hillebrand H (2004) On the generality of the latitudinal diversity gradient. Am Nat 163:192–211

Hilser H (2011) An assessment of primate health in the Sabangau peat-swamp forest, central Kalimantan, Indonesian Borneo. Masters thesis, Oxford Brookes University, Oxford

Holzmann I, Agostini I, Areta JI, Ferreyra H, Beldomenico P, Di Bitetti MS (2010) Impact of yellow fever outbreaks on two howler monkey species (*Alouatta guariba clamitans* and *A. caraya*) in Misiones, Argentina. Am J Primatol 72:475–480

Huffman MA (1997) Current evidence for self-medication in primates: a multidisciplinary perspective. Yearbook Phys Anthropol 40:171–200

Hunter PR (2003) Climate change and waterborne and vector-borne disease. J Appl Microbiol 94:37S–46S

Jagai JS, Castronovo DA, Monchak J, Naumova EN (2009) Seasonality of cryptosporidiosis: a meta-analysis approach. Environ Res 109:465–478

Köndgen S, Kühl H, N'Goran PK, Walsh PD, Schenk S, Ernst N, Biek R, Formenty P, Mätz-Rensing K, Schweiger B, Junglen S, Ellerbrok H, Nitsche A, Briese T, Lipkin WI, Pauli G, Boesch C, Leendertz FH (2008) Pandemic human viruses cause decline of endangered great apes. Curr Biol 18:260–264

Kowalewski MM, Garber PA (2010) Mating promiscuity and reproductive tactics in female black and gold howler monkeys (*Alouatta caraya*) inhabiting an island on the Parana River, Argentina. Am J Primatol 72:734–748

Kowalewski MM, Gillespie TR (2009) Ecological and anthropogenic influences on patterns of parasitism in free-ranging primates: a meta-analysis of the Genus *Alouatta*. In: Garber PA, Estrada A, Bicca-Marques JC, Heymann EW, Strier KB (eds) South American primates. Comparative perspectives in the study of behavior, ecology, and conservation. Springer, New York

Kowalewski MM, Salzer JS, Deutsch JC, Raño M, Kuhlenschmidt MS, Gillespie TR (2011) Black and gold howler monkeys (*Alouatta caraya*) as sentinels of ecosystem health: patterns of zoonotic protozoa infection relative to degree of human-primate contact. Am J Primatol 73:75–83

Kowalzik BK, Pavelka MSM, Kutz SJ, Behie A (2010) Parasites, primates, and ant-plants: clues to the life cycle of *Controrchis* sp. in black howler monkeys (*Alouatta pigra*) in southern Belize. J Wildl Dis 46:1330–1334

Laurance WF (2000) Do edge effects occur over large spatial scales? Trends Ecol Evol 15:134–135

Laurenson K, Sillero-Zubiri C, Thompson H, Shiferaw F, Thirgood S, Malcolm J (1998) Disease as a threat to endangered species: Ethiopian wolves, domestic dogs and canine pathogens. Anim Conserv 1:273–280

Leendertz FH, Pauli G, Maetz-Rensing K, Boardman W, Nunn C, Ellerbrok H, Jensen SA, Junglen S, Boesch C (2006) Pathogens as drivers of population declines: the importance of systematic monitoring in great apes and other threatened mammals. Biol Conserv 131:325–337

Lindblade KA, Walker ED, Onapa AW, Katungu J, Wilson ML (2000) Land use change alters malaria transmission parameters by modifying temperature in a highland area of Uganda. Trop Med Int Health 5:263–274

Lourenco de Oliveira R, Deane LM (1995) Simian malaria at two sites in the Brazilian Amazon. The infection rates of Plasmodium brasilianum in non-human primates. Mem Inst Oswaldo Cruz 90:331–339

Luo Z, Tang S, Li C, Fang H, Hu H, Yang J, Ding J, Jiang Z (2012) Environmental effects on vertebrate species richness: testing the energy, environmental stability and habitat heterogeneity hypotheses. PLoS One 7(e35514):1–7

