REVISTA CHILENA DE HISTORIA NATURAL

Revista Chilena de Historia Natural 83: 435-442, 2010

RESEARCH ARTICLE

River crossings by *Ateles geoffroyi* and *Alouatta pigra* in southern Mexico: A preliminary report

Habilidad para cruzar ríos en *Ateles geoffroyi* y *Alouatta pigra* en el sur de México: Un reporte preliminar

ÓSCAR M. CHAVES* & KATHRYN E. STONER

Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México, Antigua Carretera a Pátzcuaro No. 8701, Ex Hacienda de San José de la Huerta, 58190 Morelia, Michoacán
*Corresponding author: ochaba@gmail.com

ABSTRACT

During a nine month field study, we assess the ability of spider (*Ateles geoffroyi*) and howler (*Alouatta pigra*) monkeys to cross a large Mesoamerican river, and if this behavior is related to deforestation and/or human population size on the disturbed riverbank. The study was conducted along the Lacantún River, southern Mexico, which divides the Montes Azules Biosphere Reserve and the Marqués de Comillas disturbed region. We collected data on river crossings by both monkey species from 428 hours of surveys along the river and 58 questionnaires completed by knowledgeable local informants. Furthermore, we determined the frequency of river crossing by the two species, location and direction of river-crossing, bank-to-bank river width at the location of reported sighting, and the relationship with deforestation rates and/or human population size in the Marqués de Comillas region. We observed on two separate occasions spider monkeys crossing the river from the disturbed area to the reserve, but howler monkeys were never observed crossing. Interviews suggest, however, that howler monkeys cross the river more frequently than spider monkeys (13 versus 8 reports, respectively). We found that bank-to-bank river width was smaller at river crossing locations in each study site than along the river in general. Furthermore, we found no relationship between river crossings and some human pressures such as deforestation and population size in the region. Whatever the underlying pressures that drive river-crossing events in these two primate species in this region, they appear to be sufficiently strong to stimulate this behavior to occur from time to time.

Key words: *Alouatta pigra*, *Ateles geoffroyi*, fragmentation, Lacantún River, river crossings.

RESUMEN

Durante nueve meses evaluamos si los monos araña (*Ateles geoffroyi*) y los monos aulladores (*Alouatta pigra*) tenían la capacidad para cruzar uno de los ríos más grandes de México, y si este comportamiento estaba relacionado con la deforestación y/o el tamaño de las poblaciones humanas en la margen alterada del río. Este estudio se realizó a lo largo del río Lacantún, sur de México, el cual divide la Reserva de la Biósfera Montes Azules de la región altamente deforestada de Marqués de Comillas. Con base en 428 horas de monitoreos a lo largo del río y en entrevistas a 58 residentes en cuatro comunidades de Marqués de Comillas determinamos si los monos eran capaces de cruzar el río, así como la frecuencia de estos eventos en ambas especies de monos y su dirección. Además, determinamos si este comportamiento estaba relacionado con la tasa de deforestación y/o el número de habitantes en los sitios de estudio. Solamente en dos ocasiones observamos monos araña cruzando el río, de Marqués de Comillas hacia la reserva. Sin embargo las entrevistas indicaron que pese a su rareza, este comportamiento ocurría en ambas especies y era más frecuente en los monos aulladores que en los monos araña (13 versus 8 avistamientos, respectivamente). En los puntos en que se reportaron estos eventos, el ancho del río fue menor que en otras zonas del río. Sin embargo, el número de registros de monos cruzando el río no estuvo significativamente relacionado con la tasa de deforestación ni con el tamaño de las poblaciones humanas estudiadas. Cualesquiera que sean las causas que promueven este comportamiento, es indudable que estas deben ser lo suficientemente importantes como para que de vez en cuando ambas especies de monos estén dispuestas a tomar el riesgo de cruzar el río Lacantún.

Palabras clave: *Alouatta pigra*, *Ateles geoffroyi*, capacidad para cruzar ríos, fragmentación, río Lacantún.

INTRODUCTION

Animal movements across the landscape are critical in determining gene flow and hence population and species survival (Johnson et al. 1992, Haddad et al. 2003). In a particular landscape, there are diverse physical barriers, such as large rivers (i.e., rivers > 100 m in bank-to-bank width), that can impede or limit movements and dispersal abilities in a

number of terrestrial (e.g., lizards: Lamborot & Eaton 1997, primates: Anthony et al. 2007) and volant animals (birds: Hayes & Sewlal 2004).

