VI Congresso de Ecologia do Brasil – Anais de Trabalhos Completos, pp.286–287. Editora da UFCE, Fortaleza.

Neville, M. K., Glander, K. E., Braza, F. e Rylands, A. B. 1988. The howling monkeys, genus *Alouatta*. Em: *Ecology and Behavior of Neotropical Primates, Vol. 2*, R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho e G. A. B. da Fonseca (eds.), pp.349–453. World Wildlife Fund, Washington, DC.

Queiroz, H. L. 1995. *Preguiças e Guaribas: Os Mamíferos Folívoros Arborícolas do Mamirauá*. CNPq, Brasília e Sociedade Civil Mamirauá, Tefé.

Rylands, A. B. e Chiarello, A. G. 2003. Official list of Brazilian fauna threatened with extinction – 2003. *Neotrop. Primates* 11(1): 43–49.

Silva, E. C. 1981. A preliminary survey of brown howler monkeys (*Alouatta fusca*) at the Cantareira Reserve (São Paulo, Brazil). *Rev. Bras. Biol.* 41(4): 897–909.

Souza, G. R. 2002. Florística do estrato arbustivo-arbóreo da Floresta da Cicuta, um fragmento de Floresta Atlântica no município de Volta Redonda, Estado do Rio de Janeiro. Dissertação de Mestrado, Universidade Federal Rural do Rio de Janeiro, Seropédica.

Steinmetz, S. 2001. Densidade e conservação do bugio (*Alouatta fusca*) no Parque Estadual Intervales. *Neotrop. Primates* 9(2): 69–73.

Zaú, A. S. 1998. Fragmentação da Mata Atlântica: Aspectos teóricos. *Floresta e Ambiente* 5(1): 160–170.

A PRELIMINARY STUDY OF PROXIMITY PATTERNS AMONG AGE-SEX CLASSES IN A POPULATION OF CENTRAL AMERICAN BLACK HOWLERS (*ALOUATTA PIGRA*)

Lisa C. Corewyn
M. S. M. Pavelka

Introduction

Affiliative interactions reflect the nature of social bonds within primate social groups, which in turn can reflect the pattern of dispersal. In female resident societies, related females tend to affiliate more closely with one another, and the reverse is reported for male resident groups (Strier, 1994; Strier *et al.*, 2002). Bisexual or female dispersal may be associated with stronger bonds between adult males and females (Printes and Strier, 1999; Di Fiore and Fleischer, 2005), and weaker bonds between females (Strier, 1999).

Central American black howler monkeys (*Alouatta pigra*), recently upgraded to Endangered by the IUCN (IUCN, 2003), are folivore/frugivores (Silver *et al.*, 1998; Pavelka and Knopff, 2004) that live in small groups of 2–10 individuals. Groups are usually comprised of one or more adult males plus one or more adult females and juveniles (Horwich *et al.*, 2001; Ostro *et al.*, 2001). Preliminary reports indicate bisexual dispersal (Brockett *et al.*, 2000a; Pavelka, unpub. data), as seen in other howler monkey species (Crockett and Eisenberg, 1997; Di Fiore and Campbell, 2007), but long-term data on known individuals is not yet available. Despite the highly cohesive nature of howler monkey social groups (Bernstein, 1964; Stevenson *et al.*, 1998), overt social interactions are few. In black howler monkeys, less than 4% of time is typically spent in social interactions such as grooming and hand-holding among adults (Silver *et al.*, 1998; Brockett *et al.*, 2000b; Pavelka and Knopff, 2004; Brockett *et al.*, 2005).

Spacing patterns are important indicators of the underlying social relationships that aid in establishing affiliative contacts, and in avoiding agonistic interactions and predation (Altmann, 1980; White and Chapman, 1994). Kummer (1971: 221) argued that "social affinity and spatial proximity are so highly correlated that the distribution of animals in space can be used as a first reading of their social structure". Female social relationships in black howler monkeys appear to be, like those of other howler monkeys, undifferentiated and egalitarian (Pavelka, unpub. data). Crockett and Eisenberg (1987) have suggested that measures of inter-individual proximity may be one of the few ways to quantify affiliative social relationships within howler monkey groups. In this paper we describe the results of a preliminary study of proximity patterns to help elucidate the nature of within-group social bonds in *A. pigra*.