Marsh LK (2003) The nature of fragmentation. In: Marsh LK (ed) Primates in fragments: ecology and conservation. Kluwer Academic, New York

Martins SS, Ferrari SF, Silva CS (2008) Gastro-intestinal parasites of free-ranging red-handed howlers (*Alouatta belzebul*) in Eastern Amazonia. In: Ferrari SF, Rímoli J (eds) A Primatologia no Brasil—9 (.) Aracaju, Sociedade Brasileira de Primatologia, Biologia Geral e Experimental—UFS, pp 114–124

Mbora DNM, McPeek MA (2009) Host density and human activities mediate increased parasite prevalence and richness in primates threatened by habitat loss and fragmentation. J Anim Ecol 78:210–218

Milozzi C, Bruno G, Cundom E, Mudry MD, Navone GT (2012) Intestinal parasites of *Alouatta caraya* (Primates, Ceboidea): preliminary study in semi-captivity and in the wild in Argentina. Mastozool Neotrop 19:271–278

Milton K (1980) The foraging strategy of howler monkeys: a study in primate economics. Columbia University, New York

Milton K (1996) Effects of bot fly (*Alouattamyia baeri*) parasitism on free-ranging howler monkey (*Alouatta palliata*) population in Panama. J Zool 239:39–63

Milton K, Lozier JD, Lacey EA (2009) Genetic structure of an isolated population of mantled howler monkeys (*Alouatta palliata*) on Barro Colorado Island, Panama. Conserv Genet 10:347–358

Muchiri JM, Ascolillo L, Mugambi M, Mutwiri T, Ward HD, Naumova EN, Egorov AI, Cohen S, Else JG, Griffiths JK (2009) Seasonality of *Cryptosporidium* oocyst detection in surface waters of Meru, Kenya as determined by two isolation methods followed by PCR. J Water Health 7:67–75

Nunn CL, Altizer SM (2005) The global mammal parasite database: an online resource for infectious disease records in wild primates. Evol Anthropol 14:1–2

Nunn CL, Altizer SM (2006) Infectious diseases in primates: behavior, ecology, and evolution. Oxford University, Oxford

Nunn CL, Heymann EW (2005) Malaria infection and host behavior: a comparative study of Neotropical primates. Behav Ecol Sociobiol 59:30–37

Nunn CL, Altizer SM, Sechrest W, Cunningham AA (2005) Latitudinal gradients of parasite species richness in primates. Divers Distrib 11:249–256

Odongo-Aginya E, Ssegwanyi G, Kategere P, Vuzi PC (2005) Relationships between malaria infection intensity and rainfall pattern in Entebbe peninsula, Uganda. Afr Health Sci 5:238–245

Palacios G, Lowenstine LJ, Cranfield MR, Gilardi KVK, Spelman L, Lukasik-Braum M, Kinaki JF, Mudakikwa A, Nyirakaragire E, Busetti AV, Savji N, Hutchison S, Egholm M, Lipkin WI (2011) Human metapneumovirus infection in wild mountain gorillas, Rwanda. Emerg Infect Dis 17:711–713

Pascual M, Cazelles B, Bouma MJ, Chaves LF, Koelle K (2008) Shifting patterns: malaria dynamics and rainfall variability in African highland. Proc R Soc B 275:123–132

Patz JA, Graczyk TK, Geller N, Vittor AY (2000) Effects of environmental change on emerging parasitic diseases. Int J Parasitol 30:1395–1405

Peres CA (2001) Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. Conserv Biol 15:1490–1504

Phillips KA, Haas ME, Grafton BW, Yrivarren M (2004) Survey of the gastrointestinal parasites of the primate community at Tambopata National Reserve, Peru. J Zool 264:149–151

Pianka ER (1966) Latitudinal gradients in species diversity: a review of concepts. Am Nat 100:33–46

Pope BL (1966) Some parasites of the howler monkey of northern Argentina. J Parasitol 52:166–168

Poulin R (2006) Global warming and temperature-mediate increases in cercarial emergence in trematode parasites. Parasitology 132:143–151

