Pleistocene primate evolution on the continent.

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Characteristics of Two Types of Habitat and the Status of the Howler Monkey (*Alouatta caraya*) in Northern Argentina

In Argentina the black howler monkey, *Alouatta caraya*, inhabits upland semideciduous forests, and flooded forests on the islands of the large rivers, Paraná and Paraguay (Cabrera, 1939; Brown and Zunino, 1994). Field studies done on this species in these habitats revealed differences in density, social organization, diet, and behavior, related to the floristic structure (Rumiz, 1987, 1990; Rumiz *et al.*, 1986; Zunino, 1986, 1989; Bicca-Marques, 1994; Brown and Zunino, 1994).

Currently, *A. caraya* is not considered as threatened (Emmons, 1990; Rylands *et al.*, 1995). However, in Argentina the continuous extensive deforestation for timber, land use, and dam construction, suggests a progressive degradation and reduction of the habitat available for this species. The aims of the project reported here consisted in the definition of three types of habitat occupied by *A. caraya*, evaluating as such the relation between habitat and population characteristics and the effects of alteration.

Study Site and Methods

The study was carried out in the northwest of the Corrientes Province, Argentina (27° 30'S, 58° 50'W), comprising riparian forest patches along the Riachuelo river, and flooded forest in the Paraná river.

In the Riachuelo river area, the forest is a mosaic of tall and low patches of about 10 ha separated by grasslands. The forest patches show different degrees of alteration, some suffering a selective logging while in others most of the trees have been eliminated.

On the islands, the terrain is inundated almost yearly defining as such the floristic structure which is characterized by the presence of fast-growing tree species (Rumiz *et al.*, 1986). Occasionally, floods persist over long periods resulting in the loss of trees, and reducing dramatically the presence of howler monkeys. Due to the low quality of the timber, and the fact that the soils are not suitable for agriculture, logging is not a serious problem.

To compare the habitats, inventories of trees were carried out in three sites inhabited by the howler monkeys. On the Riachuelo river, a tall forest patch was selected which had suffered little alteration (BPA), along with a second which had been heavily exploited (BMA). The criteria used to select these sites were based on qualitative evaluations of the tallness of the canopy, the presence of species of economic importance, abundance of thin-trunked trees, and evidence of exploitation. The study of the flooded forest patch (SI) was carried out on the island of Brasilera, near the confluence of the Paraná and Paraguay rivers.

The species, height, and diameter at breast height (DBH) were recorded for all trees with a DBH greater than 10 cm. They were plotted in quadrats of 10 x 10 m. For comparisons between habitats we employed the following variables: NiH>10 m = Number of trees belonging to each species with a height greater than 10m; DBHm = Mean DBH; Nsp = Number of species; Ni/Nsp = Number of individuals of each species with respect to the total number of species; and NiDBH>20 cm = Number of individuals with a DBH greater than 20 cm. We also calculated the density, and used Shannon's index as a measure of diversity. Differences between habitats were analyzed by applying a discriminant analysis. To evaluate the effect of logging, we compared our results with previous inventories of 174 ha at BPA and BMA in 1987.

The density of howler monkeys was estimated in BPA, BMA, and SI. Daily censuses by transect were carried

Table 1. Habitat characteristics. Mean values and SD of tree density expressed as individuals per ha (Di); Total number of species (Nsp); Shannon's Index (H'); Diameter at breast height (DBH); Mean height (Hm); BPA: Unexploited forest; BMA: Disturbed forest; SI: Flooded forest.

Site	Di	Nsp	H'	DBH	Hm
BPA	500 (26.8)	20	4.61	16.68 (7.5)	6.58 (1.6)
BMA	745 (75.8)	14	1.92	19.95 (2.9)	5.99 (1.5)
SI	300 (76.5)	7	1.15	32.47 (11.4)	15.15 (3.6)

Table 2. Results of classification among the three habitats.

Site	N	BMA	BPA	SI
BMA	20	70.0	25.0	5.0
BPA	19	36.8	63.2	0.0
SI	29	0.0	6.2	93.1

out during at least three weeks at each site. The area surveyed was estimated by multiplying the distance traveled by 40 m. The estimated density values were obtained applying the Non-Linear Density Plot Method (Struhsaker, 1981).

Results and Discussion

The floristic analysis (Table 1) showed that the BPA and BMA had more slender trees than the SI. BMA showed the greatest abundance of trees with a DBH between 10 and 30 cm, with a few individuals in the largest categories. At BPA we also observed a predominance of slender trees (DBH=10-30 cm), but some larger trees were also present. SI showed the highest frequency of large trees, with a peak of DBH between 20 and 50 cm.

Small trees were most abundant at BMA; almost 50% of those recorded were between 4-6 m. BPA also showed a high frequency of low trees, with more than 40% grouped between 6-8 m. SI, on the other hand, showed the greatest spread, with individuals ranging in height from eight to 24 m.

