
Stella de la Torre
Charles T. Snowdon
Monserrat Bejarano

Introduction
Ecotourism has been proposed as an alternative form of sustainable use in protected areas (Yu-Douglas *et al.*, 1997). However, very little has been done to determine the impact of this activity on these habitats and on the animal populations, especially in Neotropical rain forests. A possible effect of the noise caused by tourism-related activities (e.g., motor engines and human voices) on the vocal communication and other behaviors of animals has been suggested by Payne and McVay (1971) and Edington and Edington (1986). ArboREAL primates in Neotropical rain forests, where visibility is poor, are highly dependent on vocal communication (Marler, 1965; Seyfarth, 1987). Among these Neotropical primates, howler monkeys are well known for their vocal behavior (Whitehead, 1987; Neville *et al.*, 1988). The dawn choruses of howling involve ritualized aggression in the males' defense of the females and infants of their groups, and are used also as location cues among groups (Chivers, 1969; Sekulic, 1982).

To evaluate the effects of tourism-related activities on the howling behavior of red howler monkeys, *Alouatta seniculus*, we carried out morning censuses of dawn choruses at two sites which differed in the amount of tourism and motor boats in the Cuyabeno Reserve in northeastern Ecuador.

Study Area and Methods
The Cuyabeno Reserve is a protected area of tropical rain forest located in northeastern Ecuador. The annual mean precipitation is about 3,000 mm and two seasons can be distinguished: the rainy season (March-August) with more than 250 mm of monthly rainfall, and the dry season (September-February) with less than 250 mm of monthly rainfall (de la Torre *et al.*, 1995). The high faunal diversity of this area, which includes ten primate species (de la Torre *et al.*, 1995), has attracted considerable tourism along the rivers of the Cuyabeno Reserve. In 1992, there were about 10 tourist agencies working in the Reserve. Today there are 20, and most of them use motor boats in all stages of their itineraries.

Two sites were selected to carry out the study. The first was the Laguna Grande, approximately 95 ha, in the Cuyabeno basin, located between 0°2'N-0°3'S and 76°11'W-76°15'W (Ron, 1995). In the rainy season, water levels reach 5 m in the deepest part; while in the dry season, water levels gradually drop and the lake may dry out completely from December through February. The area is consistently visited by 17 tourist agencies that use motor boats on almost every trip. The second site was the Zancudochocha, black-water, lake approximately 100 km south-east of La Hormiga Island, and larger than the Laguna Grande, covering an area of about 150 ha, although both are similar in shape. The water levels in the Zancudochocha lake reach 5 m in the deepest part in the rainy season but drop to about 4 m in the dry season (Vallejo, 1995). This lake was visited by just one tourist agency and thus supported much less tourism compared to the Laguna Grande. In addition, motor boats were not permitted at Zancudochocha.

Morning censuses of howling groups in the lake areas were carried out for two consecutive days in each rainy season at the Laguna Grande (May, 1997) and 2 consecutive days in the rainy season at Zancudochocha (July, 1997). The censuses were carried out only in the rainy season (the season with the highest number of tourists in both areas) to obtain data when the highest tourism pressure occurred in an area; we also tried to control for seasonal differences between the habitats of the two lakes (since the Zancudochocha lake does not dry out); and, finally, it was logistically easier to go to the middle of Laguna Grande during the rainy season than during the dry season. Censuses were carried out only on days with no rain and minimal wind.

All the censuses were carried out from a fixed point considered to be the center of the lake. Each census began at 0500 and lasted two hours. The direction and distance from the center of the lake of the howling groups were recorded. The direction of calls was recorded with a compass (accuracy 5°) and the distance was estimated, by ear, in three categories: far, middle and close. Since the roars of a howling group can be heard at a distance of about 2 km (pers. obs.), we considered that a group estimated to be far away was at two or more kilometers from the lake center; a group howling at a medium distance was at about 1 km from the lake center; and a group close to the lake was at about 400 m in Laguna Grande, or 600 m in Zancudochocha, from the lake center (equivalent to the approximate radius of each lake). The distance estimates were confirmed by periodical observations of some of the howler groups in areas around both lakes at varying distances from the shore, ranging from groups observed close to the lakeside (0-50 m) to groups observed far away (approximately 1.5 km).

The howling monkey groups in each lake were well identified from the first census by their direction and distance. Since all of the groups howled more than once in each census, the direction of each group was the average of the group directions in a census. The distance estimates did not vary within and between censuses for any of the groups. The average direction and distance from the estimated center (corresponding to the fixed center point in the field censuses) was plotted on a map for all groups; once plotted, its distance to the closest lake shore was recorded. Mann-Whitney non-parametric tests were used to compare the estimates of group distances from the shores between the two lakes.