Poulin R, Morand S (2000) The diversity of parasites. Q Rev Biol 75:277–293

Rifakis PM, Benítez JA, Pineda JDLP, Rodríguez-Morales AJ (2006) Epizootics of yellow fever in Venezuela (2004-2005). Ann N Y Acad Sci 1081:57–60

Rode KD, Chapman CA, McDowell LR, Stickler C (2006) Nutritional correlates of population density across habitats and logging intensities in redtail monkeys (*Cercopithecus ascanius*). Biotropica 38:625–634

Rohde K (1992) Latitudinal gradients in species diversity: the search for the primary cause. Oikos 65:514–527

Rosenberger AL, Halenar L, Cooke SB (2011) The making of Platyrrhine semifolivores: models for the evolution of folivory in primates. Anat Rec 294:2112–2130

Rovirosa-Hernández MJ, Cortés-Ortiz L, García-Orduña F, Guzmán-Gómez D, López-Monteon A, Caba M, Ramos-Ligonio A (2013) Seroprevalence of *Trypanosoma cruzi* and *Leishmania mexicana* in free-ranging howler monkeys in Southeastern Mexico. Am J Primatol 75:161–169

Rudran R, Fernandez-Duque E (2003) Demographic changes over thirty years in a red howler population in Venezuela. Int J Primatol 24:925–947

Rwego IB, Isabirye-Basuta G, Gillespie TR (2008) Gastrointestinal bacterial transmission among humans, mountain gorillas, and domestic livestock in Bwindi Impenetrable National Park, Uganda. Conserv Biol 22:1600–1607

Santa Cruz ACM, Borda JT, Patiño EM, Gomez L, Zunino GE (2000) Habitat fragmentation and parasitism in howler monkeys (*Alouatta caraya*). Neotrop Primates 8:146–148

Santos MVS, Ueta MT, Setz EZF (2005) Levantamento de helmintos intestinais em bugio- ruivo, *Alouatta guariba* (Primates, atelidae), na mata de ribeir˜ao cachoeira no Distrito de Souzas/Campinas, SP. Congresso Brasileiro de Parasitologia, Porto Alegre, RS, Brasil

Silver SC, Ostro LET, Yeager CP, Horwich R (1998) Feeding ecology of the black howler monkey (*Alouatta pigra*) in northern Belize. Am J Primatol 45:263–279

Smith KF, Acevedo-Whitehouse K, Pedersen AB (2009) The role of infectious diseases in biological conservation. Anim Conserv 12:1–12

Stoner KE (1996) Prevalence and intensity of intestinal parasites in mantled howling monkeys (*Alouatta palliata*) in Northeastern Costa Rica: implications for conservation biology. Conserv Biol 10:539–546

Stoner KE, González Di Pierro AM (2006) Intestinal parasitic infections in *Alouatta pigra* in tropical rain forest in Lacandona, Chiapas, Mexico: implications for behavioral ecology and conservation. In: Estrada A, Garber PA, Pavelka MSM, Luecke L (eds) New perspectives in the study of Mesoamerican primates: distribution, ecology, behavior, and conservation. Springer, New York

Stuart MD, Greenspan LL, Glander KE, Clarke MR (1990) A coprological survey of parasites of wild mantled howling monkeys, *Alouatta palliata palliata*. J Wildl Dis 26:547–549

Thompson RCA (2000) Giardiasis as a re-emergence infectious disease and its zoonotic potential. Int J Primatol 30:1259–1267

Travi BL, Colillas OJ, Segura EL (1986) Natural trypanosome infection in Neotropical monkeys with special reference to *Saimiri sciureus*. In: Taub DM, King FA (eds) Current Perspectives in primate biology. Van Nostrand Rehinold, New York

Trejo-Macías G, Estrada A, Mosqueda Cabrera MA (2007) Survey of helminth parasites in populations of *Alouatta palliata mexicana* and *A. pigra* in continuous and in fragmented habitat in southern Mexico. Int J Primatol 28:931–945

Valdespino C, Rico-Hernández G, Mandujano S (2010) Gastrointestinal parasites of howler monkeys (*Alouatta palliata*) inhabiting the fragmented landscape of the Santa Marta mountain range, Veracruz, Mexico. Am J Primatol 72:539–548