Methods

This study was conducted at Monkey River in the Toledo district of Belize. The 52 ha study site is located within a 100 km^2 lowland semi-evergreen riparian forest along the river. The area exhibits a distinctive dry season, generally from January to May, and a wet season from June to December. The average annual temperature in the area is 26°C, with an average annual rainfall of approximately 2,460 mm (Pavelka and Knopff, 2004). Over 160 hours of focal animal data were collected on 11 adults and juveniles (infants were not sampled) living in three groups (A, D, and Q). Each of the three groups contained one adult male and two adult females, and group Q also had two juveniles (defined as independent offspring over one year of age). Ten-minute focal animal samples were collected from each group member, with no individual sampled more than once each hour, in order to maintain independence across sample points. The first individuals were sampled opportunistically and on a rotating basis thereafter. Though individuals could not always be reliably identified, we used age-sex class and location relative to other group members to ensure individuals were as equally represented as possible. At the start of each focal animal sample, we conducted a proximity scan to record the age-sex class of each neighbor within 2 m of the focal animal (following the proximity categories established for *A. pigra* [Schneider *et al.*, 1999; Treves *et al.*, 2001], and other howler monkey species such as *A. palliata* [Zucker and Clarke, 1998] and *A. seniculus* [Stevenson *et al.*, 1998]). Each group was followed from dawn to dusk once per week over the wet season study period of July 2003 to January 2004.

From the 960 proximity scans, we calculated proximity scores for dyads using a formula adapted from Matsumura and Okamoto (1997):

$$\textbf{a)}\ \frac{f_A(B) + f_B(A)}{F(A) + F(B)} \times 100 \qquad \textbf{b)}\ \frac{f_A(A)}{F(A)} \times 100$$

Where **a)** F(A) was the total number of proximity scans for a given age-sex class A; F(B) was the total number of proximity scans for a given age-sex class B; f_A (B) was the total number of proximity scans in which B was found within 2 m of A when A was scanned; and f_B (A) was the total number of proximity scans in which A was found within 2 m of B when B was scanned. Although this formula was originally intended for individual dyad analyses, we have adapted it for age-sex classes. Given that there were different numbers of individuals and different numbers of samples for each age-sex class, for dyads with the same age-sex class, we **b)** divided the number of near proximity scans for that dyad by the total number of proximity scans for that focal age-sex class. Dyads with an unknown age-sex class were dropped from this part of the analysis. Proximity data from the three groups were pooled, with the exception of dyads involving juveniles, which were calculated by group, as juveniles were only present in one group. Chi-square tests were used due to the small sample sizes and the categorical nature of the data (Siegel and Castellan Jr., 1988).

Maintenance of proximity was calculated using Hinde's index (Hinde and Atkinson, 1970) for each of the proximity dyads using the frequency of approaches (when one individual approached and settled within one meter of another) and leaves (when one animal moved away from another with whom it had been in one meter proximity) from the focal animal data:

$$\frac{APP_a}{APP_b + APP_a} - \frac{LEA_a}{LEA_b + LEA_a} \times 100$$

Where APP_a was the number of approaches by age-sex class *a* towards age-sex class *b*; APP_b was the number of approaches by age-sex class *b* towards age-sex class *a*; LEA_a was the number of leaves by age-sex class *a* from age-sex class *b*; and LEA_b was the number of leaves by age-sex class *b* from age-sex class *a*. If the percentage was positive, then age-sex class *a* was more responsible than *b* for maintaining proximity, and vice versa if the percentage was negative. Low values of Hinde's index indicated a tendency for individuals in those dyads to be equally responsible for maintenance of proximity.

Results

Confirming the cohesive nature of Central American black howler monkeys, in 70.6% of the 960 proximity scans (divided into 347, 247, and 366 total scans for each group respectively) the focal animal had another individual within 2 m significantly more often than not (29.4%, or 284 scans with no individual within 2 m; $\chi^2 = 611.2$, *df* = 2, $p < 0.001$). Proximity scores were highest for juveniles (80%), followed by adult females (72.5%) and then males (65.8%). Fig. 1 shows the overall proximity scores within and across each age-sex class for each group. Adult females were in close proximity to other adult females as often as they were to adult males. However, analysis of the strength of the adult dyads revealed that females associated with one another more than expected given the availability of congeners in each group ($\chi^2 = 6.24$, *df* = 1, $p = 0.01$). It is possible that the percentage of time adult males spent in close proximity to adult females in each