Although field observations of terrestrial vertebrates crossing large rivers are extremely scarce and anecdotic (e.g., deer: Miller 1930, Long 2006, elephants: Johnson 1980, proboscis monkeys: Matsuda et al. 2008), various genetic studies suggest that the ability of terrestrial vertebrates, such as primates, to cross large rivers either rafting or swimming is influenced by some ecological and morphological factors (e.g., body size, use of particular forest strata, river width). In primates this ability is related to body size (Ayres 1986), a high degree of terrestriality (i.e., the frequent use of the ground), and narrow headwater sections of the rivers (Yeager 1991, Ayres & Clutton-Brock 1992, Matsuda et al. 2008). Thus, some larger primates are capable of selecting river locations with reduced bank-to-bank width (e.g., *Nasalis larvatus*: Matsuda et al. 2008), which may reduce both the predation risk (by aquatic predators such as crocodiles) and the probability of drowning. The ability to locate narrow river sections is probably related to higher cognitive abilities and the frequent utilization of mental maps, such as found in many larger primates, including some Neotropical primates (e.g., howler and spider monkeys: Garber et al. 2009).

Since Neotropical primates are highly arboreal and hence rarely visit the ground (e.g., spider monkeys: Campbell et al. 2005), it is reasonable to expect that river crossing behavior could be negligible compared to Old World primates, which are more terrestrial (e.g., chimpanzees, gorillas: McCrossin et al. 1998, snub-nosed monkeys: Li 2007). Nevertheless, the possibility that river crossings also occur in some Neotropical primates is suggested by a number of genetic (e.g., saddle-back tamarins: Peres et al. 1996) and biogeographic studies (e.g., Amazonian primates: Ferrari 2004) in South American.

Possible proximate causes promoting river crossings in primates have been studied only in the large-bodied (10-20 kg) proboscis monkeys, indicating that river crossings are mainly related to antipredator behavior (Yeager 1991, Matsuda et al. 2008). However, no other possible explanations, such as anthropogenic pressures (e.g., deforestation and/or human population size) have been evaluated. For example, our preliminary observations along the Lacantún River, Southern Mexico, suggest the possibility that a high level of deforestation, and the consequent fragmentation along one riverbank (Marqués de Comillas region) may promote howler and spider monkeys to visit the ground and swim to the opposing undisturbed riverbank (Montes Azules Biosphere Reserve) which contains a greater abundance of key food plants for both monkey species (Chaves et al. 2010). A similar argument was suggested to explain why some African elephants swim for kilometers until arriving to some islands (see Johnson 1980).

In spite of the above, in Mesoamerica these important topics remain practically unexplored and to date there are no previous studies reporting river crossings (and its potential proximate causes) by Atelinae large-bodied primates (6.4-11.4 kg) such as the black-handed spider monkey *Ateles geoffroyi vellerosus* (Gray) or the black howler monkey *Alouatta pigra* (Lawrence) (Di Fiore & Campbell 2007). Nevertheless, a recent biogeographic study in southeastern Mexico suggests that current distributions of the black howler monkey and the closely-related mantled howler monkey (*Alouatta palliata*) are not affected by the Usumacinta river (> 100 m in width) (Baumgarten & Williamson 2007), and hence individuals of both species are likely capable of swimming (or rafting) from one side of the river to the other.

In this study we used direct observations and data from local informants, to assess for the first time, if howler and/or spider monkeys are able to cross a Mesoamerican large river such as the Lacantún River, Southern Mexico. We address five questions: (1) Can howler and/or spider monkeys move between the Marqués de Comillas region (MCR) riverbank and the Montes Azules Biosphere Reserve (MABR) riverbank? (2) Are there differences in the frequency of river crossing by the two species? (3) Is bank-to-bank river width smaller at river crossing locations compared to other regions of the river? (4) Are river crossings more common in one direction than the other? (5) Is there a

negative relationship between annual deforestation rates and/or number of inhabitants in human populations and the number of river crossings? Since howler and spider monkeys are the largest Neotropical primates (Di Fiore & Campbell 2007) and both are able to use detailed mental maps in their home ranges (Ramos-Fernández et al. 2004, Garber et al. 2009) we expect that at least some individuals of both species will be able to cross the river at narrow widths. Furthermore, since the MCR riverbank is a highly deforested region (Marquez-Rosano 2006), and both primate species are vulnerable to habitat loss, we also expect that most river crossings will occur from MCR riverbank to MABR riverbank, particularly in the case of spider monkeys because they are less tolerant than howler monkeys to human disturbances (Ramos-Fernández & Wallace 2008).

