Activity patterns and diet of the howler monkey *Alouatta belzebul* in areas of logged and unlogged forest in Eastern Amazonia

A. C. B. Pinto, C. Azevedo–Ramos & O. de Carvalho Jr.

Abstract

Activity patterns and diet of the howler monkey Alouatta belzebul *in areas of logged and unlogged forest in Eastern Amazonia.*— This work compared the activity patterns and diet of a group of *Alouatta belzebul* in areas of logged and unlogged forest in eastern Amazonia. An instantaneous scan sampling procedure was used for the behavioral study (9.3 ± 1.9 complete observation days/month) from February to November 2000. Fruit availability was estimated monthly. Activity budgets were not significantly different between sites. Rest was the predominant activity in both sites (53.6 % and 48.7 %, respectively). Average daily path length was 683.5 ± 215.1 m (n = 93), and the home range was 17.8 ha, including 7 ha in unlogged forest and 10.8 ha in the logged forest. Neither fruit availability nor diet varied significantly between sites. The diet was predominantly folivorous (43.4 % and 46.6 % in unlogged and logged forest, respectively) and frugivorous (43.9 % and 42.8 %). The spatial use by the group was positively related to fruit sources. This study documented the ability of a ranging group of *A. belzebul* to survive in a habitat influenced by reduced impact logging without dramatically influencing its activity patterns and diet.

Key words: *Alouatta belzebul*, Activity patterns, Diet, Reduced impact logging, Tropical rain forest, Amazonia.

Resumen

Patrones de comportamiento y alimentación del mono aullador Alouatta belzebul *en zonas de selva talada y sin talar del este de la Amazonia.*— En este trabajo se comparan los patrones de comportamiento y alimentación de un grupo de *Alouatta belzebul* en zonas de selva deforestada y sin deforestar del este de la Amazonia. Para el estudio del comportamiento se utilizó un muestreo de barrido temporal instantáneo (observación completa durante 9,3 ± 1,9 meses/días) entre los meses de febrero y noviembre de 2000. La disponibilidad de fruta se calculó mensualmente. Las actividades realizadas no fueron significativamente diferentes en ninguna de las dos ubicaciones. El descanso fue la actividad predominante en ambas, 53,6 % y 48.7 % respectivamente. La media de la longitud de los recorridos diarios era de 683,5 ± 215,1 m (n = 93) y el área de acción era de de 17,8 hectáreas, incluyendo 7 hectáreas de selva sin talar y 10,8 hectáreas de bosques talados. Ni la disponibilidad de fruta ni la dieta variaron significativamente entre las zonas. La dieta era eminentemente folívora (43,4 % y 46,6 % en las zonas de selva sin talar y deforestada, respectivamente) y frugívora (43,9 % y 42,8 %). El uso que el grupo hacía del espacio estaba relacionado de manera positiva con las fuentes de suministro de frutas. En este estudio se ha documentado la habilidad de un grupo de *A. belzebul* en libertad para sobrevivir en un hábitat afectado por una tala de impacto reducido sin que ello afectase dramáticamente a sus patrones de comportamiento y alimentación.

Palabras clave: *Alouatta belzebul*, Patrón de comportamiento, Alimentación, Tala de impacto reducido, Selva tropical, Amazonia.

Andréia C. B. Pinto & Claudia Azevedo–Ramos, Núcleo de Altos Estudos Amazônicos (NAEA), Univ. Federal do Pará (UFPA), CEP 66.075–900, Belém–PA, Brasil.

Claudia Azevedo–Ramos & Oswaldo de Carvalho Jr, Inst. de Pesquisa Ambiental da Amazônia (IPAM), Av. Nazaré 669, CEP 66.075–900, Belém–PA, Brasil.

Introduction

Brazilian Amazonia contains more than one third of the world's forests and the richest Neotropical primate fauna. However, of the 123 primate *taxa* occurring in Amazonia (including species and sub-species), 18% are threatened (RYLANDS et al., 1997). Deforestation and timber harvesting are the main disturbing factors affecting the region, especially in Eastern Amazonia. Selective logging invariably involves alterations in the physical structure of the vegetation and availability of food resources, which may have considerable impacts on primates (JOHNS, 1983; JOHNS & SKORUPA, 1987; GREISER JOHNS, 1997). Despite these negative impacts, logged forests have a potential for conservation, as they contain a great share of native fauna, including primates. However, a better understanding of primate ad-aptations to logged forests is urgently needed to allow the elaboration of more effective forest resource management and conservation strate-gies. It is reasonable to assume that behavioral flexibility would allow a better chance of surviving in altered habitats.

The howler monkeys (*Allouatta*) are known for their capacity to adapt in forest fragments (RYLANDS & KEUROGHLIAN, 1988; CHIARELLO, 1993; BICCA–MARQUES & CALEGARO–MARQUES, 1994; ESTRADA & COATES–ESTRADA, 1996; ESTRADA et al., 1999; JUAN et al., 2000; GÓMEZ–MARIN et al., 2001), which made us question how they would re-spond to logging activity. This study compares the activity patterns and diet of a group of Red–Handed howler monkeys, *Alouatta belzebul*, which lives in a mosaic of logged and unlogged forests in Eastern Brazilian Amazonia.

