

# A Primatologia no Brasil

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# **A PRIMATOLOGIA NO BRASIL**

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**BLACK HOWLERS' (*Alouatta pigra*) SOCIAL BEHAVIOR:  
A DESCRIPTION OF SOCIAL INTERACTIONS AMONG  
ADULTS AND AN ANALYSIS OF REPERTOIRE  
COMPLETENESS**

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**ABSTRACT**

The description of the behavioral repertoire of a species is basic to the study of animal behavior, as this information can help understanding proximate and ultimate aspects of behavior. The aim of our study was to describe the social interactions repertoire of adult black howlers and to analyze its completeness. We studied four groups that lived in different locations in Campeche, Mexico. We used the behavioral sampling method to record the social interactions of adults. In addition to describing the social interactions, we analyzed similarities between groups in the expression of behaviors with the Sorensen's coefficient. We assessed repertoire completeness through a modification of the accumulation curves methodology, which is generally employed to study biodiversity. We observed 39 interactions during 480h of observations, and mostly were affiliative. Although only eight interactions were observed in all groups, similarity levels

indicate that a medium-to-high proportion of acts were shared. We found that repertoire completeness increased with increasing sampling effort and that a satisfactory proportion of the repertoire was observed. We conclude that the repertoire described in this paper is representative of black howlers' social interactions, and can be useful for future studies. Additionally, we propose that the methods used to analyze the repertoire are valuable to assess within and between-repertoire completeness and efficacy.

## INTRODUCTION

A fundamental stage in the study of animal behavior is the description of the behavioral patterns displayed by a species. When the descriptions are exhaustive and all possible behavioral acts have been observed, this information can be gathered in an ethogram (Martin & Bateson, 1993). Allied with field observations, ethograms allow analyzing the biological, ecological and evolutionary contexts of behavior (Lehner, 1979). At the present, the ethograms of a wide range of species have been described, from invertebrates (e.g. *Ilhaia cuspidata*: Pereira *et al.*, 2004), to reptiles (e.g., *Sceloporus cyanogenys*: Greenberg, 1977), birds (e.g. *Ardeotis kori*: Lichtenberg & Hallager, 2007), and mammals (Muñoz-Romo, 2006).

Most frequently researchers focus on specific behavioral subsamples, usually labeled as catalogues or repertoires. Such is the case of primate studies that have described sexual behavior (e.g. *Cebus apella*: Carosi & Visalberghi, 2002), positional behavior (e.g. *Cacajao calvus*: Walker & Ayres, 1996), or social behavior (e.g. *Macaca thibetana*: Zhao, 1997).

Although the genus *Alouatta* is one of the most thoroughly studied primate *taxa* in the Neotropics, there are currently only a few descriptions of their social interactions; most come from classical studies on mantled howlers (*Alouatta palliata*: Altmann, 1959; Bernstein, 1964; Carpenter, 1934, 1965; *Alouatta caraya*: Albuquerque & Codenotti, 2006). Additionally, some particular behavioral patterns have been reported in other studies, such as playing (*A. palliata*: Baldwin & Baldwin, 1978), ritual behaviors (*A. palliata*: Glander,

1980; Jones, 1980), grooming (*A. guariba*: Oliveira & Ades, 1998; *A. palliata*: Jones, 1979; *A. pigra*: Brockett *et al.*, 2000; *A. seniculus*: Neville, 1972; Sánchez-Villagra *et al.*, 1998), threats (*A. palliata*: Jones, 2005), gestural communication (*A. pigra*: Brockett *et al.*, 2005), and sexual behavior (*A. palliata*: Córtes-Ortiz & Morales, 1996).

Currently, there are only a few descriptions of the social interactions of black howlers (*Alouatta pigra*), an endangered species endemic to the Mesoamerican region (Cuarón *et al.*, 2003). Therefore, the aim of the present study was to describe the social interactions repertoire of adult black howlers based on the observation of four free-ranging groups in Campeche, Mexico.