METHODS

Study area and sites

This study was carried out during a nine month period in the Lacandona rainforest located in southern Chiapas, Mexico (16°05'58" N, 90°52'36" W). The Lacantún River is the largest and widest river found in Chiapas (range: 65-155 m in width) dividing our study area in two different regions: the Montes Azules Biosphere Reserve (MABR) on the west side, and the Marqués de Comillas region (MCR) on the east side. MABR is an undisturbed 3,312 km^2 protected area (Fig. 1). Conversely, MCR is a highly disturbed area (Marquez-Rosano 2006) consisting of 25 small rural settlements, with a total population of 8,538 inhabitants (INEGI 2005). Field work focused on four settlements located along the east side of the Lacantún River: Loma Bonita, Chajul, Reforma Agraria, and Pico de Oro (Table 1; Fig. 1).

Data collection

Due to the rarity of river crossings and the challenge of tracking animals through a complex landscape (Johnson et al. 1992), we used two complementary methods: surveys along the river and semi-structured

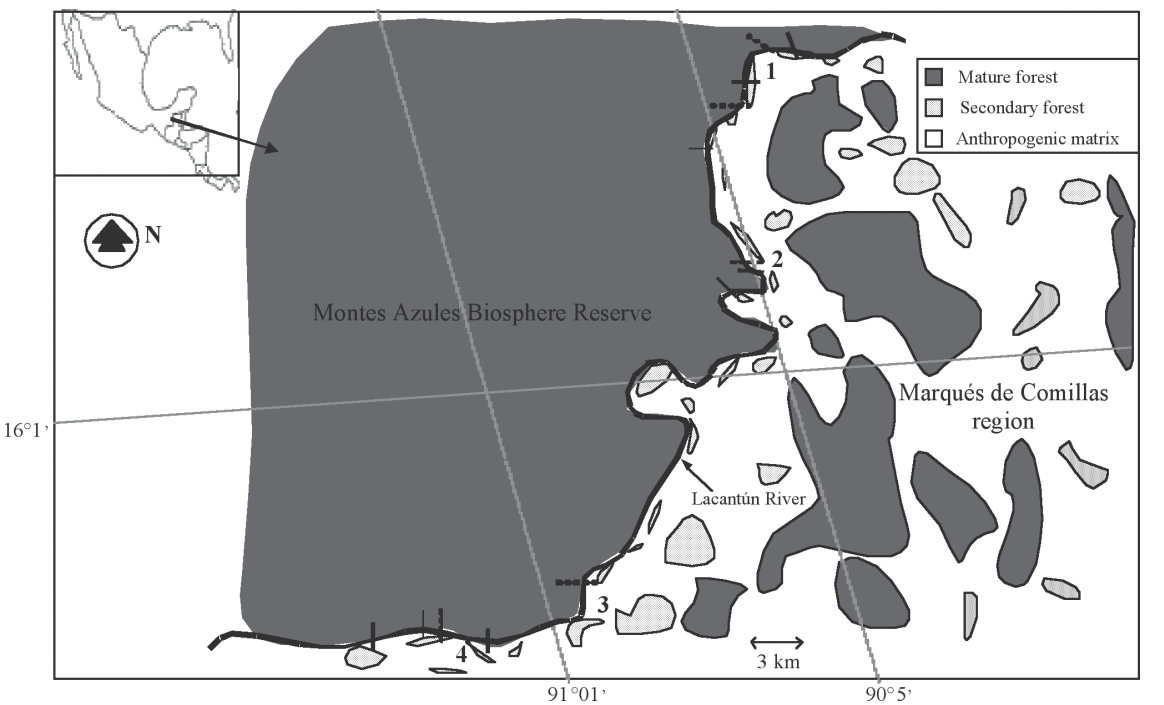

Fig. 1: Scheme of the study site showing the Lacantún River, the Montes Azules Biosphere Reserve (west side of river) and the four studied settlements of the Marqués de Comillas region (east side of river): (1) Zamora Pico de Oro, (2) Reforma Agraria, (3) Chajul, and (4) Loma Bonita. Successional status of remnant vegetation is based on recent satellite images and field samplings during 2007. Solid lines indicate river-crossing events of *A. pigra*, and dotted lines indicate river-crossing events of *A. geoffroyi*.

