zonas. Por isto, apesar de boa parte do Cerrado ter sido incluída na hipótese de distribuição potencial, *C. nigritus* e *C. robustus* estão provavelmente restritas aos entornos da Mata Atlântica. O ponto empírico situado na chamada "savana uruguaia" foi localizado numa região limítrofe com a Mata Atlântica, por isso a freqüência de ocorrências ter sido muito baixa (Tabela 1). Claramente, primatas não ocorrem nesta região, a não ser nas florestas de galeria e na Mata Atlântica limítrofe.

É interessante notar que em ambas as espécies analisadas, a hipótese inicial de distribuição potencial, resultante das análises dos fatores de clima e vegetação, indica uma distribuição maior do que a realizada. Isto sugere que estas espécies poderiam ocupar uma distribuição mais ampla do que a área de ocorrência atual determinada pelos registros de ocorrência, e que fatores históricos (cladogenéticos) e ecológicos (competição interespecífica) podem ter atuado para determinar o padrão de distribuição observado hoje. Desta maneira, podemos concluir que além dos fatores climáticos e de macrohabitat (aqui representados pelas ecoregiões), a presença de outras espécies de *Sapajus* parece ser também um fator importante, definindo os limites norte e oeste de *C. nigritus*, e os limites norte, sul e oeste de *C. robustus*, pois estas espécies não ocorrem em simpatria. Portanto, tanto fatores independentes como dependentes da densidade explicam os limites geográficos destas espécies.

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STRUCTURE AND COMPOSITION OF WILD BLACK HOWLER TROOPS (*ALOUATTA CARAYA*) IN GALLERY FORESTS OF THE ARGENTINEAN CHACO

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Introduction

The genus *Alouatta* occurs from the south of Mexico to northern Argentina and from the South American Pacific Coast to the Brazilian Atlantic Forest (Defler, 2003). *A. caraya* is the southernmost species, inhabiting central and southern Brazil, eastern Bolivia, Paraguay, and northern Argentina (Thorington *et al.*, 1984). Although there are adequate demographic data from populations in the forests of the Río Paraná in Argentina (Pope, 1968; Thorington *et al.*, 1984; Rumiz, 1990; Arditi and Placci, 1994; Brown and Zunino, 1994; Zunino *et al.*, 1996, 2001), the data are comparatively limited for populations in the Argentinean Chaco (Arditi and Placci, 1990; Brown and Zunino, 1994; Dvoskin *et al.*, 2004).

In this preliminary study we describe the composition and structure of wild troops of *A. caraya* that inhabit the gallery forests along the Riacho Pilagá in Formosa Province and compare them with data obtained from this area two decades ago.

Methods

The *A. caraya* population we studied occupies forests on the Guaycolec Ranch (58°13'W, 25°54'S), a spread of 25,000 ha, 25 km northeast of the city of Formosa. The ranch covers a mosaic of grasslands, savannas, dry forest, and semideciduous gallery forests. Our study area consisted of approximately 300 ha of gallery forest along the banks of the Riacho Pilagá. We mapped the area using a transect grid, marked every 50 m with colored tape.

In July and August 2001, two people surveyed the study area for black howler troops from 07:30 h to 17:00 h working together for 11 days and independently for 13 days, making a total of 24 days. Troops were found by following the loud, characteristic vocalizations, or by spotting resting individuals or moving branches. All visible individuals in each troop were classified into age and sex categories as suggested by Rumiz (1990):

• *Adults*: Females with blonde body color but darker and grayish back, barely noticeable clitoris, and broad vulvar lips with irregular pigmentation; if nursing, with swollen breasts and long nipples. Males entirely black with orange testicles.
• *Subadults*: Females with narrow vulvar lips, shorter and broader clitoris, and smaller body size than adults. Males with whitish or yellowish testicles and an almost entirely brownish-black coat, or black with golden highlights.
• *Juveniles*: We distinguished small, medium, and large juveniles. Females had a long thin clitoris, thin vulvar lips, body color usually paler than adult females but never red-

dish. Males were yellowish ventrally with a darker back, dark stripe on forehead, testicles descended and visible.
• *Infants*: Females had a penniform clitoris and narrow vulvar lips. Male testicles were broader than the female vulvar lips.

Results

We made contact with troops on 19 occasions, for a total observation time of 24.5 h; each troop was observed for an average of 1.1 h. The two observers encountered monkeys on nine occasions while surveying together and on ten occasions while working independently.

We identified 111 individuals in thirteen mixed-gender reproductive troops (Table 1). Two additional individuals were found ranging alone, but we found no temporary associations of males or females in the area. The reproductive troops ranged in size from 5 to 15 individuals (mean 8.5, SD ± 3.4). The study population consisted of mixed-gender troops with one or several adult males. Uni-male troops were more common (n = 10) than multi-male troops (n = 3). Uni-male troops were also smaller than multi-male troops (mean of 7.5 ± 2.7 vs. 12.0 ± 3.6 individuals). There were a relatively large number of infants (n = 22) compared to adult females (n = 28).