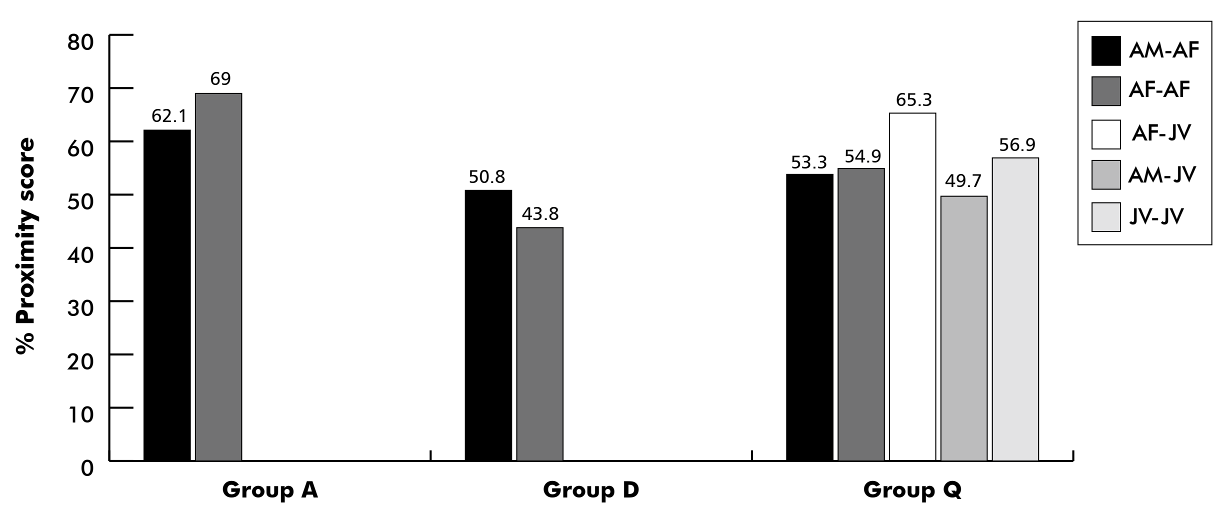

Figure 1. Proximity score by age-sex dyad for each group. AM = adult male; AF = adult female; JV = juvenile.

group was artificially low, given that males could have had both group females in close proximity at once; however, only dyadic interactions were analyzed as part of this study. In the only group with juveniles (group Q), the proximity score for adult females with juveniles was 65.3%, and juveniles were in close proximity to other juveniles in 56.9% of their proximity scans. The least commonly occurring dyad in this group was adult males and juveniles (49.7%).

Maintenance of proximity was calculated to determine which age-sex class was responsible for maintaining the "relationship" within each dyad (Table 1). Between adult females and adult males, females were slightly more responsible for maintaining proximity (5.5%), although the low score suggested fairly even responsibility. Juveniles were 15.3% more responsible for maintaining the spatial relationship with adult females; however, adult males and juveniles appeared to be equally responsible.

Discussion

Despite low levels of conspicuous social interaction and undifferentiated social relationships in *A. pigra*, the proximity data presented here support the overall impression that the groups were nonetheless very cohesive. If spatial proximity is taken as an indication of social affinity, as has been suggested (Kummer, 1971; Altmann, 1980; White and Chapman, 1994), the spacing patterns reported here further revealed variation among age-sex classes in strength of social bonds. Juveniles exhibited a higher degree of affiliation than adults, and females exhibited a higher degree of affiliation than males. Being smaller in size and less experienced than adults, young monkeys may be more vulnerable to predation and might spend more time near other individuals, particularly their mothers, as a result. Proximity patterns and vigilance rates (a measure of predation risk through scanning behavior) have been found to be related in *A. pigra*, with vigilance decreasing as the number of close neighbors increases (Treves *et al.*, 2001). Moreover, juveniles spend more time in social play than adults, increasing the amount of time in close proximity.

Individual adult female proximity scores were higher than those of adult males, as expected given the likely association between adult females and their own juvenile offspring. However, the analysis of the strength of different dyadic combinations revealed a surprising affiliation between adult females. In this study, adult females had equal opportunity to interact with another female or with the adult male. Adult males, conversely, could only associate with adult females. Thus, the finding that the male-female and female-female dyads occurred equally was surprising, with female-female dyads occurring more than would be expected given availability of congeners — and certainly given the bisexual dispersal pattern and unimale groups, which would predict weaker female-female associations than male-female associations.

