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THE PARASITE BEHAVIOR HYPOTHESIS AND THE USE OF SLEEPING SITES BY BLACK HOWLER MONKEYS (*ALOUATTA CARAYA*) IN A DISCONTINUOUS FOREST

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Introduction

Primates are particularly susceptible to parasitic infections because they live in social groups that facilitate their transmission (Stoner, 1996). The costs and benefits of living in smaller and larger social groups have been examined in a number of primate field studies (Struhsaker, 1969; Eisenberg *et al.*, 1972; Clutton-Brock and Harvey, 1977; Van Schaik, 1989; Janson, 1992; Sterck *et al.*, 1997; Chapman and Chapman, 2000; Kappeler and van Schaik, 2002). Several factors influence social group living: 1) the availability, abundance, and distribution of food resources—limiting the number of animals that an area can support or influencing foraging efficiency in groups of different sizes (Wrangham, 1980; Chapman, 1990); 2) historical and social traits, including changes in group size or population size (Stevenson *et al.*, 1998); 3) life history traits such as birth rates, sex ratios, mortality, and dispersal patterns (Altmann, 1980; Dunbar, 1988; Crockett, 1996); 4) predation pressure (Stanford, 2002); 5) cooperation and affiliation among individuals (Sussman and Garber, 2004); and 6) traits related to social organization that are phylogenetically conservative and do not change in different environments (DiFiore and Rendall, 1994). There are few studies that consider parasite transmission as a factor in limiting group size or affecting group structure in social primates (Freeland, 1976; Janson, 2000).

Parasitism has density-dependent costs related to disease transmission; therefore, it may play an important role in increasing the fitness of individuals living in smaller social groups, who benefit from an enhanced amount of grooming. Because parasitic infections can cause a fitness decrease in animals, some parasite-avoidance behaviors (e.g., mammals licking their own fur, auto- and allogrooming, mud wallows, and dust baths) can be expected (Alexander, 1974; Pulliam and Caraco, 1984; Mooring and Hart, 1992; Loehle, 1995). Parasites can directly affect host survival by increasing predation risk or decreasing competitive abilities (Scott, 1988). In addition, if parasite loads affect health and physical appearance, they can influence patterns of female mate choice or the ability of individuals to compete directly for access to sexual partners (Freeland, 1981; Hamilton and Zuk, 1982).

Due to their use and re-use of a limited ranging area, primates living in small forest patches with restricted home ranges will be more exposed to infection and re-infection (increasing the amount of the re-infecting dose) with parasite ova and larvae (Freeland, 1976, 1980; Gilbert, 1997). Behaviors that avoid and/or reduce parasite infections (Freeland, 1980; Hausfater and Meade, 1982) constitute an alternative to physiological immunity (Keymer and Read, 1991) and may contribute to the survival of some individuals. Howler monkeys (*Alouatta*) host a number of intestinal parasites that are eliminated in their feces (Stuart *et al.*, 1998; Santa Cruz *et al.*, 2000; Muller *et al.*, 2000). This study examines the black howler monkey's (*Alouatta caraya*) use of defecation and night resting sites as a strategy to avoid parasite re-infection in a forest fragment in northern Argentina.

A number of hypotheses have been offered to explain the selection of sleeping sites in primates (Anderson, 1984; Di Bitetti *et al.*, 2000): 1) Parasite hypothesis: different trees are chosen every night to avoid recontamination with parasites; 2) Predation hypothesis: a) different and inaccessible trees are used so that predators cannot predict the locations of the sleeping sites, or b) contrariwise, the persistent use of the same trees that provide the most effective escape routes from predators; 3) Thermoregulatory hypothesis: energy conservation associated with individuals huddling together when it is cold; 4) Social hypothesis: monkeys choose sleeping sites that allow social contact and social bonding; 5) Safety hypothesis: howlers select trees that offer secure and sheltered platforms to sleep in relaxed positions or to avoid severe weather; and 6) Feeding site hypothesis (von Hippel, 1998): monkeys prefer to sleep near or in feeding trees. If howlers select sleeping sites to reduce the chances of parasitic infections then they will defecate in places different from those where they sleep (avoiding the contamination of sites they use often). They should also defecate from low branches in order to avoid sullying supports used as potential traveling routes or sleeping sites.