This species is endemic to Brazil and can be found in the Amazon and Atlantic forests (BONVICINO et al., 1989). The diet of the genus *Alouatta* can best be defined as folivorous–fru-givorous (CROCKET & EISENBERG, 1987). Its diversi-fied diet favors *Alouatta*'s occurrence under sev-eral environmental conditions (MILTON, 1980; NEVILLE et al., 1988; CROCKETT, 1998; HORWICH, 1998). During periods of food shortage, howler mon-keys may compensate for fruit scarcity by con-suming leaves and decreasing physical activities to offset the low energetic return from leaves (MILTON, 1980; NEVILLE et al., 1988). Because selec-tive logging may remove important tree species from the monkey's frugivorous diet, the hypoth-esis of this work was that the abundance of fruits in the logged site would be lower, inducing howler monkeys to become more folivorous. As a conse-quence, the size of home range, as well as the time dedicated for locomotion should be smaller in the logged site. Changes in activity and diet may potentially modify the ecological services of this howler monkey group (e.g., from seed disperser to seed predator), a subtle effect of logging activities, which —if replicated in other animal groups— may affect long–term environ-mental sustentability.

Materials and methods

The study was conducted in Cauaxi Ranch (3° 45' 32" S; 48° 10' 06" W), Paragominas Munici-pality, northeast of Para, Brazil. The area is cov-ered by *Terra Firme* (up–land) rain forest, with total annual rainfall about 2,200 mm. This ranch has approximately 20,000 hectares, comprising a mosaic of logged and unlogged forests, and pas-ture areas. The logged site used for this study was harvested using reduced–impact techniques in 1996 (VERÍSSIMO et al., 1992; VIDAL et al., 1997). The logging intensity was 25 m^3/ha (~3 trees/ha).

The group of howler monkeys observed in-cluded six individuals (one adult male, two adult females, one sub–adult female, one young male, and an infant female). The group became accus-tomed to the observer for a period of 50 hours before data collection began. In order to quan-tify their home range, their localization in the area, and the resources that they utilized, a 50 x 50 m grid system was cleared in 80 ha (40 ha in a logged area and 40 in an unlogged area). This area represents approximately 4 times the home range previously reported for this species (e.g. BONVICINO, 1989; SOUZA, 1999).

Activities of the *Alouatta belzebul* group were monitored using instantaneous scan samplings (ALTMANN, 1974) for ten days per month from 6.00 to 19.00 h, from February to November 2000. The observations totaled 1203.25 h, and were distributed in 105 observation days (93 com-plete and 12 incomplete days). During this pe-riod, a total of 5003 scans were conducted and 21300 behavioral records were obtained. Obser-vations were made using binoculars, and a dis-tance of at least 10 m was maintained between the observer and the monkeys at all times. The group's activities were recorded every 15 minutes (see QUEIROZ, 1995; JARDIM, 1997; PINA, 1999; SOUZA, 1999). In each scan and for each individual we recorded: (1) behavioral category, (2) age and sex and (3) location in the 50 x 50 m grid system.

Four behavioral categories were established based on previous studies (BONVICINO, 1989; JARDIM, 1997; PINA, 1999; SOUZA, 1999), and preliminary field observations: resting, moving, feeding and social interaction. When all individuals were out of sight during a scan, but their location was known, the record was attributed to the category of rest (PINA, 1999; SOUZA, 1999). During feeding events, the ingested item was categorized (fruit, leaf, flower, or termite's nest), identified to spe-cies level whenever possible, and its source was plotted in the map area. When the ingested item was a fruit or leaf, the stage of maturity was also recorded.

The group's home range was estimated by summing the visited grids. For this purpose we divided the larger 50 x 50 m grids into four 25 x 25 m^2 when estimating their location. In or-der to determine the daily range, the route of the group was traced on the map containing the

trail grid and then measured using a curvemeter, with its scale converted to meters.

A fruit abundance index for each area was calculated using an adaptation of ZHANG & WANG's (1995) forest floor fruit counting methodology. In an area of 60 ha (30 ha for each site) a 1 ha sampling area (0.5 ha for each site) was selected at random each month and divided into 10 transects of 5 x 200 m. The fruit counting was conducted at the end of each month in both sites. All pre–existent fruits found on the floor were removed 10 days before each sample to avoid recording fruits whose availability did not correspond to that month. During the census, all fruits (mature, immature or fragmented) were counted along each transects. Fruits were identified to species level whenever possible or classified as morphospecies.

The differences in behavioral and feeding categories between logged and unlogged sites during the ten–month sampling were tested using the Wilcoxon non–parametric test for dependent samples (SIEGEL, 1979; AYERS et al., 2000). The difference between the fruit abundance index estimated for both sites was evaluated using the Mann–Whitney Test for independent samples. The Sorensen index was used to measure the similarity of fruit composition between the areas (KREBS, 1989).