Results and Discussion
Nine groups of howler monkeys were recorded during the censuses at the Laguna Grande and eight groups at Zancudochocha. The estimated mean distance of the howling groups was significantly different between the two lakes (Mann-Whitney Z = -2.08; p = 0.037); groups at Laguna Grande howled farther from the shores (mean = 839 m ±
103), than did groups at Zancudococha (mean = 478 m ±

The fact that howler monkey groups howled closer to the
shore in the lake with no motor boats suggests a possible
effect of the noise of motor boats on the calling behavior
of this species. The sound frequency of the roars of red howler
monkeys is centered on 300-700 Hz (Whitehead, 1995), and
thus greatly overlaps with the frequency of the noise of
outboard engines for which most of the sound energy is
below 1 kHz (pers. obs.). The shores of the Laguna Grande
and Zancudococha have similar forest types, with areas of
non-flooded terra firme forest and flooded forests (igapó)
(Prance and Prance, 1985; Ron, 1995; Vallejo, 1995). Although
it is not possible to entirely exclude differences in the habi-
tat quality between the two lake shores that may influence
the spatial distribution of the howler monkey groups, it
would seem likely that those at the Laguna Grande were
howling further from the shores to avoid the negative sound
interference with the motor noise, or that howler monkey
groups that were closer to the shores at the Laguna Grande
howled less, not only to avoid sound interference with
motor noise but to avoid being detected by humans. Given
the importance of howling behavior to these monkeys,
changes in the vocal behavior and/or the spatial distribu-
tion of the groups would predictably have long-term nega-
tive effects on their reproductive performance (Chivers,
1969; Sekulic, 1982; Neville et al., 1988).

These data suggest an impact of tourism-related activities
on the vocal behavior of the howler monkeys and are
complementary to data obtained on pygmy marmosets
(Cebuella pygmaea) in the Cuyabeno Reserve that also
point to a negative effect of human activities, including
tourism, on their behavior. Groups of pygmy marmosets
living in areas with intense tourism and human traffic
showed lower rates of social play and used less the lower
strata of the forests than groups of marmosets living in
areas with reduced tourism and traffic. These behavioral
changes appeared to be an effort of the marmosets to avoid
contact with humans and were possibly related to differ-
ences in the reproductive performance of the groups (de la
Torre et al., submitted). It has been assumed that primates
habituate to human presence without any special effort
(Griffith and van Schaik, 1993), but we believe our findings
challenge this assumption and that more studies monitor-
ing the effect of ecotourism and human traffic in Neotro-
pical rain forests are required to minimize the potential en-
vironmental damage of these human activities and to improve
the current conservation policies in protected areas.

Acknowledgments

We are greatly indebted to the following persons and insti-
tutions: Daniel Payaguaje, Lucía de la Torre, Xavier Burbano
and Stephan Amend from PROFORS (Forestry Program for
the Province of Sucumbios), Lcdo. Luis Borbor, Director of
the Cuyabeno Reserve and all the park guardians, for their
most valuable support during the field work. Anthony
Rylands, Lisa Naughton, Karen Strier, Adrian Treves,
Cristina Lázaro-Perea and Mariano Sironi provided useful
comments on the manuscript. INEFAN (Ecuadorean Insti-
tute of Forestry and Wildlife), permitted us to conduct the
research in the Cuyabeno Reserve. Most of the tourist agen-
cies that work in the Reserve helped us logistically at some
point in our study, we are especially thankful to Transturi
that greatly facilitated our work at Zancudococha. This re-
search was supported by the Grant 5806-96 from the Na-
tional Geographic Society, with additional support from
the Milwaukee Zoological Society, the Tinker-Nave Fund, the
University of Wisconsin Davis Fund and the Latin Ameri-
can Studies Program in American Universities, LASPAU.

Stella de la Torre, Department of Zoology, University of
Wisconsin, Madison, WI 53706, USA, Charles T. Snowdon,
Department of Psychology, 1202 West Johnson Street,
University of Wisconsin, Madison, WI 53706, USA, and
Monserrat Bejarano, Departamento de Biología, Pontificia
Universidad Católica del Ecuador, Quito, Ecuador.

References

Chivers, D. J. 1969. On the daily behaviour and spacing of
howling monkey groups. Folia Primatol. 10: 48-102.
de la Torre, S., Campos, F. and de Vries, T. 1995. Home range
and birth seasonality of Saginus nigricollis graelisi in
de la Torre, S. Snowdon, C. T. and Bejarano, M. Submitted.
Effects of human activities on pygmy marmosets in Ecu-
dorian Amazonia.

traffic on the abundance and activity periods of Sumatran

Marler, P. 1965. Communication in monkeys and apes. In: Pri-
mate Behavior, I. de Vore (ed.). Holt, Rinehart and Winston,
New York.

Neville, M. K., Glander, K. E., Braza, F. and Rylands, A. B.
and Behavior of Neotropical Primates, Vol. 2., R. A.
Mittermeier, A. B. Rylands, A. F. Coimbra-Filho and G. A. B.
da Fonseca (eds.), pp.349-453. World Wildlife Fund. Wash-
ington, D. C.

Science 173: 585-597.

Pires, J. M. and Prance, G. T., 1985. The vegetation types of
the Brazilian Amazon. In: Amazonia, Key Environments, G.
Press, Oxford.