Further, evidence of seasonal mating appeared to be absent as copulations were not observed. This result has been found in other howler monkey studies, suggesting that the dispersal patterns of female primates may not be a consistent predictor of social bonds, at least as measured by proximity patterns. Wang and Milton (2003) reported that adult male howlers (*A. palliata*) at Barro Colorado Island were most often in close association with adult females, as would be expected for a female-dispersing species; these findings were in contrast to those of Zucker and Clarke (1998) and Kovacovsky (2002), who found *A. palliata* females spent more time in close proximity with one another than expected. Zucker and Clarke (1998) reported that adult dyads varied in frequency and intensity across years and among individuals, and suggested that female bonds were likely influenced by female reproductive status and parity, and by changing memberships of adult males within the groups.

When comparing *A. pigra* with red-tailed monkeys (*Cercopithecus ascanius schmidtii*) and red colobus monkeys (*Procolobus badius tephrosceles*), Treves and Baguma (2002) unexpectedly found that females in the two species with female transfer — black howler monkeys and red colobus monkeys — were significantly more cohesive than the female red-tailed monkeys, who are female-resident. Though kinship was not known in our study, some individuals could have been related, thereby affecting differential proximity. Further, the data on the maintenance of proximity presented here revealed that females were not more responsible for maintaining proximity with adult males than males were with them. Females may derive more benefit from associating with males when in unimale groups, as their groups can be more vulnerable to takeovers by extragroup males (Crockett and Janson, 2000). Not surprisingly, juveniles were more responsible for maintaining

Table 1. Number of approaches and leaves attributed to each age-sex class. AM = adult male; AF = adult female; JV = juvenile; N App = number of approaches over study period; N Lea = number of leaves over study period; H Index = Hinde's index (%).

Age-sex class to which action was attributed	Received AM			Received AF			Received JV		
	N App	N Lea	H Index	N App	N Lea	H Index	N App	N Lea	H Index
AM	–	–	–	88	93	-5.5	35	36	2.6
AF	98	83	5.5	–	–	–	69	112	-15.3
JV	83	97	-2.6	196	159	15.3	–	–	–

proximity to adult females, as they may derive more benefit from close associations with females for predator protection, and to gain social, survival, and maternal skills.

Though infants were not sampled, they were present in each of the three groups at various times through the study period and could conceivably have affected proximity results, particularly among lactating and non-lactating females (see Corewyn, 2005). We caution against broad generalizations given the small sample size in the number of groups, particularly with regard to juvenile proximity, since these data were only representative of one group. We are unable to comment on male-male social relationships in *A. pigra*, and look to future research to address these limitations.

Acknowledgements

We would like to thank the people of Monkey River and Placencia for their help and support. For his help with statistical analyses, we gratefully acknowledge Dr. Tak S. Fung of the Department of Mathematics and Statistics, University of Calgary. We are grateful to Travis Steffens, Keriann McGoogan, Alison Behie, Grainne McCabe, and Allison Maclean for their help with data collection, and to Tracy Wyman for technical assistance. Support for this project was provided by the Calgary Zoo Conservation Fund, Natural Sciences and Engineering Research Council of Canada, Province of Alberta Graduate Scholarship, National Geographic Society, Calgary Institute for the Humanities, Department of Anthropology, and the Faculties of Social Sciences and Graduate Studies at the University of Calgary.

Lisa C. Corewyn, Department of Anthropology, University of Texas at San Antonio, One UTSA Circle, San Antonio, TX 78249-0649, USA, e-mail: <monkeythesis@yahoo.ca> and **M. S. M. Pavelka,** Department of Anthropology, University of Calgary, 2500 University Drive N.W., Calgary, AB T2N 1N4, Canada.

References

Altmann, J. 1980. *Baboon Mothers and Infants*. Harvard University Press, Cambridge, Massachusetts.

Bernstein, I. S. 1964. A field study of the activities of howler monkeys. *Anim. Behav*. 12: 92–97.

Brockett, R. C., Horwich, R. H. and Jones, C. B. 2000a. Female dispersal in the Belizean black howling monkey (*Alouatta pigra*). *Neotrop. Primates* 8: 32–34.

Brockett, R. C., Horwich, R. H. and Jones, C. B. 2000b. A model for the interpretation of grooming patterns applied to the Belizean black howling monkey (*Alouatta pigra*). *Primate Report* 56: 23–32.

Brockett, R. C., Horwich, R. H. and Jones, C. B. 2005. Hand-holding by Belizean black howler monkeys: Intentional communication in a Neotropical primate. *Folia Primatol.* 76: 227–230.