Esquema del sitio de estudio mostrando el río Lacantún, la Reserva de la Biósfera Montes Azules (lado oeste de río) y las cuatro comunidades estudiadas en la región de Marqués de Comillas (lado este del río): (1) Zamora Pico de Oro, (2) Reforma Agraria, (3) Chajul, y (4) Loma Bonita. El estatus sucesional de la vegetación remanente está basado en imágenes satelitales y muestreos de campo durante 2007. Los registros de monos cruzando el río están indicados con líneas continuas para *A. pigra*, y en líneas punteadas para *A. geoffroyi.*

interviews with local informants. Although data derived from questionnaires present some limitations (e.g., difficulty to asses the reliability of informants and the accuracy of the information), interviews are valuable tools in biology and have been used to study rare primate behaviors and distribution patterns (e.g., attacks on humans by chimpanzees: Hockings et al. 2009, distribution of Peruvian uakari monkeys across a major river barrier: Bowler et al. 2009).

To sample the river, two days per week (from January-March, May-October 2007) we traveled roundtrip (42 km each way) in a boat along the river between Loma Bonita and Pico de Oro searching for monkeys that were crossing or about to cross the river. To increase the probability of observing monkeys, in all surveys we traveled at a velocity of 14-20 km h^{-1}. We monitored the entire river and riverbanks (i.e., vegetation strips bordering both sides of the river) using the simple visual inspection method and binoculars with two trained observers searching different sides of the river simultaneously. Surveys consisted of 3-4 h periods and began at 700 h or 1500 h, alternating hour of initiation each week. When a sighting occurred, we observed the monkey(s) until the river crossing was successfully completed or aborted. We recorded: species, sex and age class of the individual(s), and direction of swimming (i.e., MCR to MABR or viceversa).

Semi-structured interviews were conducted with 11-19 people from each settlement between 25-65 years old. These informants were selected because they had some knowledge about the mammals of the region (i.e., they were subsistence hunters, fishermen, town elders, park rangers, landowners, and eco-tourism guides familiarized with primates and other nonvolant mammals of the region). The interview was designed to establish if participants had observed either monkey species crossing the river (i.e., if they observed monkeys swimming or rafting in the river) within their lifetime, and to record details of the frequency of sightings both within the past year and historically. We began the interview by briefly talking about monkeys and showing pictures to establish if the people could distinguish the two species from each other. Questionnaires consisted of four questions: (1) Have you seen spider or howler monkeys crossing the river? (if your answer is affirmative, describe briefly), (2) In which direction did the animal cross: from MABR bank to MCR bank, or vice versa? and (3) When and where did these river crossings occur? (if you remember, please indicate the approximate month, year and place). As an indicator of reliability of the answers provided by informants, at the end of each question we included a complementary query: Honestly, how sure are you about your answer? Please select one of the following levels of certainty: I am not sure; I am almost sure; I am absolutely certain. Overall we interviewed 72 local inhabitants, but the questionnaires from 14 of them were discarded because they were not absolutely sure about their answers. We recorded approximate location of each sighting (as reported in the questionnaires) using a GPS unit, and measured its bank-to-bank river width in five points (separated by 25 m) using a laser distance meter. Furthermore, we calculated the average width of the Lancantún River in the region by choosing randomly 40 points separated by ca. 1 km and hence we compared this bank-to-bank river width estimated from the sightings of the spider and howler monkeys. Finally, the annual deforestation rates in the studied settlements on the MCR bank were estimated using the information provided by SEMANART (Mexican Office for Environment, unpublished data) for the 2004-2007 period. The number of inhabitants in each settlement at the time of the river crossings was calculated using the population data provided by the Instituto Nacional de Estadística y Geografía, Mexico (INEGI, unpublished data).

Since in each of the four settlements we interviewed independent knowledgeable informants at different times, we assume that each one of their answers to the four questions is a replicate. For this reason, the data from the questionnaire are suitable for the statistical analyses described below.

TABLE 1

Overall characteristics of the study sites in the Marqués de Comillas region, Lacandona, Chiapas. [a]Number of houses are indicated in parenthesis. [b]Annual deforestation rate provided by SEMANART (Mexican Office for Environment, unpublished data) for 2004-2007 period. [c]Mean (± SD) bank-to-bank river width for all river crossings recorded (n = 5 in each case). [d]Number of river crossings for spider monkeys (S) and howler monkeys (H) are indicated in parenthesis.

Características generales de los sitios de estudio en la región de Marqués de Comillas, Lacandona, Chiapas. [a]El número de viviendas se indica entre paréntesis. [b]La tasa de deforestación anual fue suministrada por SEMANART (Secretaría de Medio Ambiente y Recursos Naturales de México, datos no publicados) para el periodo 2004-2007. [c]Ancho promedio (± DE) del río para todos los registros (n = 5 en cada caso). [d]El número de monos araña (S) y monos aulladores (H) que fueron reportados cruzando el río se indica entre paréntesis.