There are multiple factors that may limit or bias the observation of animal behavior, and as a result, decrease the completeness of the repertoires. Among these, sampling decisions are particularly important, as the inclusion or exclusion of subjects and groups, or changes in the amount of time dedicated to observations, will usually affect the quality of the repertoire. In species with a high diversity of behavioral acts, as most primates (Fagen & Goldman, 1977), a compromise must be reached between the sampling effort and the exhaustiveness of the catalogues. We therefore tested the quality of the social behavior repertoire that was defined in the present study. Based on methods developed to study biodiversity, we analyzed the completeness of the repertoire by estimating the proportion of behavioral acts that were actually observed, and by calculating the sampling effort required to describe a hypothetically complete behavioral repertoire of this species.

## MATERIAL AND METHODS

### *STUDY SITE AND SUBJECTS*

The state of Campeche is located in southeastern Mexico, in the Yucatan peninsula. The climate is warm and wet, with a mean annual temperature of 24.1°C and annual rainfall ranging from 900 to 2,000mm. According to the precipitation levels, two seasons are distinguished, a wet season from June to October, and a dry season from November to May (Vidal-Zepeda, 2005).

The first study group occupied a forest fragment with approximately 96ha (2080995 N, 712630 W; zone 15 UTM); the vegetation at this site was mainly medium semi-deciduous forest. This fragment was situated inside a forestry ranch named 'El Álamo' and it was undisturbed for more than five years. The population density was approximately 52ind/km<sup>2</sup>, and in addition to several other howler groups, there was also a resident group of spider monkeys (*Ateles geoffroyi yucatanensis*). This group (El Álamo hereafter) included one adult male, two adult females, and one male infant (born at the beginning of the observations). Observations at El Álamo were made during November and December 2005.

The second group lived inside the southern core area of the Calakmul Biosphere Reserve (ca. 150000ha). At this study site (2027515 N, 198000 W; zone 16 UTM) the vegetation was medium and tall semi-deciduous forest. Population density was 15.2ind/km<sup>2</sup> (Estrada *et al.*, 2004), and at this site spider monkeys were also regularly observed. The study group (Calakmul hereafter) was composed by three adult males, two adult females, and four infants, two females and two males (two of which were born during the study). Data were collected during January and February 2006, and during this period no other groups were seen or heard in the area.

The third study group was observed near the Nuevo Ontáριο settlement (2090933 N, 722414 W; zone 15 UTM). This was an extremely disturbed area, where the few remaining trees were scattered throughout plantations of maize and jalapeño chili pepper; as tree crowns were not connected, howlers had to go down to the ground to move from one tree to another. Due to the described landscape characteristics, it was not possible to calculate neither population density nor area; two other black howler groups were seen at this site. The group (El Chilar hereafter) included two adult males, three adult females, two juvenile females, and one juvenile male. In this group we collected data in April and May 2006.

Finally, the fourth group occupied a forest fragment in the vicinity of the Ejido Chicbul (2077858 N, 717331 zone 15 UTM). The main types of vegetation at this 4ha fragment were low and medium semi-deciduous forest. Our study group (Chicbul hereafter) was the

only resident group (population density of 150ind/km<sup>2</sup>), and comprised one adult male, two adult females, one juvenile male, and two infants (one female and one male). Observations were made in November and December 2006.

### *BEHAVIORAL OBSERVATIONS*

To define the behavioral sampling protocol we developed a preliminary repertoire based on unpublished descriptions of mantled howlers' social behavior (Dias, 2002, 2007). We then used this repertoire to identify behavioral acts in several black howler groups through *ad libitum* sampling (Altmann, 1974), during a total of 120h of preliminary observations. As social interactions are infrequent in howlers, we selected the behavioral sampling method with a continuous recording technique (Martin & Bateson, 1993). To increase the probability of observing different behavioral acts, and therefore describe a representative catalogue, we studied groups with different sizes and compositions that lived in different habitat conditions.

For each group, after a preliminary period (ca. 36hrs) of observations aimed at recognizing each individual, A.R.N. systematically recorded all social interactions (as events) in which adult group members were involved. All individuals were easily identified by their natural markings (body size, scars, broken fingers, and genital and facial features). During sampling periods each observed interaction was described. We observed each group for 30 days and a total of 120h, during which observations were divided into morning (7:00h to 12:00h) and afternoon (12:00h to 17:00h) schedules.