Corewyn, L. C. 2005. Proximity patterns in the Central American black howler (*Alouatta pigra*) at Monkey River, Belize. Master's thesis, University of Calgary, Alberta, Canada.

Crockett, C. M. and Eisenberg, J. F. 1987. Howlers: Variations in group size and demography. In: *Primate Societies*, B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker (eds.), pp.54–68. University of Chicago Press, Chicago and London.

Crockett, C. M. and Janson, C. H. 2000. Infanticide in red howlers: Female group size, male membership and a possible link to folivory. In: *Infanticide by Males and its Implications*, C. P. van Schaik and C. H. Janson (eds.), pp.75–98. Cambridge University Press, Cambridge.

IUCN. 2003. *Alouatta pigra*. 2003 IUCN Red List of Threatened Species. Website: <http://www.redlist.org>. Accessed 26 May 2004.

Di Fiore, A. and Fleischer, R. C. 2005. Social behavior, reproductive strategies, and population genetic structure of *Lagothrix poeppigii*. *Int. J. Primatol.* 26: 1137–1173.

Di Fiore, A. and Campbell, C. J. 2007. The Atelines: Variation in ecology, behavior, and social organization. In: *Primates in Perspective*, C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger and S. K. Bearder (eds.), pp.155–185. Oxford University Press, New York.

Hinde, R. A. and Atkinson, S. 1970. Assessing the roles of social partners in maintaining mutual proximity, as exemplified by mother-infant relations in rhesus monkeys. *Anim. Behav.* 18: 169–176.

Horwich, R. H., Brockett, R. C., James, R. A. and Jones, C. B. 2001. Population structure and group productivity of the Belizean black howling monkey (*Alouatta pigra*): Implications for female socioecology. *Primate Report* 61: 47–65.

Kovacovsky, S. 2002. Proximity patterns of adult female mantled howler monkeys (*Alouatta palliata*): Evidence for female-bonding. *Am. J. Primatol.* 57 (S1): 24–25.

Kummer, H. 1971. Spacing mechanisms in social behavior. In: *Man and Beast: Comparative Social Behavior*, J. F. Eisenberg and W. S. Dillon (eds.), pp.220–234. Smithsonian Institution Press, Washington, DC.

Matsumura, S. and Okamoto, K. 1997. Factors affecting proximity among members of a wild group of moor macaques during feeding, moving and resting. *Int. J. Primatol.* 18: 929–940.

Ostro, L. E. T., Silver, S. C., Koontz, F. W., Horwich, R. H. and Brockett, R. 2001. Shifts in social structure of black howler (*Alouatta pigra*) groups associated with natural and experimental variation in population density. *Int. J. Primatol.* 22: 733–748.

Pavelka, M. S. M. and Knopff, K. H. 2004. Diet and activity in black howler monkeys (*Alouatta pigra*) in southern Belize: Does degree of frugivory influence activity level? *Primates* 45: 105–111.

Printes, R. C., and Strier, K. B. 1999. Behavioral correlates of dispersal in female muriquis (*Brachyteles arachnoides*). *Int. J. Primatol.* 20: 941–960.

Schneider, E. C., Hunter, L. F. and Horwich, R. H. 1999. Adoption of a young juvenile in black howler monkeys (*Alouatta pigra*). *Neotrop. Primates* 7: 47–51.

Siegel, S. and Castellan Jr., N. J. 1988. *Nonparametric Statistics for the Behavioral Sciences*. McGraw-Hill, Boston.

Silver, S. C., Ostro, L. E. T., Yeager, C. P. and Horwich, R. 1998. Feeding ecology of the black howler monkey (*Alouatta pigra*) in northern Belize. *Am. J. Primatol.* 45: 263–279.

Stevenson, P. R., Quinones, M. J. and Ahumada, J. A. 1998. Effects of fruit patch availability on feeding subgroup size and spacing patterns in four primate species at Tinigua National Park, Colombia. *Int. J. Primatol.* 19: 313–324.

Strier, K. B. 1994. Brotherhoods among Atelins: Kinship, affiliation, and competition. *Behaviour* 130: 151–167.

Strier, K. B. 1999. Why is female kin bonding so rare? Comparative sociality of neotropical primates. In: *Comparative Primate Socioecology*, P. C. Lee (ed.), pp.300–319. Cambridge University Press, Cambridge, UK.

Strier, K. B., Dib, L. T. and Figueira, J. E. C. 2002. Social dynamics of male muriquis (*Brachyteles arachnoides hypoxanthus*). *Behaviour* 139: 315–342.