Because the spatial use patterns of a group of primates may be influenced by food sources and the presence of other groups (MILTON, 1980; TERBORGH, 1983; JARDIM & OLIVEIRA, 1997), the spatial use of the habitat by these howler monkeys was evaluated using Pearson linear correlation relating the monthly home range with (1) the number of fruit sources used monthly by the group, (2) the number of fruits recorded through counting, and (3) inter–group encounters, based on the absolute number of encounters (visual or agonistic) between neighboring groups. The effect of the diet on howler monkey behavior was also tested by correlating the speed of locomotion with percentage of fruit ingestion.

Results

The howler monkey group spent more time in the logged site (65.1 %) than in the unlogged site (34.9 %). Approximately half of the activity period of the howler monkeys in logged and unlogged sites was dedicated to rest (48.7 % and 53.6 %, respectively). The remaining time was divided among moving (28.7 % and 29.3 %), feeding (21.6 % and 15.9 %) and social interactions (0.8 % and 1.2 %). The howler monkey's diet at both sites was characterized by the consumption of fruits (42.8 % and 43.9 %) and leaves (46.6 % and 43.4 %), followed by a lower percentage of flowers (10.0 % and 12.5 %). Soil ingestion events (0.6 % and 0.2 %), representing the intake of nest termites, were more frequent in *ad libitum* records due to the rarity of this activity.

There was no significant difference in the time spent in each behavioral category between the sites within the 10 months of sampling (Wilcoxon Test, rest: $Z = -1.784$; $P = 0.075$; moving: $Z = -0.051$; $P = 0.959$; feeding: $Z = -1.784$; $P = 0.075$; social interactions: $Z = -0.866$; $P = 0.386$, $n = 10$ for all comparisons; fig. 1).

There were no significant differences within the same feeding category between sites: fruits (Wilcoxon Test, $Z = -0.2801$; $n = 10$; $P = 0.779$), young leaves ($Z = -0.6625$; $P = 0.508$), mature leaves ($Z = -0.4146$; $P = 0.678$) and flowers ($Z = -0.5601$; $P = 0.575$). In both sites, it was verified that the decrease in fruit consumption and the consequent higher intake of leaves and flowers was more accentuated during the beginning of the dry season (fig. 2).

The fruit abundance sample registered a total of 39 species / morphospecies, of which 19 (48.7 %) were exclusive to the unlogged site, 14 (35.9 %) were only present in the logged site, while six (15.4 %) were present in both. The similarity found between the sites was only 0.27 according to the Sorensen Index (values range from 0 to 1), indicating a strong difference in fruit composition. However, the absolute difference in fruit abundance between the logged and unlogged sites was not statistically significant (Mann–Whitney, $U = 50$; $n = 10$; $P = 1.00$). The temporal distribution of fruit species / morphospecies was very heterogeneous. Thirty (76.9 %) were recorded only once in ten months. The greatest abundance of fruits at both sites was in February which was also the richest month in the unlogged site (11 species, 5 for the logged site), followed by March and November (5 species at each site). Fifty six percent of the species (22 species) showed mature fruits (table 1).

The home range of the focal howler monkey group comprised 17.8 ha, including 7 ha of unlogged forests and 10.8 ha of logged forests was used by the howler monkeys (fig. 3). In the logged site, the howler monkeys did not avoid areas affected by harvesting trails and tree removals. The logging removed 23 trees within the group's home range (fig. 3). However, when the logging intensity within the group's home range (2.1 trees removed/ha) was compared to the logging intensity in the surrounding 16 ha (3 trees removed/ha; fig. 3), it was observed that the home range of the howler monkeys was confined to an area that was somewhat less impacted by tree removals.