Methods

Alouatta caraya is an arboreal folivore-frugivore. Its range in northern Argentina marks the extreme southern distribution of the genus (Brown and Zunino, 1994). The study was carried out in a fragment of semideciduous gallery forest in northern Argentina (27°30'S and 58°41'W) in the basin of the Río Riachuelo, a tributary of the Río Paraná (Fig. 1). The area is between 50 and 60 m above sea level. The climate is subtropical, with an annual average temperature of 21.7° C and annual average precipitation of 1230 mm (Servicio Meteorológico Nacional, from 1901–1950). Rains are frequent year-round, but decrease considerably in July and August. The vegetation forms a mosaic of tall and low forests, savannas with palms, grasslands and lowland zones with lagoons and "esteros" (marshes). The primary forest has been and is currently being logged intensively.

A group of black howlers was followed for 15 days in August 1994 (winter) and 15 days in February 1995 (summer) from sunrise till sunset. There were 10 individuals in the group in the winter period (1 adult male, 2 subadult males, 3 adult females, 1 subadult female, 2 juveniles and 1 infant) and 9 individuals in the summer (1 adult male, 3 subadult males, 2 adult females, 1 subadult female, 1 juvenile and 1 infant). The forest fragment of 8.5 ha was subdivided into 212 quadrates of 20 x 20 m. We recorded the quadrates where the group defecated and slept at night, and then compared the frequencies of quadrate use with a G-test (Sokal and Rohlf, 1995). We also recorded the height and species of trees in which the monkeys defecated and slept. The height differences were analyzed with a Mann-Whitney test. The floristic composition and vegetation structure were taken from Zunino (1986) and Rumiz *et al.* (1986).

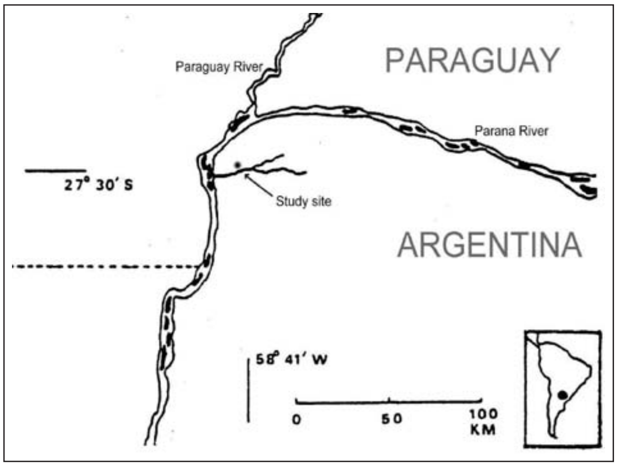

Figure 1. Location of the study site.

Results

Black howler monkeys defecate 2.63 times a day (sd = 0.49, n = 205 [total number of defecations of all individuals, excluding infants]), generally after resting (when they wake up in the morning and after an afternoon nap) and before going to sleep at night. In 60% of the 205 defecations recorded, the entire group defecated at about the same time. In 21%, all of the individuals but one defecated, and in 19% all but two defecated. The distribution and the frequency of quadrates used for night resting showed that the howlers were selective in the areas used for sleeping sites (site fidelity). They used different quadrates and locations in the forest to sleep and to defecate ($G_{\text{Williams}} = 112.36$, df =1, $p < 0.001$). The heights at which they defecated (8.33 ± 2.97 m) and at which they slept (18.07 ± 4.88 m) were significantly different ($U = 189$, $N_1 = 110$, $N_2 = 205$, $p < 0.001$). They slept in the crowns of the trees and defecated from the lower branches directly onto the ground. The group used six trees as night resting sites: five *Ficus monckii* trees (90.1%) and a *Tabebuia ipe* (9.9%). The troop defecated in 23 trees of nine different species.

Ficus monckii trees were commonly used as both sleeping (90.1%) and defecating sites (35.12%) (Table 1). These fig trees are the largest in this semideciduous forest (Rumiz *et al.*, 1986). The importance of *F. monckii* may also be its asynchrony in leafing and fruiting phenology, as it thus provides a year-round source of fruits and leaves (Zunino, 1987, 1989). The monkeys fed in these trees before going to sleep at night and when they woke up in the morning. In total, they used six different sleeping sites on the 20 nights of our two study periods, suggesting site fidelity. All group members slept together each night. Three times they used the same tree for three consecutive nights, and three times they used the same tree on two consecutive nights, again indicating site fidelity.