Settlement	Location	No. inhabitants[a]	ADR (ha)[b]	River width (m)[c]	No. river crossings[d]
Loma Bonita	16°05'99.8" N, 91°00'16.5" W	349 (58)	160	63 ± 6	14 (3 S, 11 H)
Chajul	16°06'39.5" N, 90°56'04.6" W	346 (68)	155	74 ± 7	8 (0 S, 8 H)
Reforma Agraria	16°15'12.2" N, 90°49'59.5" W	111 (30)	50	71 ± 11	22 (7 S, 15 H)
Pico de Oro	16°19'24.5" N, 90°50'43.7" W	1,788 (371)	380	79 ± 9	23 (6 S, 17 H)

Data analysis

To compare the reported number of river crossings between monkey species, we conducted Chi-square tests with Yates's correction for continuity in two by two contingency tables. To compare the bank-to-bank river width between the sighting locations for both species and the average width of the river, we used a generalized linear model (GLM; Crawley 2002). GLM is a statistical test that is analogous to analysis of variance (ANOVA). However, whereas in ANOVA the data must have a normal distribution and similar variances, in GLM the structure of the error distribution is analyzed by a link-function, which is related to a specific distribution function (e.g., Poisson, normal, gamma, binomial) and the analysis is not affected by heteroscedasticity (Crawley 2002). To identify which river widths in river crossing locations were statistically different from each other we used post-hoc analyses with contrasts. We conducted Chi-square tests with Yates's correction for continuity to compare direction of river crossings (MABR and MCR). To determine the effect of the annual deforestation rate and the number of inhabitants on the number of river crossings in each settlement, we used a multiple regression analysis of log-transformed data. All statistical analyses were performed using JMP software (version 8.0, SAS Institute, Cary, N.C.).

RESULTS

We observed four spider monkeys crossing the river on two different occasions during 68 river surveys (428 observation hours) traveling more than 3000 km. One adult male crossed the river from Reforma Agraria (MCR bank) to the MABR bank at the beginning of the rainy season (first week of June 2007). Three females (two adults and one sub-adult) crossed from the MABR bank to Chajul (MCR bank) during the middle of the rainy season (first week of September 2007). No howler monkeys were observed crossing during the river surveys, despite the frequent presence of howler troops along both riverbanks.

Interviews indicate that historically, similar crossing-events have been observed for howler and spider monkeys during the 1983-1987 period (six and three sightings, respectively) and during the 1996-2007 period (seven and five sightings, respectively). From a total of 58 interviewees in the four settlements, 37 (63.8 %) had never seen monkeys crossing the river, 13 (22.4 %) affirmed seeing howler monkeys crossing the river, and eight (13.8 %) reported seeing spider monkeys crossing. Bank-to-bank river width differed significantly among river locations ($X^2 = 29$; df = 4; $P < 0.0001$), being smaller in river crossing locations in each settlement (Table 1) than average width along the Lacantún River (mean ± SD: 111.6 ± 24 m; contrast tests; $P < 0.05$ in all cases). Number of river crossings was significantly higher for howlers than for spider monkeys ($X^2 = 18.3$; df = 1; $P = 0.001$; Fig. 1). We found a higher number of river crossings from MCR to MABR than in the opposite direction for both howler (68 %; $X^2 = 12$; df = 1; $P < 0.003$) and spider monkeys (77 %; $X^2 = 9$; df = 1; $P = 0.001$), and for both species most river crossings occurred during the dry season (71.2 %). However, number of river crossings was not significantly related to the annual deforestation rate ($R^2 = 0.02$; $P = 0.07$) or the number of inhabitants in each settlement ($R^2 = 0.09$; $P = 0.06$).

DISCUSSION

In concurrence with our predictions, our findings indicate that the Lacantún River does not function as an impassable barrier for movements of spider and howler monkeys between the MABR and MCR riverbanks. We found that river crossings were extremely rare, only being observed in four adult spider monkeys during the study. Nevertheless, interviews indicate that historically river crossings have been observed for both species on various occasions (Table 1). These differences between survey results and questionnaire results likely occur because nine months is a very short study period to record these rare events. It is also likely that we underestimated the number of river crossings in both species because sampling cannot be ubiquitous and at all times. In spite of this, our observations demonstrate for the first time that spider monkeys can and do swim across large rivers. In concordance with our findings, other studies have concluded that rivers do not impose impassable barriers for large-bodied primates (Ferrari 2004, Aguiar et al. 2007). For example, in Malaysia, river crossings are frequently observed in proboscis monkeys (*Nasalis larvatus*) (Yeager 1991, Matsuda et al. 2008). Similarly, based on historical biogeography analyses, Goldani et al. (2006) found that Amazonian rivers are not significant barriers for dispersal for many primate species including *Ateles chamek* and *Alouatta* spp.