## **DATA ANALYSIS**

### *REPERTOIRE DESCRIPTION*

We classified social interactions into three categories: affiliation, agonism, and sexual behaviors. In the repertoire presented in Results, each behavior is described as a structural unit, i.e., considering the body movements exhibited by actors and receivers. As the observation of sexual interactions depends on the reproductive status of females, these were not included in the analyses of similarities between groups



and repertoire completeness.

As gross measures of behavioral diversity (richness), we calculated the total number of observed behavioral acts (i.e., types of social interactions, which were operationally defined as the way the behavior of one individual was affected by the presence or behavior of another, excluding vocalizations; Whitehead, 2008), the total number of acts per category, and the number of acts per group. To study between-group variations in the expression of behavioral acts, we performed a cluster analysis using the Sorensen's coefficient:  $S=2C/(2C+A+B)$ ; where  $A$  is the number of behavioral acts observed in group  $A$  but not in group  $B$ ,  $B$  the number of acts observed in group  $B$  but not in group  $A$ , and  $C$  is the number of acts observed in both groups. The Sorensen coefficient is particularly indicated for comparisons of richness between sampling units with high similarity (Krebs, 1999). Such is the expected trend for behavioral repertoires.

#### *ANALYSIS OF REPERTOIRE COMPLETENESS*

Fagen & Goldman (1977) and Fagen (1978) have proposed a method for analyzing completeness of behavioral catalogues based on a lognormal Poisson distribution fitting. However, in addition to its computational complexity, this method fails to estimate repertoire size when it is composed by many rare behaviors (Fagen & Goldman, 1977). Such is the expected trend for howlers' social interactions, as it has been frequently stated that in this genus social interactions are infrequent (e.g. Crockett & Eisenberg, 1987). Therefore, we followed a different methodology to analyze repertoire completeness.

Flora and fauna inventories have been frequently analyzed through the construction of species accumulation curves (or collector's curves), where some measure of sampling effort is plotted against the cumulative number of species observed (Colwell & Coddington, 1994; Gotelli & Colwell, 2001). Effort can be measured as the number of individuals observed, samples, traps, or some other assessment of area or time (Colwell & Coddington, 1994; Moreno & Halffter, 2000; Soberón & Llorente, 1993). In species accumulation models the curves reach an asymptote when the probability of observing new species approaches zero (Soberón & Llorente, 1993), allowing

therefore assessing repertoire completeness (For full descriptions of this methodology see: Colwell, 2000; Colwell & Coddington, 1994; Gotelli & Colwell, 2001; Moreno & Halffter, 2000; Soberón & Llorente, 1993).

In the case of black howlers' social interactions repertoire, the observation of new behavioral acts can be represented as a function of the number of sampling hours. Specifically, we expected that the addition of new behavioral acts to the repertoire would decrease as the number of observation hours and groups increased. Thus, repertoire completeness was analyzed by adding new groups, and consequently, sampling effort, to the sample successively.

To project the behavior accumulation curves we first transformed observation periods into 1-h samples, and identified the number of acts observed in each sample. These data were then gathered in matrices, where the rows represented the behavioral acts (scored as 1 for presence and 0 for absence) and the columns the 1-h sampling periods. We prepared four matrices, each corresponding to the total number of samples at the end of each sampled group (i.e., 120, 240, 360, and 480 1-h samples). We analyzed these matrices with the EstimateS software (after 100 randomizations; Colwell, 2000) to calculate the mean number of new behavioral acts for each 1-h sample (*Sobs*) accumulated up to the total sample size (Gray, 2002).

To describe the curves we then applied the Clench equation to the *Sobs*:  $S(t)=at/(1+bt)$  ; where  $S(t)$  is the predicted number of species at  $t$ ,  $t$  is a measure of effort (in this study the number of 1-h samples),  $a$  is the rate of increase at the beginning of sampling, and  $b$  represents the accumulation of behavioral acts. This model is particularly appropriate when the probability of adding new acts to the repertoire increases with increasing sampling effort (Soberón & Llorente, 1993), as is expected in the case of primate interactions.