Discussion

The differences in the frequency of quadrate use and the heights at which the howlers defecated and slept may well reflect their attempts to diminish contact with feces in areas where they carry out much of their daily activity. Defecating in specific areas without understorey vegetation (low heights) could diminish the individual's chance of infection and re-infection by parasite ova or larvae on sullied branches or the leaves they may later come to eat. Following the hypotheses proposed above, however, the choice of sleeping trees did not appear to be related to parasite avoidance, at least as stated (Hypothesis 1: they used the same trees on consecutive nights), but instead could be related to behav-

Table 1. Use of different tree species by *A. caraya* for defecation, sleeping, and eating.

Species	% of use as defecation sites	% of use as sleeping sites	% in diet (from Zunino 1989)	DBH[1] m	Height m
Tabebuia ipe	3.41	9.10	4.2	0.40	20.0
Ficus monckii	35.12	90.90	45.83	0.52	12.25
Allophylus edulis	3.90	0	0.1	0.14	4.0
Celtis sp.	5.85	0	6.8	0.16	6.33
Enterolobium contortisiliquum	6.34	0	1.04	0.5	15.17
Gleditsia amorphoides	28.29	0	5.26	0.17	6.42
Myrcianthes pungens	4.39	0	0	0.23	6.46
Pithecelobium scalare	4.87	0	0.05	?	?
Phytolacca dioica	7.80	0	4.06–10	0.3	13.0
Other	0	0	32.66–26.72	-	-

[1] DBH: diameter at breast height.

iors designed to decrease predation risk. Braza *et al.* (1981) described a behavior in *A. seniculus* in which the monkeys rubbed their anus on a tree branch after defecating, behavior that could expose other group members to parasites. We observed a similar behavior in *A. caraya*. These howler behaviors do not appear to be consistent with avoiding exposure to parasites.

Sleeping high up in the trees is a common pattern in primates (Anderson, 1984). In this study howlers slept in tall trees characterized by a closed crown. This may be related to reducing predation risk from terrestrial predators while the closed crown minimizes risk from aerial predators. Although black howler monkeys do not have many predators at this site, potential predators include the jaguarondi (*Herpailurus yagouaroundi*) and dogs (*Canis domesticus*). We did not observe any predation or predator attacks, and reports of predation on atelines are rare anyway (Di Fiore, 2002). The relationship between the selection of sleeping trees and predation avoidance remains unclear. Selectivity in the trees used as sleeping sites was evident in that they were not the most abundant trees in the forest. As such, the selection of sleeping trees was consistent with a predator avoidance hypothesis: *Ficus* and *Tabeuia* trees were the tallest in the forest and possibly provided protection against predators.

We also found evidence in support of the thermoregulation hypothesis: they always slept huddled as a group. The social hypothesis was supported because the large crowns of the trees allowed the group members to sleep together. The safety hypothesis could not be discounted because the selected trees offered large branches and crowns to accommodate the individuals (pers. obs.).

Lastly, the feeding site hypothesis fits because *Ficus* trees were the major source of food in the howlers' diet (Table 1). *Ficus monckii* was the most frequent tree used as a sleeping site and the most important species in the black howler monkey diet (Zunino, 1987, 1989), representing 45.8% of the feeding time (Zunino, 1989). The leaves and fruits of *F. monckii* were available during almost all the year owing to the asynchronous phenology of this species (Zunino, 1986, 1987, 1989). During the winter when other species such as *Celtis* sp. and *Tabebuia ipe* (Zunino, 1987, 1989) increase in dietary importance (depending on their phenology), these species also were used as sleeping sites. Although we cannot discount a social function for sleeping site selectivity, the selection of large feeding trees as sleeping sites might best represent a foraging strategy.