As we predicted, bank-to-bank river width was smaller at river crossing locations than along the river in general. This same phenomenon has been reported in other primates of Malaysia (Matsuda et al. 2008) and South America (Ayres & Clutton-Brock 1992). For instance, in a biogeographic study in South America, Ayres and Clutton-Brock (1992) have shown that populations of *Ateles* spp. and other primates may be separated at the mouth of a major river but are not separated at its headwaters because: (1) at the mouth of the river, fast flow rates reduce the ability of primates to cross the river, in comparison to the relatively slow flow present at the headwaters, and (2) at the mouth of the river, meanders increase the overall width of the river. In addition, Matsuda et al. (2008) indicate that in proboscis monkeys selection of narrow river locations reduces the predation risk by aquatic predators such as crocodiles. Unfortunately, we cannot establish if this phenomenon occurs at our study site, because crocodiles populations and distributions along the Lacantún River are unknown (Procuraduría Federal de Protección al Medio Ambiente, Mexico, personal communication 2009).

Although we did not observe river crossings in howler monkeys, interviews suggested crossings were more frequent in howler than in spider monkeys (Table 1, Fig. 1). We suggest that this phenomenon is likely explained by the greater ability of howler monkeys for swimming (Goldani et al. 2006) and their greater abundance and distribution in the region compared to spider monkeys. Along the Lacantún River on the MABR side and in one large fragment on the MCR side Estrada et al. (2004) found that howler monkeys are consistently more abundant (14.4 and 13.3 individuals km^{-2}, respectively) than spider monkeys (2.9 and 9.3 individuals km^{-2}, respectively). Populations of spider monkeys on the MCR side are restricted to a few of the medium and larger (30-1475 ha) private forest fragments found in the region.

Evidence suggests that, irregardless of the ecological motivation, river crossings in some primates may be facilitated by river dynamics (e.g., reduction of water level: Goldani et al. 2006). This may explain, at least in part, the observation that in this study most reported events of monkeys crossing the Lacantún River occurred during the dry season, the time of the year with minimal water flow. During the dry season the water level and the stream velocity of the Lacantún River can be reduced by more than 50 %, and in some areas the river is only 1 m deep or less (Comisión Federal de Electricidad, Mexico, personal communication 2008). Furthermore, we suggest that the finding that most river crossings occurred from the MCR bank to the MABR bank may be related to both the seasonal changes in plant phenology and the differential food availability along each riverbank. Fruits and young leaves are the most important plant items in the diet of spider (González-Zamora et al. 2009) and howler monkeys (Pavelka & Knopff 2004), and in Neotropical forests both items are often more scarce during the dry season than in the rainy season (Zimmerman et al. 2007). Furthermore, food availability for monkeys is lower in the MCR disturbed region than in MABR (Chaves et al. 2010). Based on these facts we suggest that food scarcity likely promotes river crossings from the MCR bank to the MABR bank.

We found no relationship between river crossings and deforestation or population size in each settlement and hence it is necessary to study other alternative explanations (see above). The antipredator value of river crossing behavior in spider and howler monkeys was not evaluated in our study because of the methodological and logistical complications of recording predation events. However, in other Neotropical forests there are records of predation of howler and spider monkeys by jaguars (*Panthera onca*) and pumas (*Puma concolor*) (reviewed by Ferrari 2009), suggesting that this possibility needs to be systematically studied in Lacandona. Whatever the underlying pressures that drive river-crossing events in these two primate species in this region, they appear to be sufficiently strong to stimulate this behavior to occur over time. Our results are preliminary and should be taken with caution because there are some important limitations including a low number of direct observations of river crossings, a short study period, a low number of settlements sampled, and limitations in evaluating the reliability of local informants. Further long-term studies analyzing how river crossings and gene flow are affected by

different ecological factors (e.g., monkey population density, seasonality, predation, food availability) and anthropogenic pressures, such as deforestation and hunting, are crucial to improve our understanding of factors driving river crossing behavior in both howler and spider monkeys (and other Neotropical primates). We suggest that semi-structured interviews with local inhabitants, and direct field observations (complemented with genetic techniques if possible) may be useful tools to achieve this goal.