Van Belle S, Estrada A, Ziegler TE, Strier KB (2009) Sexual behavior across ovarian cycles in wild black howler monkeys (*Alouatta pigra*): male mate guarding and female choice. Am J Primatol 71:153–164

Venturini L, Santa Cruz AM, González JA, Comolli JA, Toccalino PA, Zunino GE (2003) Presencia de *Giardia duodenalis* (Sarcomastigophora, Hexamitidae) en mono aullador (*Alouatta caraya*) de vida silvestre. Comunicaciones Científicas y Tecnológicas, Universidad Nacional del Nordeste

Vitazkova SK (2009) Overview of parasites infecting howler monkeys, *Alouatta* sp., and potential consequences of human-howler interactions. In: Huffman MA, Chapman CA (eds) Primate parasite ecology. The dynamics and study of host-parasite relationships. Cambridge University, Cambridge

Vitazkova SK, Wade SE (2006) Parasites of free-ranging black howler monkeys (*Alouatta pigra*) from Belize and Mexico. Am J Primatol 68:1089–1097

Vitazkova SK, Wade SE (2007) Effects of ecology on the gastrointestinal parasites of *Alouatta pigra*. Int J Primatol 28:1327–1343

Vittor AY, Gilman RH, Tielsch J, Glass G, Shields T, Sanchez Lozano W, Pinedo-Cancino V, Patz JA (2006) The effect of deforestation on the human-biting rate of *Anopheles darlingi*, the primary vector of falciparum malaria in the Peruvian Amazon. Am J Trop Med Hyg 74:3–11

Volney B, Pouliquen JF, De Thoisy B, Fandeur T (2002) A sero-epidemiological study of malaria in human and monkey populations in French Guiana. Acta Trop 82:11–23

Volotao AC, Junior JC, Grassini C, Peralta JM, Fernandes O (2008) Genotyping of *Giardia duodenalis* from southern brown howler monkeys (*Alouatta clamitans*) from Brazil. Vet Parasitol 158:133–137

Weyher AH, Ross C, Semple S (2006) Gastrointestinal parasites in crop raiding and wild foraging *Papio anubis* in Nigeria. Int J Primatol 27:1519–1534

Wilcox BA, Ellis B (2006) Forest and emerging infectious diseases of humans. Unasylva 57:11–18

Wilson K, Grenfell BT (1997) Generalized linear modelling for parasitologists. Parasitol Today 13:33–38

Wilson K, Bjørnstad ON, Dobson AP, Merler S, Poglayen G, Randolph SE, Read AF, Skorping A (2002) Heterogeneities in macroparasite infections: patterns and processes. In: Hudson PJ, Rizzoli A, Grenfell BT, Heesterbeek H, Dobson AP (eds) The ecology of wildlife disease. Oxford University, Oxford

Wright PC, Arrigo-Nelson SJ, Hogg KL, Bannon B, Morelli TL, Wyatt J, Harivelo AL, Ratelolahy F (2009) Habitat disturbance and seasonal fluctuations of lemur parasites in the rain forest of Ranomafana National Park, Madagascar. In: Huffman MA, Chapman CA (eds) Primate parasite ecology. The dynamics and study of host-parasite relationships. Cambridge University, Cambridge

Young H, Griffin RH, Wood CL, Nunn CL (2013) Does habitat disturbance increase infectious disease risk for primates? Ecol Lett 16:656–663

Zamora-Vilchis I, Williams SE, Johnson CN (2012) Environmental temperature affects prevalence of blood parasites of birds on an elevation gradient: implications for disease in a warming climate. PLoS One 7(e39208):1–8

Zhou G, Minakawa N, Githeko AK, Yan G (2004) Association between climate variability and malaria epidemics in the East African highlands. Proc Natl Acad Sci U S A 101:2375–2380

Zommers Z, Macdonald DW, Johnson PJ, Gillespie TR (2012) Impact of human activity on chimpanzee ground use and parasitism (*Pan troglodytes*). Conserv Lett 6:264–273