Although the selection of sleeping trees was consistent with several alternative hypotheses, it was not consistent with parasite avoidance in so far as they used the same trees for defecating and sleeping on consecutive nights and only six sites during the 20 days of the study. Their tendency to move down in the forest to defecate, and do so in areas with sparse understoreys, however, might well be adaptive in terms of avoiding parasitism.

Other howler species such as *Alouatta palliata* (*v.* Dudley and Milton, 1990; Stuart *et al.*, 1990; Stoner, 1996), *A. seniculus* (*v.* Braza *et al.*, 1981; Gilbert, 1994, 1997) and *A. guariba* (*v.* Stuart *et al.*, 1993) have been recorded showing similar behavior in terms of selectivity of sleeping trees and defecation sites. Braza *et al.* (1981) reported that *A. seniculus* defecated directly over the ground as a way to avoid contaminating possible foraging routes. Gilbert (1997) showed that *A. seniculus* used specific trees to defecate from, defecating from lower branches and avoiding contact with underlying vegetation. Gilbert (1997) argued that defecation site choice may represent a parasite avoidance behavior in red howlers, and that this behavior could contribute to the relatively low abundance of endoparasite infection in howlers (Thatcher and Porter, 1968; Stuart *et al.*, 1990; Gilbert, 1994). Finally, a number of howler species, including black howlers, are reported to show behaviors associated with the reduction of disease transmission, such as the selection of defecation sites near the ground. Phylogeny may play an important role in the evolution of this behavior.

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NEWS

A RESERVA BIOLÓGICA FEDERAL DA MATA ESCURA E SUA IMPORTÂNCIA COMO UNIDADE DE CONSERVAÇÃO PARA OS PRIMATAS DO MÉDIO RIO JEQUITINHONHA, MINAS GERAIS

Fabiano R. Melo

Introdução

Antes mesmo da chegada dos Bandeirantes no vale do Jequitinhonha, em pleno século XVII, criadores de gado já ocupavam a região (Mascarenhas *et al.*, 1989). Entretanto, somente com a descoberta do ouro nas décadas finais de 1600 e da extração do diamante no século seguinte que, de fato, esta região ganhou espaço na história econômica brasileira e seu povoamento se deu de forma mais efetiva (Mascarenhas *et al.*, 1989). Este processo rápido de urbanização alcançado promoveu dificuldades no abastecimento de gêneros alimentícios para a região, o que favoreceu o surgimento de uma frágil agricultura de subsistência, associada, quase sempre, à pecuária de corte (Mascarenhas *et al.*, 1989). Ainda assim, nos anos de 1840, a zona de ocupação nativa da Mata Atlântica em Minas Gerais se limitava à região entre os rios Doce e Jequitinhonha, onde índios Botocudos vagavam livremente, atacando intrusos com certa freqüência (Dean, 1997).

Ainda hoje, o índice de pobreza ostentado pela região é elevado, ocasionando uma intensa migração da zona rural para os grandes centros urbanos e um esvaziamento demográfico persistente (Brasil, IBGE, 2004). Com mais de dois terços da população vivendo na zona rural, ela tem sido caracterizada em vários estudos como "região deprimida", onde os índices de pobreza, miséria, desnutrição, mortalidade, analfabetismo, desemprego e infra-estrutura sócio-econômica imperam desfavoravelmente em grande parte dos municípios (Gonçalves, 1997; Dias *et al.*, 2002; Ribeiro e Galizoni, 2003).

A média bacia do rio Jequitinhonha estende-se da foz do rio Araçuaí até a cidade de Salto da Divisa, no limite dos Estados de Minas Gerais e Bahia. Neste trecho, são registradas formações vegetais adaptadas a baixos índices pluviométricos e altas temperaturas, destacando-se a caatinga de porte arbustivo, indicando intervenção antrópica (Veloso *et al.*, 1991; SEI, 1997).

A floresta estacional semidecidual e decidual, especialmente de terras baixas, de porte mais desenvolvido, intercala-se à caatinga, que desaparece progressivamente enquanto se avança para leste, em direção do litoral. Pelo menos em três municípios dentro de Minas Gerais há presença de floresta ombrófila densa sub-montana e montana: Bandeira, Santa Maria do Salto e Salto da Divisa (Veloso *et al.*, 1991; Silva e Casteleti, 2003; Andrade, 2004). O antropismo adqui-