The most diverse of the three plots was BPA due to the high number of tree species. The diversity values in BMA were approximately half those of BPA, suggesting the possibility that a wider range of food sources was to be found in the less altered environments. At SI, however, diversity was lower than in the other two habitats, due to fewer species. Finally, the highest density values were obtained at BMA, were found to be intermediate in BPA, and lowest in SI.

The vegetation quadrats were grouped in 3 OTUS, each corresponding to the previously defined habitats. The first discriminant function explained 95% of the variance, and suggested that the first two functions could explain the relationships between the ecological factors. The variables with greatest discriminant value were: Hm, Ni, and Ni/Nsp on the first function, and Hm on the second. The first discriminant function separated most of the SI quadrats with respect to BPA and BMA (Table 2). However, the analysis did not discriminate clearly between BPA and BMA. The partial overlap suggested a degree of similarity between them. This was expected due the common origin of the two areas, differentiated only by the degree of exploitation.

Regarding the howler census, we found that the mean group size was significantly lower at BMA, and only slightly smaller at BPA than at SI (Table 3). However, larger groups were more frequent at SI than at BPA.

Table 3. Population characteristics of black howler monkeys. Mean values (SD), and comparisons by ANOVA among habitats.

Variable	BMA	BPA	SI	P
Density (inds./ha)	0.50 (0.17)	0.88 (0.18)	2.37 (0.74)	<0.01
Group size	4.60 (1.42)	7.80 (1.64)	13.00 (7.10)	<0.01
Sex ratio	1.60 (0.62)	2.00 (0.70)	1.90 (0.60)	>0.05

The density values showed significant differences between habitats, the lowest was at BMA, and the highest at SI. In spite of the differences in density and group size, sex ratio was not significantly different between habitats. The sex ratio appeared as a constant, independent of the environmental differences, but with many multimale groups in SI and a predominance of unimale groups in the other habitats.

A continuous reduction in quality and size of the useful habitat for howlers was observed for the Riachuelo area between 1987 and 1994. Currently 21.14% of the 123 ha of BPA studied in 1987 is being exploited, which is consequently becoming more similar to BMA, and considering the 174 ha of habitat comprising BPA and BMA, 16.1% has been eliminated altogether. Considering the islands occupied by howlers, the recently inaugurated dam of Yacireté has eliminated habitats containing between 4000 and 14000 howlers due to inundation (Neris *et al.*, 1994; Zunino and Ruiz, 1995).

The density of howler monkeys in the flooded forest is higher than has been recorded for other populations of *Alouatta* living in tropical environments (Crockett and Eisenberg, 1987). The flooded forest offers a less diverse diet (Brown and Zunino, 1994), but seasonality is less marked than in the *terra firme* forest patches at the same latitude (Rumiz *et al.*, 1986). The availability of potential food resources in the flooded forest appears to be more uniform in space and time.

In the last decades forest exploitation in the study site has resulted in a loss of habitat for the black howler monkeys, reducing the populations and increasing the isolation of the groups. If this trend continues in the future, the mainland population will be seriously threatened. The status of *A. caraya* in flooded forest, however, remains uncertain. Other projects threaten this environment, such as the Corpus and Paraná Medio dams and the waterway project that intends to permit navigation as far as Bolivia. Protected areas where these howlers occur are limited to the National Parks of Chaco and Pilcomayo, with an estimated population of about 10,000 howlers, and none of them includes flooded forests, the most important habitat for this species

(Brown and Zunino, 1994).

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Temporal Division of Labor in a Primate: Age-Dependant Foraging Behavior

Introduction

Division of labor based on age or size may reflect the reproductive condition of individuals in social groups. In 1967, West proposed the general hypothesis that hierarchical relations may be advantageous to both dominants and subordinates and that individuals of low rank may be inferior reproductives who benefit genetically from associations with and contributions to reproductively superior individuals. Since increasing age or size eventually entails decreasing reproductive value (V_x), several authors have noted that the display of social behavior, such as foraging behavior that benefits all members of a group, should increase with age as the benefits from individual (selfish) reproduction decline (e.g., West-Eberhard, 1975; Hrdy and Hrdy, 1976). As individual reproductive value decreases, benefits (genetic or other) from assisting the reproduction of conspecifics (social behavior) may increase because costs (genetic or other) of social behavior decrease with decreased benefits from individual reproduction. In order to test this hypothesis, I studied the relationship between adult female age, dominance rank, reproductive value, and social foraging behavior (food search and pursuit) for adult female mantled howler monkeys (*Alouatta palliata* Gray).

Subjects and Methods

During an extended period of study at Hacienda 1a. Pacifica, Cañas, Guanacaste, Costa Rica, I studied two marked, aged groups of mantled howler monkeys in two tropical dry forest habitats (see Jones, 1980; Table 1). For this species, age and dominance rank are negatively correlated in both sexes (Jones, 1978, 1980).

Foraging was operationally defined as the behavioral series: feed-rest-move (at least 100m) - feed, by a unit of more than three adults. These criteria were adopted in order to standardize measurement and to eliminate periods of food search within unusually large patches