During the study, 42 inter–group encounters were observed. Of these, 15 involved competition for food sources, two for sexual partners, two for sleeping sites and the other 23 had no direct cause identified, but were possibly for territorial defense. Twenty of the total encounters (47.6 %) were characterized by agonistic interaction, including violent chases between the males of rival groups, and reciprocal vocalizations. The other 22 encounters (52.4 %) were classified as
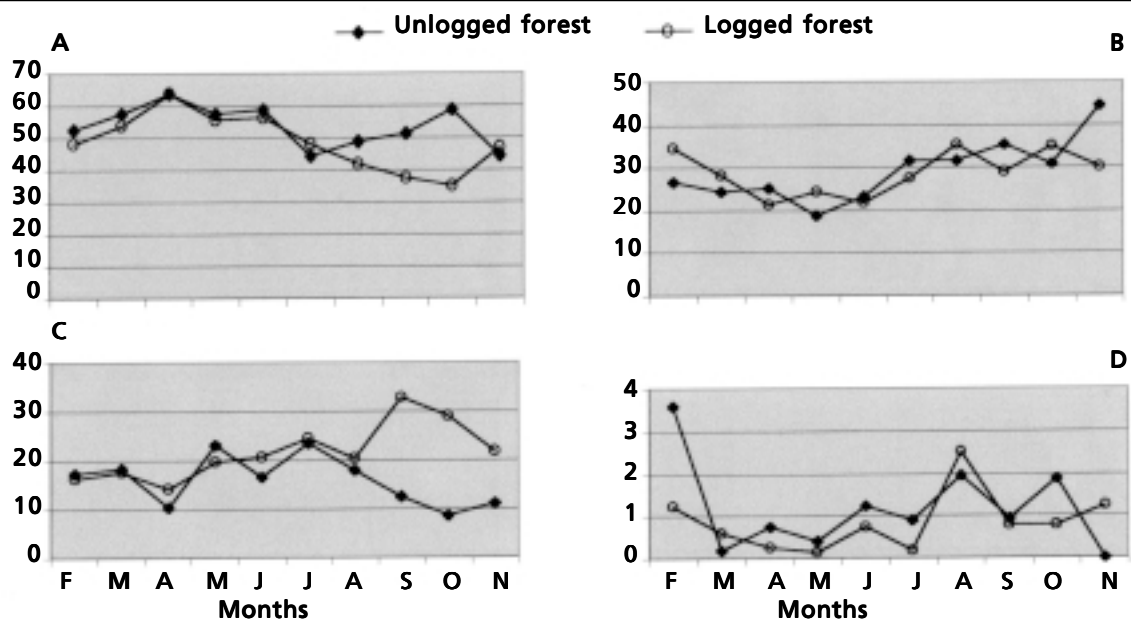
Fig. 1. Monthly variation in the proportion of the main behavioral categories of *Alouatta belzebul* in unlogged (*n* = 7562 behavioral records) and logged forests (*n* = 13 738.35), from February to November 2000, in Paragominas, Para, Brazil: A. % resting; B. % moving; C. % feeding; D. % social.

Fig. 1. Variación mensual de la proporción de categorías de comportamiento principales de Alouatta belzebul *en zonas sin talar (n = 7562 datos sobre comportamiento) y en zonas deforestadas (n = 13 738,35), entre los meses de febrero y noviembre de 2000, en Paragominas, Pará, Brasil: A. % en reposo; B. % en movimiento; C. % alimentándose; D. % social.*
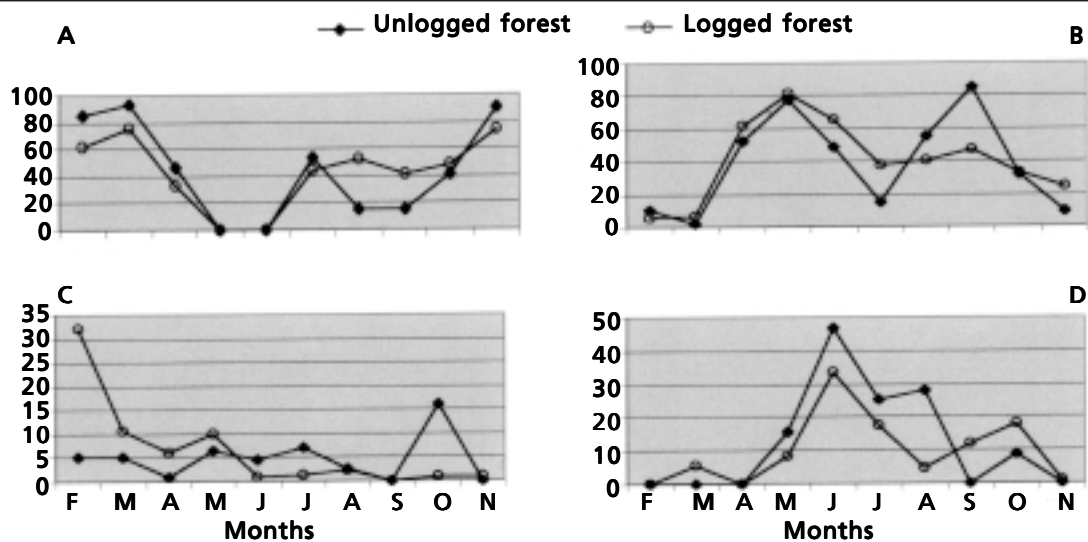

Fig. 2. Monthly variation in the proportion of the main feeding categories of *Alouatta belzebul* in unlogged (*n* = 1261 feeding records) and logged forests (*n* = 2941), from February to November 2000, in Paragominas, Para, Brazil: A. % fruits; B. % young leaf; C. % madure leaf; D. % flowers.

Fig. 2. Variación mensual en el porcentaje de categorías de alimentos principales de Alouatta belzebul *en zonas sin talar (n = 1261 datos de alimentación) y en zonas deforestadas (n = 2941), de febrero a noviembre de 2000 en Paragominas, Pará, Brasil: A. % frutos; B. % hojas jóvenes; C. % hojas maduras; D. % flores.*

Table 1. Monthly fruit census in the unlogged and logged sites from February to November 2000 at the Cauaxi Ranch in Paragominas, Para, Brazil: N. Number of fruits; % Montly percentage; * Species utilized by *Alouatta belzebul*'s group as fruit resource.