We adjusted this function to the *Sobs* using a non-linear estimation method with the Simplex & Quasi-Newton algorithm (StatSoft Inc, 2001). From these tests we obtained a value for the fitting of the model to the observed data ( $R^2$ ), as well as the  $a$  and  $b$  parameters; the later were used to study repertoire completeness. First, we calculated the asymptote of the curves; i.e., the predicted number

of behavioral acts, as  $a/b$ . Second, we calculated the proportion of observed behavioral acts:  $P_{Sobs} = T_{Sobs} / (a/b)$ ; where  $P_{Sobs}$  is the proportion of observed behaviors, and  $T_{Sobs}$  is the total number of observed behaviors. Finally, as we approach the total number of behaviors in the repertoire the effort required to register a new act will be increasingly higher; therefore, by definition an infinite effort would be necessary to observe 100% of the behaviors. We selected 90% of the total behaviors as a conservative level for repertoire completeness (Moreno & Halfpter, 2000), and estimated the sampling effort required to observe this proportion of the complete repertoire:  $t_{0.90} = 0.90 / [b * (1 - 0.90)]$ . We used the first two measures to assess repertoire completeness, and the third to discuss research planning.

## RESULTS

### *BLACK HOWLERS' SOCIAL INTERACTIONS REPERTOIRE, REPERTOIRE DIVERSITY AND SIMILARITIES BETWEEN GROUPS*

During the 480-h of observations we recorded 39 different interactions between adult black howlers (Table 1), 29 of which occurred in non-sexual contexts. The majority of behavioral acts were affiliative (51.3%), followed by sexual (25.6%) and agonistic interactions (23.1%). With the exception of mounting, which was observed once in El Álamo, all sexual interactions occurred in the El Chilar group.

The number of non-sexual behavioral acts observed in the four groups was very similar: 18 interactions in El Álamo; 19 interactions in Calakmul; 18 interactions in El Chilar; 17 interactions in Chicbul. Comparing the interactions observed across the four groups, the average ( $\pm$ SD.) Sorensen's similarity coefficient was  $0.67 \pm 0.04$  (range = 0.61–0.74). These results indicate that a medium-to-high proportion of interactions were common to the groups (>60%), and that in the pair-wise comparisons the variation among groups was low. The greatest similarities were between Chicbul and El Álamo, whereas the lowest were between Calakmul and Chicbul (Figure 1).

**Table 1.** Black Howlers' social interactions repertoire with descriptions of the behavioral acts recorded and number of groups that displayed the behavioral act.

	#	Behavioral act	Description*	Groups
	1	Embracing	A stretches one or both arms towards R and surrounds its body. This behavior may be reciprocal.	2
	2	Tail embracing	A moves its tail towards R's body and surrounds some part of it. Always longer than 5-s.	3
	3	Grooming solicitation	A approaches R, presents its truck, broadside, or another body part and repeatedly looks at R. This solicitation may or may not be responded.	2
	4	Grooming	A touches R's body, and slowly and gently picks through its fur with both hands.	4
	5	Mutual grooming	A and R participates as both actors and receivers of grooming.	1
	6	Scratching	A repeatedly moves one of its hands on some part of R's body; while performing this behavior, A sometimes looks away from the scratched area.	2
	7	Finger stroking	Both A and R extend one of their hands until contact is established; both begin to slowly tickle each others' fingers while staring at the hands. Always longer than 5-s.	3
Affiliative	8	Hand-holding	A extends one or two hands towards R and grasps one of its hands (Brockett <i>et al.</i> , 2005). Always longer than 5-s.	4
	9	Play face	While facing R, A performs rapid and repetitive head movements from side to side and exposes its teeth.	1
	10	Playing solicitation	A stretches repeatedly and rapidly one or more extremities towards R; it may include jumping, touching, and/or play face. Solicitations may be responded or ignored.	1
	11	Playing	A and R perform rapid movements directed at each other that may include touching, pulling and pushing, biting, and/or chasing.	2
	12	Contact	A approaches R, and some part of its body touches R's body. Always longer than 5-s	4
	13	Chest contact	A approaches R and presses its chest against R's chest. Always shorter than 5-s.	1
	14	Smelling	A brings its nose close to some R's body part (excluding genitals) without touching it and smells it.	4
	15	Foot touching	A touches R with one of its feet; we have observed foot touching towards the face and the shoulder of receptors. Always shorter than 5-s.	2
	16	Head touching	A and R touch each others' forehead. Always shorter than 5-s.	2
	17	Hand touching	A touches R with one or both of its hands; we have observed hand touching towards the arms, armpits, back, face, feet, genitals, hands, head, mouth, neck, shoulders, and tail of receptors. Always shorter than 5-s.	4
	18	Mouth touching	A touches R with its mouth (excluding genitals); we have observed mouth touching towards the arms, back, chest, face, hands, and mouth of receptors. Always shorter than 5-s.	4