ACKNOWLEDGMENTS

This research was supported by grants from the Consejo Nacional de Ciencia y Tecnología, Mexico (CONACyT Grant CB2005-C01-51043 and CB2006-56799). This study would not have been possible without the collaboration of the local people in Loma Bonita, Chajul, Reforma Agraria, and Pico de Oro. We thank A. Jamangapé and R. Lombera for providing logistic support during the monitoring of the Lacantún River. We thank C. Chapman for reviewing early and advanced drafts of this paper and for providing useful comments and suggestions. We are grateful for technical support provided by J. M. Lobato García, G. Sánchez Montoya, and H. Ferreira. We also thank one anonymous reviewer for valuable criticism and suggestions that improved the manuscript.

LITERATURE CITED

AGUIAR LM, G LUDWIG, WK SVOBODA, CLS HILST, IT NAVARRO & FC PASSOS (2007) Occurrence, local extinction and conservation of Primates in the corridor of the Upper Parana River, with notes on other mammals. Revista Brasileira de Zoologia 24: 898-906.

ANTHONY NM, M JOHNSON-BAWE, K JEFFERY, SL CLIFFORD, KA ABERNETHY et al. (2007) The role of Pleistocene refugia and rivers in shaping gorilla genetic diversity in central Africa. Proceedings of the National Academy of Sciences USA 104: 20432-20436.

AYRES JM & TH CLUTTON-BROCK (1992) River boundaries and species range size in Amazonian primates. American Naturalist 140: 531-537.

AYRES JM (1986) Uakaries and Amazonian flooded forests. Cambridge University, Cambridge, UK.

BAUMGARTEN A & GB WILLIAMSON (2007) The distributions of howling monkeys (*Alouatta pigra* and *A. palliata*) in southeastern Mexico and Central America. Primates 48: 310-315.

BOWLER M, JN MURRIETA, M RECHARTE, P PUERTAS, R BODMER (2009) Peruvian red uakari monkeys (*Cacajao calvus ucayalii*) in the Pacaya-Samiria National Reserve: A range extension across a major river barrier. Neotropical Primates 16: 34-37.

CAMPBELL CJ, F AURELI, CA CHAPMAN, G RAMOS-FERNÁNDEZ, K MATTHEWS, SE RUSSO, S SUAREZ & L VICK (2005) Terrestrial behavior of *Ateles* spp. International Journal of Primatology 26: 1039-1051.

CHAVES OM, KE STONER & V ARROYO-RODRÍGUEZ (in press) Differences in diet between spider monkey groups living in forest fragments and continuous forest in Lacandona, Mexico. Biotropica.

CRAWLEY M (2002) Statistical computing: An introduction to data analysis using S-Plus. John Wiley & Sons, Chichester, England.

DI FIORE A & CJ CAMPBELL (2007) The Atelines: Variation in ecology, behavior, and social organization. In: Campbell C, A Fuentes, KC Mackinnon, M Panger & S Bearder (eds) Primates in perspective: 155-185. Oxford University Press, Oxford, UK.

ESTRADA A, S VAN BELLE & Y GARCÍA-DEL VALLE (2004) Survey of black howler (*Alouatta pigra)* and spider (*Ateles geoffroyi*) monkeys along the Río Lacantún, Chiapas, Mexico. Neotropical Primates 12: 70-75.

FERRARI SF (2004) Biogeography of Amazonian primates. In: Mendes SL & AG Chiarello (eds) A Primatologia no Brasil: 101-122. IPEMA/SBPr, Vitória, Brasil.

FERRARI SF (2009) Predation risk and antipredator strategies. In: Garber PA, A Estrada, JC Bicca-Marques, EW Heymann & K Strier (eds) South American primates: Comparative perspectives in the study of behavior, ecology, and conservation: 251-275. Springer Press, New York, NY.

GARBER PA, JC BICCA-MARQUES & MA AZEVEDO-LOPES (2009) Primate cognition: Integrating social and ecological information in decision-making. In: Garber PA, A Estrada, JC Bicca-Marques, EW Heymann & K Strier (eds) South American primates: Comparative perspectives in the study of behavior, ecology, and conservation: 365-385. Springer Press, New York.

GOLDANI A, GS CARVALHO & JC BICCA-MARQUÉS (2006) Distribution patterns of Neotropical primates (Platyrrhini) based on parsimony analysis of endemicity. Brazilian Journal of Biology 66: 61-74.