*Tabla 1. Censo mensual de frutas en las ubicaciones deforestadas y sin deforestar, entre los meses de febrero y noviembre de 2000 en el Rancho Cauaxi de Paragominas, Pará, Brasil: N. Número de frutos; % Porcentaje mensual; * Especies utilizadas por el grupo de* Alouatta belzebul *como fuente de suministro de frutas.*

Family			Unlogged Forest		Logged Forest	
Species or morphospecies		Month	N	%	N	%
Sapotaceae						
	*Manilkara amazonica**	February	15	(4.4)	0	(0)
		March	01	(2.6)	0	(0)
	Manilkara sp.*	September	0	(0)	01	(100.0)
	*Neoxythece elegans**	February	262	(76.2)	0	(0)
	*Pouteria bilocularis**	February	01	(0.2)	0	(0)
	*Pouteria laurifolia**	November	0	(0)	03	(3.8)
	*Pouteria sagotiana**	October	50	(96.2)	45	(93.8)
		November	04	(14.8)	0	(0)
	Morphospecie # 01	February	03	(0.9)	0	(0)
	Morphospecie # 02	August	12	(17.4)	0	(0)
	Morphospecie # 03	November	0	(0)	30	(37.5)
Mimosaceae						
	*Inga heterophylla**	February	01	(0.3)	0	(0)
		July	0	(0)	12	(70.6)
	Inga sp. 1*	February	06	(1.7)	0	(0)
	Inga sp. 2	November	0	(0)	05	(6.3)
Burseraceae						
	*Protium guacayanum**	February	0	(0)	20	(14.1)
	Protium sp.*	February	0	(0)	10	(7.0)
Lauraceae						
	*Nectandra rubra**	February	0	(0)	01	(0.7)
		March	01	(2.6)	0	(0)
		August	0	(0)	01	(20.0)
		November	02	(7.4)	0	(0)
	Morphospecie # 04	July	30	(56.6)	0	(0)
Humiriaceae						
	Endopleura uchi	February	14	(4.1)	0	(0)
	*Sacoglotis guianensis**	November	0	(0)	02	(2.5)
Moraceae						
	Brosimum amplicoma	February	02	(0.6)	0	(0)
	Helicostylis sp.*	July	20	(37.7)	0	(0)
Asteraceae						
	*Heteropsis jenmani**	March	01	(2.6)	0	(0)

Table 1. (Cont.)

| Family | Month | Unlogged Forest | | Logged Forest | |
Species or morphospecies		N	%	N	%
Caryocaraceae					
Caryocar glabrum	February	01	(0.3)	0	(0)
Combretacae					
Buchenavia sp.*	March	0	(0)	87	93.5
Chrysobalanaceae					
Licania sp.*	October	01	(1.9)	0	(0)
Lecythidaceae					
Eschweillera odorata	February	0	(0)	01	(0.7)
	July	02	(3.8)	0	(0)
	October	0	(0)	02	(4.2)
	November	10	(37.0)	40	(50.0)
Passifloraceae					
*Passiflora nitida**	February	01	(0.3)	0	(0)
	August	0	(0)	01	(20.0)
Polygalaceae					
*Moutabea guianensis**	February	38	(11.0)	0	(0)
	March	28	(71.8)	0	(0)
Tiliaceae					
*Luehea speciosa**	Setember	12	(100.0)	0	(0)
	November	10	(4.4)	0	(0)
Not identified					
Morphospecies # 05	February	0	(0)	110	(77.5)
Morphospecies # 06	March	0	(0)	06	(6.4)
Morphospecies # 07	July	01	(1.9)	02	(11.8)
	August	0	(0)	03	(60.0)
Morphospecies # 08	July	0	(0)	02	(11.8)
Morphospecies # 09	July	0	(0)	01	(5.9)
Morphospecies # 10	August	57	(82.6)	0	(0)
Morphospecies # 11	November	01	(3.7)	0	(0)
Morphospecies # 12	October	01	(1.9)	0	(0)
Morphospecies # 13	October	0	(0)	01	(2.1)
Morphospecies # 14	June	0	(0)	20	(100.0)
Morphospecies # 15	March	08	(6.4)	0	(0)
Total fruits		596		406	