Approximately 40% of the individuals were adults (Table 1), while juveniles—the second largest age-class—made up slightly less than a third of the population (31%). Subadults (7%) and infants (38%) comprised the rest. Overall,

Table 1. Size and composition of troops of *Alouatta caraya* in Formosa Province, Argentina.

Group	AM	AF	SAM	SAF	LJM	LJF	MJM	MJF	MJU	SJM	SJF	I	Total
G1	3	4	1				2					3	13
G3	2	2					1	1		1		1	8
G9	2	2				1	1	2	1	2	1	3	15
G2	1	2					1	1				1	6
G4	1	2					1	1				1	6
G5	1	3	1				1	2		1	2	2	13
G6	1	2	1					1		1		2	8
G7	1	2						1				2	6
G8	1	1		1			1					1	5
G10	1	2	1								1		5
G11	1	1	1					1			1	1	6
G12	1	3						1		1		3	9
G13	1	2	2		1		1			1	1	2	11
Solitary	1												1
Solitary	1												1
Total	19	28	7	1	1	1	9	11	1	7	6	22	113

AM: Adult male; AF: Adult female; SAM: Subadult male; SAF: Subadult female; LJM: Large juvenile male; LJF: Large juvenile female; MJM: Medium juvenile male; MJF: Medium juvenile female; SJM: Small juvenile male; SJF: Small juvenile female; LJU: Large juvenile unsexed; MJU: Medium juvenile unsexed; SJU: Small juvenile unsexed; I: infant.

the numbers of females and males in the population were very similar (48 and 45, Table 1). In the adult class, the sex ratio was strongly biased in favor of females (28 and 17). The numbers of female and male juveniles were very similar for all three juvenile categories as well as for all juvenile categories combined (18 and 17). The small sample sizes of subadults and infants prevented any statistical analysis.

Discussion

The average group size of *A. caraya* has apparently increased during the last two decades: Brown and Zunino (1994) estimated a mean group size of 6.3 individuals during censuses conducted in 1981, and Arditi and Placci (1990) found no groups with more than eight individuals during a one-year study of the population in 1989-1990. Both estimates are significantly smaller than ours (range: 5 to 15 individuals, mean = 8.5). An increase in troop size may suggest that the population is expanding, as has been observed in red howlers in Venezuela (Rudran and Fernandez-Duque, 2003). In our population, the three multi-male groups were significantly larger than uni-male troops. The age structure of the troops also suggests an expanding population, as indicated by a relatively large number of juveniles and infants and by the number of reproducing adult females.

Our estimates of sex ratio should be considered tentative due to the small number of groups and the potential for age misclassification. It would be necessary to determine the sex of the large number of unsexed infants before any conclusions could be reached. Rudran and Fernandez-Duque (2003) found that the ratio of male to female infants changed in a linear association with density. In other words, more females than males were born at low population densities. If the observed trend of more male than female births were to be confirmed, it might indicate that the population is expanding. On the other hand, the strongly biased sex ratio in the subadult category needs to be considered with some caution. Although it is relatively easy to identify subadult males because they have started to show signs of the characteristic black coat of adult males, it is more difficult to classify subadult females who cannot be differentiated from adult females by coat color. The number of subadult females may, therefore, have been underestimated.

In conclusion, our preliminary data suggest that the population has expanded during the last two decades, in agreement with a previous analysis of changes in population density in the howler troops of this region (Dvoskin *et al.*, 2004). Our conclusion is mainly supported by the observed increase in average troop size and by the relatively large number of infants and juveniles. Other parameters of population structure may confirm and detail this expansion, but longer-term demographic records will be required to construct the necessary dataset. For example, the proportion of uni-male troops may also indicate the status of the population, as in Venezuela, where the proportion of uni- and multi-male troops changed dramatically over 30 years in a population of red howler monkeys (Rudran and Fernandez-

Duque, 2003). Uni-male troops accounted for a relatively larger proportion of the population when the population was declining than when it was expanding. Although the reasons for the change in the proportion of uni-male troops were not clear, if confirmed this factor could become a convenient tool for population management, helping us anticipate, with relative accuracy, changes in population size that would take decades to observe.

The vast amount of data on the population biology of howler monkeys, spanning several decades of fieldwork, has convincingly shown the limitations of short-term studies (Rudran and Fernandez-Duque, 2003; Estrada *et al.*, 1999; Fedigan and Jack, 2001). Thus, although our preliminary study offers a few solid results and several tentative findings worth examining in the future, it is imperative that we expand the database if we want to examine how social and environmental factors may be shaping the observed demographic features.

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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