GONZÁLEZ-ZAMORA A, V ARROYO-RODRÍGUEZ, OM CHAVES, S SÁNCHEZ-LÓPEZ, KE STONER & P RIBA-HERNÁNDEZ (2009) Diet of spider monkeys (*Ateles geoffroyi*) in Mesoamerica: Current knowledge and future directions. American Journal of Primatology 71: 8-20.

HADDAD NM, DR BOWNE, A CUNNINGHAM, BJ DANIELSON, DJ LEVEY, S SARGENT & T SPIRA (2003) Corridor use by diverse taxa. Ecology 84: 609-615.

HAYES FE & JN SEWLAL (2004) The Amazon River as a dispersal barrier to passerine birds: Effects of river width, habitat and taxonomy. Journal of Biogeography 31: 1809-1818.

HOCKINGS KJ, G YAMAKOSHI, A KABASAWA & T MATSUZAWA (2009) Attacks on local persons by chimpanzees in Bossou, Republic of Guinea: Long-term perspectives. American Journal of Primatology 71: 1-10.

INEGI (2005) II Conteo de población y vivienda 2005. Instituto Nacional de Estadística y Geografía, México DF.

JOHNSON AR, JA WIENS, BT MILNE & TO CRIST (1992) Animal movements and population

dynamics in heterogeneous landscapes. Landscape Ecology 7: 63-75.
JOHNSON DL (1980) Problems in the land vertebrate zoogeography of certain islands and the swimming powers of elephants. Journal of Biogeography 7: 383-398.
LAMBOROT M & L EATON (1997) The Maipo River as a biogeographical barrier to *Liolaemus monticola* (Tropiduridae) in the mountain ranges of central Chile. Journal of Zoological Systematics and Evolutionary Research 35: 105-111.
LI Y (2007) Terrestriality and tree stratum use in a group of Sichuan snub-nosed monkeys. Primates 48: 197-207.
LONG ES (2006) Landscape and demographic influences on dispersal of white-tailed deer. Ph.D. Thesis, Pennsylvania State University, Pennsylvania.
MARQUEZ-ROSANO C (2006) Environmental policy and dynamics of territorial appropriation: The tensions between the conservation of tropical forests and the expansion of cattle ranching in the Mexican tropics. URL: http://iasc2008.glos.ac.uk/conference%20papers/papers/M/Marquez-Rosano_110701.pdf (accessed January 20, 2010).
MATSUDA I, A TUUGA, Y AKIYAMA & S HIGASHI (2008) Selection of river crossing location and sleeping site by proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysia. American Journal of Primatology 70: 1097-1101.
MCCROSSIN ML, BR BENEFIT, SR GITAU, A PALMER & K BLUE (1998) Fossil evidence for the origins of terrestriality among Old World monkeys and apes. In: Strasser E, JG Fleagle, HM Mchenry & AL Rosenberger (eds) Primate locomotion: Recent advances: 353-376. Plenum, New York.
MILLER FW (1930) Notes on some mammals of Southern Matto Grosso, Brazil. Journal of Mammalogy 11: 10-22.
PAVELKA MS & KH KNOPFF (2004) Diet and activity in black howler monkeys (*Alouatta pigra*) in southern Belize: Does degree of frugivory influence activity level? Primates 45: 105-111.
PERES CA, JL PATTON & MNF DA SILVA (1996) Riverine barriers and gene flow in Amazonian saddle-back tamarins. Folia Primatologica 67: 113-124.
RAMOS-FERNÁNDEZ G, JL MATEOS, O MIRAMONTES, G COCHO, H LARRALDE & B AYALA-OROZCO (2004) Levy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*). Behavioral Ecology and Sociobiology 55: 223-230.
RAMOS-FERNÁNDEZ G & RB WALLACE (2008) Spider monkey conservation in the twenty-first century: Recognizing risks and opportunities. In: Campbell CJ (ed) Spider monkeys: Behavior, ecology and evolution of the genus *Ateles*: 351-376. Cambridge University Press, New York.
YEAGER CP (1991) Possible antipredator behavior associated with river crossings by proboscis monkeys (*Nasalis larvatus*). American Journal of Primatology 24: 61-66.
ZIMMERMAN JK, SJ WRIGHT, O CALDERON, MA PAGAN & S PATON (2007) Flowering and fruiting phenologies of seasonal and aseasonal Neotropical forests: The role of annual changes in irradiance. Journal of Tropical Ecology 23: 231-251.

Associate Editor: Juan Carlos Torres-Mura
Received September 23, 2009; accepted June 25, 2010