pacific, with only visual interactions, sometimes including few vocalizations with one of the groups leaving the area before any physical contact. The relationship between the size of the area used by the monkeys monthly and inter–group encounters was positively significant in the unlogged site ($r = 0.652$; $P = 0.041$), but not in logged site ($r = 0.164$; $P = 0.651$; fig. 4). In the later, the encounters took place manly in few areas with larger concentration of fruiting tree, without significant relationship to the exploration of new areas by the howler group. On the other hand, in
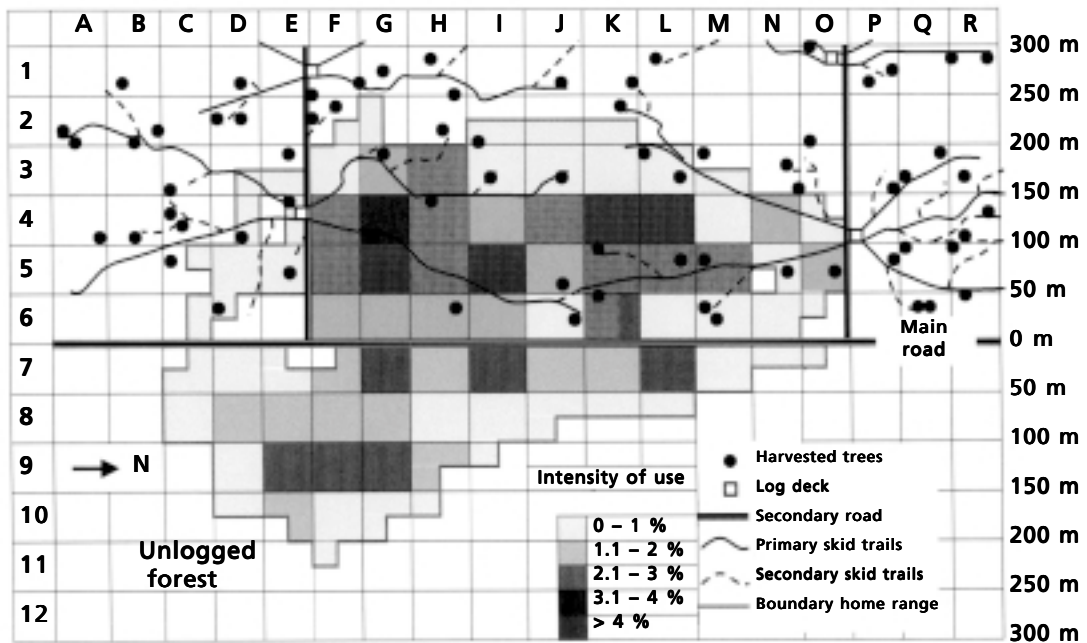
Fig. 3. Skid trails and harvested trees within / around the home range of the *Alouatta belzebul*, showing the intensity of spatial use (according to the number of scans in each 50 x 50 m²; *n* = 5003 scans), in Cauaxi farm, Paragominas, Para, Brazil.

Fig. 3. Senderos de arrastre y árboles talados dentro / alrededor del área de deambulación de Alouatta belzebul, *que muestran la intensidad de uso del espacio (de acuerdo con el número de barridos cada 50 x 50 m², n = 5003 barridos), en la granja Cauaxi, Paragominas, Pará, Brasil.*

unlogged site, most of the encounters occurred along the west margin of the focal group's home range, indicating an expansion of the home range to this direction. The expansion of the area used by the monkeys was motivated by the search for new fruit sources in logged and unlogged sites, as indicated by a linear correlation between the size of home range and the number of fruit sources used by the howler group ($r = 0.787$; $P = 0.007$; and $r = 0.759$; $P = 0.011$, respectively). Areas with low intensity use sometimes received visits exclusively focused on a specific fruit source. However, the relation between size of home range and number of fruits counted on the forest floor was not significant for either site, possibly due to low overlap between the counted species and the fruit species consumed by howlers (33.3 % in unlogged site and 23.3 % in logged sites). The daily range varied from 269 to 1300 m, with an average of 683.5 ± 215.1 m based on 93 days of complete observation. Direct comparisons of the daily path length between the sites was not possible, since the group used both sites almost on a daily basis and the locomotion behavior rarely took place exclusively in one of the sites alone. However, the relationship between the daily range and the time of permanence of the howler monkey group in each site showed that there was no difference in the speed of locomotion between the unlogged (61.0 ± 22.04 m/h) and the logged sites (66.3 ± 28.32 m/h; Mann–Whitney, $U = 45$, $n = 10$, $P = 0.706$). However, there was a significant and positive correlation between speed of locomotion and frugivory ($r = 0.660$, $P = 0.038$).

Discussion

The initial prediction that fruit availability would be lower in the logged site, and that this would press the monkeys towards a more folivorous diet, and consequently less activity in this area, was not confirmed. No significant alteration in the diet or in the behavioral pattern of the monkeys between areas was found.