Treves, A. and Baguma, P. 2002. Interindividual proximity and surveillance of associates in comparative perspective. In: *The Guenons: Diversity and Adaptation in African Monkeys*, M. E. Glenn and M. Cords (eds.), pp.161–172. Kluwer Academic/Plenum Publishers, New York.

Treves, A., Drescher, A. and Ingrisano, N. 2001. Vigilance and aggregation in black howler monkeys (*Alouatta pigra*). *Behav. Ecol. Sociobiol.* 50: 90–95.

Wang, E. and Milton, K. 2003. Intragroup social relationships of male *Alouatta palliata* on Barro Colorado Island, Republic of Panama. *Int. J. Primatol.* 24: 1227–1243.

White, F. J. and Chapman, C. A. 1994. Contrasting chimpanzees and bonobos: Nearest neighbor distances and choices. *Folia Primatol.* 63: 181–191.

Zucker, E. L. and Clarke, M. R. 1998. Agonistic and affiliative relationships of adult female howlers (*Alouatta palliata*) in Costa Rica over a 4-year period. *Int. J. Primatol.* 19: 433–449.

DENSITY OF *SAGUINUS INUSTUS* (SCHWARTZ, 1951) IN THE INTERFLUVIUM OF THE CAQUETÁ–APAPORIS RIVERS, COLOMBIAN AMAZONIA

Claudia Idaly Castillo-Ayala
Erwin Palacios

Introduction

The Amazon bioregion is considered one of the highest biodiversity areas in the world. Primates are important components of this biodiversity, and with 15 genera, 81 species and 134 taxa, they are the most emblematic faunal group of Amazonia (Mittermeier *et al.*, 2002). *Saguinus* is perhaps the most diverse of Neotropical primate genera, with 13–15 species and 33 recognized forms (Hershkovitz, 1977; Rylands *et al.*, 2000). Defler (2003a) recognizes the presence of six species of *Saguinus* in Colombia (40–46% of the total species in the genus), three of them exclusively distributed in the Colombian Amazon: *S. fuscicollis* (Spix, 1823), *S. nigricollis* (Spix, 1823), and *S. inustus* (Schwartz, 1951). *Saguinus inustus*, the mottled-face tamarin, is distributed in southeastern Colombia, west of the Andes, between the Guayabero-Guaviare rivers and the Caquetá River, and between the Mesay River and the border with Brazil; however, accurate eastern and western boundaries of its geographical range within the country are still unknown (Defler, 2003a). The species is also present in western Brazil, between the Rio Negro and the Colombian border.

Saguinus inustus is one of the least-studied species of Neotropical primates; preliminary information on its ecology (ranging and diet) comes from only two short studies carried out near La Pedrera, at Comeyafú Indigenous Reserve, an interfluvial area between the Caquetá and Apaporis rivers (Palacios *et al.*, 2004; Defler, unpublished data), and from occasional observations of foraging groups in the Amanã Sustainable Development Reserve in Brazil (de Souza *et al.*, 2004). Here we present the first data on the density of *S. inustus*. We collected this information during a primate survey in the lower Caquetá River as part of a larger effort started six years ago to document and monitor the densities of primates and 15 other large vertebrate species in eastern Colombian Amazonia (Palacios *et al.*, 2003; Palacios and Peres, 2005; Peres and Palacios, 2007).

Methods

Study area

Censuses were carried out in the interfluvial area between the lower Caquetá and Apaporis Rivers, Amazonas, near Loma Linda indigenous community (01°16'S, 69°44'W, 101 m a.s.l.; Fig. 1), Córdoba Indigenous Reserve. Primary *terra firme* and várzea forests represented the majority of the forested matrix in the study site. An area of secondary *terra firme* forest (locally called *rastrojo*) located around the indigenous settlement comprised a small proportion of such matrix. There were also patches of what is locally known as savanna forest or *varillal*, which corresponds to primary forest with a mean height of 17–18 m, and a very sparse understory growing on rocky outcrops and white sands; and another savanna type known as *sabana capotuda*, with a mean canopy height of 8 m, deep soil litter and a very dense understory with intermingled vines and lianas.

Linear transects

We used the line transect method (Burnham *et al.*, 1980) to estimate *S. inustus* densities. From a zero point located ca. 100 m away from the community secondary forest area, two transects (4.6 and 4.9 km long, oriented 40° NW and 40° NE respectively) were cut; they were