Ron, S. R. 1995. Estudio poblacional del caimán negro,
Melanosuchus niger, y del caimán blanco, Caiman
crocodilus (Crocodylia: Crocodylidae) en seis lagunas de
la Amazonía Ecuatoriana. Tesis de Licenciatura, Pontificia
Universidad Católica del Ecuador, Quito.

Sekulic, R. 1982. The function of howling in red howler mon-

Seyfarth, R. M. 1987. Vocal communication and its relation to
language. In: Primates Societies, B. B. Smuts, D. L. Cheney,


**Disappearance of Infants Following Male Takeovers in the Belizean Black Howler Monkey (Alouatta pigra)**

Robin C. Brockett
Robert H. Horwich
Clara B. Jones

Organisms are expected to employ self-interested tactics and strategies to maximize lifetime probabilities of survival and reproductive success (Trivers, 1985). Behavior programs may differ significantly between the sexes, since selection is thought to operate on the relative parental investment in offspring by males, on the one hand, and females, on the other (Trivers, 1972). Some researchers (e.g., Sugiyama, 1967; Hausfater and Hrdy, 1984) have argued that males may gain a reproductive advantage by killing infants likely to have been sired by non-kin ("infanticide"). This "sexual selection hypothesis" suggests that infanticide shortens a female's interbirth interval through the cessation of lactation and subsequent return of ovarian cycling. Infantilidal males are thought to gain a reproductive advantage by impregnating the dead infant's mother.

Dixon (1998, Table 4.4, p.68) summarizes 48 cases of infanticide observed directly in 13 primate species. Paleotropical species account for 42 of the 48 (88%) cases, and the Hanuman langer (Presbytis entellus) accounts for 21 of them (50%). The bias in this database favoring Old World primates, and P. entellus in particular, may reflect sampling error resulting from differential time-investment by researchers. Supporting this idea is the observation that infanticide has been reported most commonly in terrestrial or semi-terrestrial species for which visibility is less of a deterrent to observation.

Infanticide has been reported for four species of Alouatta (A. seniculus, the red howler monkey; Rudran [1979], Sekulic [1983]; A. caraya, the black and brown howler monkey: Zunino et al. [1986], Runisz [1940]; A. fuscata, the brown howler monkey: Galetti et al. [1994]; and A. palliata, the mantled howler monkey: Clarke [1981, 1983]). The first three species exhibit polygynous mating systems (after Dixon, 1998) while A. palliata groups vary from polygynous to multimale-multifemale (see Crockett and Eisenberg, 1987). Clarke’s (1981, 1983) study groups exhibited multimale-multifemale social organization, and infanticide was associated with turnovers in the male hierarchy. Infanticide typically occurs in polygynous (harem or age-graded) or multimale-multifemale mating systems (Dixon, 1988).

We conducted ad libitum observations of marked A. pigra at the Community Baboon Sanctuary (CBS), Belize. The CBS is a managed reserve formed in 1985 by cooperative agreement among private landowners (Horwich, 1990). Located at 17°34'N, 88°35'W, the CBS is a mosaic of small farms, pastures, and tropical moist forest fragments including riparian habitat along the Belize River (see Horwich and Lyon, 1990). The study area is composed of mapped trails, and >1000 trees have been mapped and identified. Black howlers are generally polygynous with a modal group size of one adult male to several adult females and immatures (Ostro et al., 1999), although multimale groups may be found. Studies of demography, ecology, social organization and behavior are in their early stages (e.g., Horwich, 1983; Silver et al., 1998; Ostro et al., 1999).

As part of a broader study, 5 incidents of infant disappearance associated with male takeovers were observed (Table 1). These data suggest several topics for further research. First, similar to findings for langurs (Presbytis spp.) (Sommer, 1994), there appears to be a male bias in the sex of infants which disappeared. It would be interesting to obtain larger sample sizes in order to evaluate the sex ratios of infants killed, since an offspring's "value" will differ according to its sex and, possibly, the condition of the mother (see Hrdy, 1987). It is possible that infanticide generally occurs in response to some threshold of benefits to costs to the potential victimizer and that the "value" of the po-

<table>
<thead>
<tr>
<th>Dates of Takeover</th>
<th>Troop</th>
<th>Male(s) displaced</th>
<th>Displacing male</th>
<th>Mother of infant</th>
<th>Post Takeover copulation observed</th>
</tr>
</thead>
<tbody>
<tr>
<td>2 Feb. - 20 Feb. 1995</td>
<td>Roxie</td>
<td>BBLT , UM</td>
<td>BWB</td>
<td>BBLT</td>
<td>yes(^1)</td>
</tr>
<tr>
<td>27 Feb. - 30 Mar. 1995</td>
<td>Baizar</td>
<td>O</td>
<td>BBLT</td>
<td>ORT</td>
<td>no(^2)</td>
</tr>
<tr>
<td>15 Feb. - 19 Mar. 1997</td>
<td>Robin</td>
<td>W LT</td>
<td>BBLT</td>
<td>Baizar</td>
<td>yes (\text{LET})</td>
</tr>
</tbody>
</table>

\(^1\)BBRT gave birth to a male offspring on 13 October 1995 and BBLT to a male offspring on 1 December 1995.

\(^2\)Copulation attempt observed.