Three factors may have contributed to the absence of behavioral modifications in the logged area. First, the low logging intensity (25 m³/ha) and the reduced–impact operational model may not have altered the area considerably in terms of food resources availability, at least not to the point of provoking a change in the monkeys' behavior. That was partially confirmed by the fruit
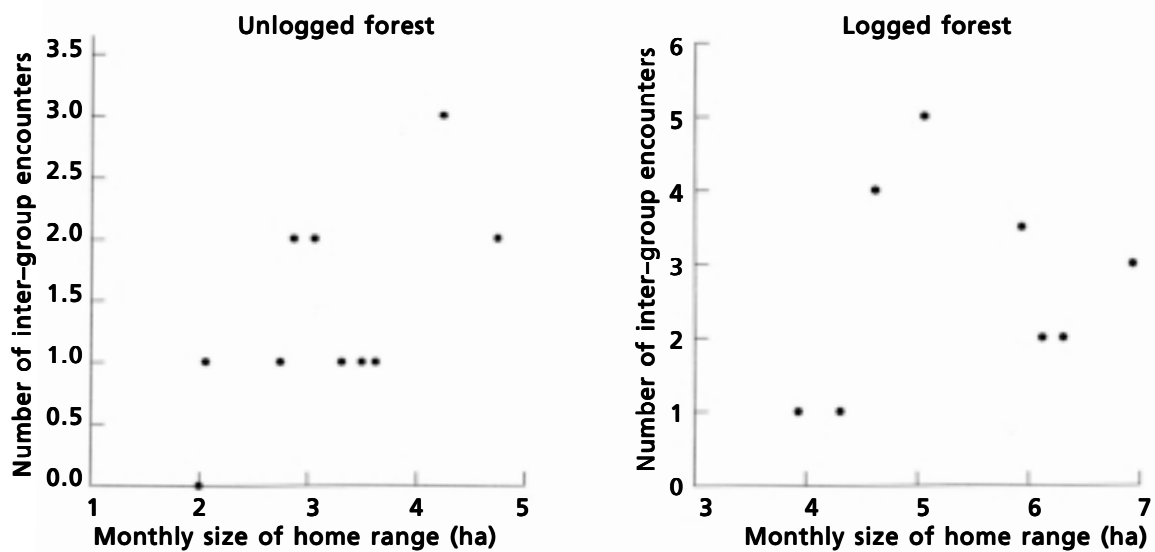
Fig. 4. Relationship between the size of the area used monthly by the monkeys and inter–group encounters in the unlogged (*r* = 0.652; *P* = 0.041) and logged sites (*r* = 0.164; *P* = 0.651), from February to November 2000, in Paragominas, Para, Brazil.

Fig. 4. Relación entre las dimensiones del área que los monos utilizan mensualmente y los encuentros entre diferentes grupos en las zonas sin talar (r = 0,652; P = 0,041) y en las deforestadas (r = 0,164; P = 0,651), desde febrero a noviembre de 2000 en Paragominas, Pará, Brasil.
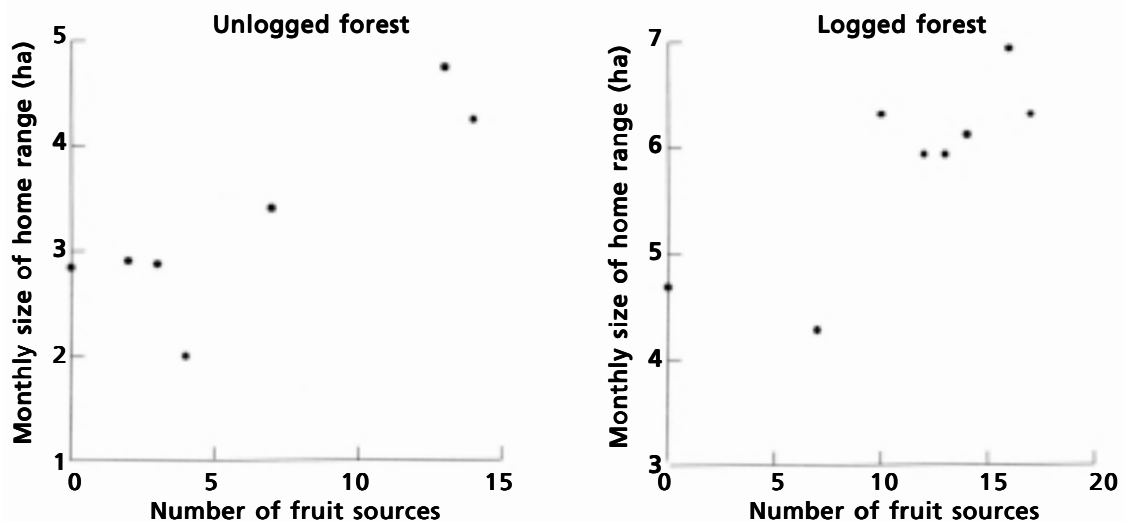

Fig. 5. Relationship between the size of the area used monthly by the monkeys and the number of fruit sources used by the howler group in the unlogged (*r* = 0.759; *P* = 0.011) and logged sites (*r* = 0.787; *P* = 0.007), from February to November 2000, in Paragominas, Para, Brazil.

Fig. 5. Relación entre las dimensiones del área que los monos utilizan mensualmente y el número de fuentes de suministro de frutas utilizadas por el grupo de monos aulladores en las zonas sin talar (r = 0,759; P = 0,011) y en las deforestadas (r = 0,787; P = 0,007) desde febrero a noviembre de 2000 en Paragominas, Pará, Brasil.

census, which indicated similar fruit abundance between the sites, although the species composition was different. Second, the adjacent unlogged site possibly acted as a refuge for the monkeys, at least, minimizing possible harsh conditions due to logging activities, such as clime changes (e.g. CHIARELLO, 1993; ESTRADA et al., 1999). Third, the time period between the harvesting and this study, approximately three years, could have been sufficiently long for the monkeys to reestablish their pre–harvesting behavior. Other studies (JOHNS, 1983; JOHNS & SKORUPA, 1987; GRIESER JOHNS, 1997) have shown a relatively short re-adaptation period for various animal species following logging and in the absence of subsequent anthropogenic pressures (e.g. hunting and/or agriculture). Likewise, leaves and flowers that show a decline in abundance immediately following logging, may show production peaks after logging (JOHNS, 1986, 1988, 1994). Additionally, some of Alouatta's inherent characteristics, such as a recognized diet flexibility, and tolerance to disturbed habitats (MILTON, 1980; ESTRADA & COATES–ESTRADA, 1996; CROCKETT, 1998; HORWICH, 1998; SILVER et al., 1998; ESTRADA et al., 1999; GÓMEZ–MARIN et al., 2001) may help to explain how this group was able to persist in the logged area without significant changes in its behavioral patterns.

The lack of information on the behavior of A. belzebul in other logged forests makes it difficult to generalize from our results. However, the activity pattern and diet of our group were similar to those found for other groups of red–handed howler monkey in the Caxiuanã National Forest, in Pará, Brazil (PINA, 1999; SOUZA, 1999), an area of continuous rainforest with climatic similarities with our study site. In general, the behavioral budget of the focal group was typical for the Alouatta genus, with resting activities dominating other activities (BICCA–MARQUES & CALEGARO–MARQUES, 1994; SILVER et al., 1998; ESTRADA et al., 1999; JUAN et al., 2000). As to the home range, other studies on A. belzebul recorded a variation from 9.5 to 18.1 ha (BONVICINO, 1989; SOUZA, 1999, respectively); our group occupied an area at the high end of this range (17.8 ha). However, the average daily range of A. belzebul in this study was 50 % less than that recorded by JARDIM (1997) and SOUZA (1999), but similar to that reported by BONVICINO (1989) in an Atlantic Forest fragment.

As a general rule, the temporal and spatial distribution of food resources, the location of sleeping sites, and the degree of territoriality of the species, influence the spatial use pattern of primates (TERBORGH, 1983). For this study, fruit source distribution was a key element in explaining the howler monkeys' spatial use patterns; the expansion of the home range was positively correlated with the search of new fruit sources. In general, the Amazonian species of Alouatta exhibits a pronounced frugivorous diet, as compared with howler species from others regions (e.g., JULLIOT & SABATIER, 1993; QUEIROZ, 1995;

JARDIM, 1997; PINTO, 2002), reinforcing the importance of this food source.

A close link between home range and food source availability has been demonstrated for howler monkeys. The study of STONER (1996) on habitat selection by Alouatta palliata in Costa Rica clearly showed that the density of the principal food resources was the most important factor driving habitat selection. The same species studied in forest fragments of different sizes in Mexico showed a higher index of frugivory and travelling activities among the groups living in larger fragments that also contained the highest number of food sources (JUAN et al., 2000). Additionally, CLARKE et al. (2002) observed a new arrangement in the home range of one group of A. palliata in Costa Rica. This group incorporated new stands of the fruit tree Muntingia calabura (Elaeocarpaceae) when this source became available and was located close to their original home range.

As a consequence of their dietary preference for ripe fruits, the howlers monkeys have played an important role as seed dispersers (see ESTRADA & COATES–ESTRADA, 1984, 1986; JULLIOT, 1996, 1997; PINTO, 2001); and as a result of their feeding flexibility, the howlers present considerable ability to survive in altered areas. Thus, these monkeys may to persist under conditions of reduced–impact logging and contribute to regeneration of the logged area (through of the seed dispersal), since fruit sources not had been severely harvested. The intensity and type of logging (e.g. high–impact or reduced–impact logging) are certainly key factors for the maintenance of environmental conditions that will allow the permanence of primates species in logged forests (see JOHNS, 1983; JOHNS & SKORUPA, 1987; GREISER JOHNS, 1997). Therefore, this study suggests that forest management plans should foresee the maintenance of a temporal and spatial availability of fruits that allow a larger spatial use by the monkeys, and, therefore, improve the ecological services they might provide. Additionally, the maintenance of unlogged fragments next to logged forests may help as a faunal refuge and seed stock for forest regeneration. The control of indirect effects of logging, such as the increase in hunting due to the facilitated access to remote areas, is also important. This may represent the major threat to the survival of large primates after logging (see JOHNS, 1983; PERES, 1990, 1997).

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