\* A is actor, R is receiver.

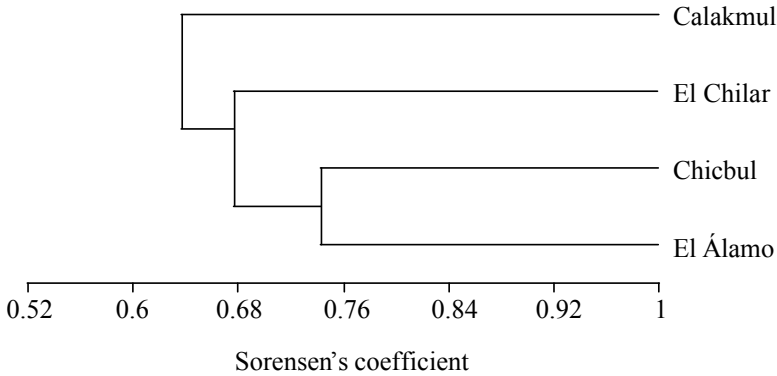
Behavioral repertoire completeness of *Alouatta pigra*

	#	Behavioral act	Description*	Groups
Affiliative	19	Tail touching	A touches R with its tail; we have observed tail touching towards the back, hands, head, and tail of receptors. This contact is always shorter than 5-s.	3
	20	Tongue touching	A touches R with its tongue; we have observed tongue touching towards the armpits and face of receptors. Always shorter than 5-s.	1
Agonistic	21	Chasing	A runs towards R, while the later flees.	2
	22	Running toward	A runs towards the place occupied by R. As a response R may flee, retreat, or ignore A's approach.	1
	23	Approach- retreat	Without displaying threatening behaviors, A approaches the area where R is standing and the later abandons it.	4
	24	Supplanting	Without displaying threatening behaviors, A approaches the area where R is standing and the later abandons it; A then occupies the area where R was before.	3
	25	Avoiding	A repeatedly moves away from R although the later does not seem to display any behaviors. This behavior is usually preceded by or accompanied by brief rapid glances from A to R.	4
	26	Fleeing	In response to A's agonistic behaviors (usually chasing, running toward, or slapping), R quickly moves away.	2
	27	Submissive position	As a response to A's agonistic behaviors (displacing or slapping), R lowers its shoulders and back approaching its body to the surface where it stands. This act sometimes includes a facial expression where R opens widely its mouth and eyes, and produces low tone vocalizations.	3
	28	Slapping	A hits some part of R's body with one or both hands; A's hand are usually opened.	2
	29	Fighting	A and R quickly bite, push, pull, and slap each other.	1
Sexual	30	Tongue-flicking	Facing R, A sticks its tongue out and in repeatedly.	1
	31	Sexual presentation	A approaches R, turns around, and directs its anogenital area to R's face with its tail raised. This behavior is frequently combined with tongue-flicking.	1
	32	Genital smelling	A brings its nose close to R's genitals, without touching it, and smells it.	1
	33	Mutual tongue touching	A and R touch each others' tongues.	1
	34	Tongue-vulva touching	A touches R's vulva with its tongue.	1
	35	Copulation solicitation	A repeatedly displays tongue flicking and genital presentations in front of R; this behavior may also include genital smelling, hand touching, mouth touching, or tongue touching.	1
	36	Mounting	A lays above R's body, either in a dorso-ventral or ventro-ventral position.	1

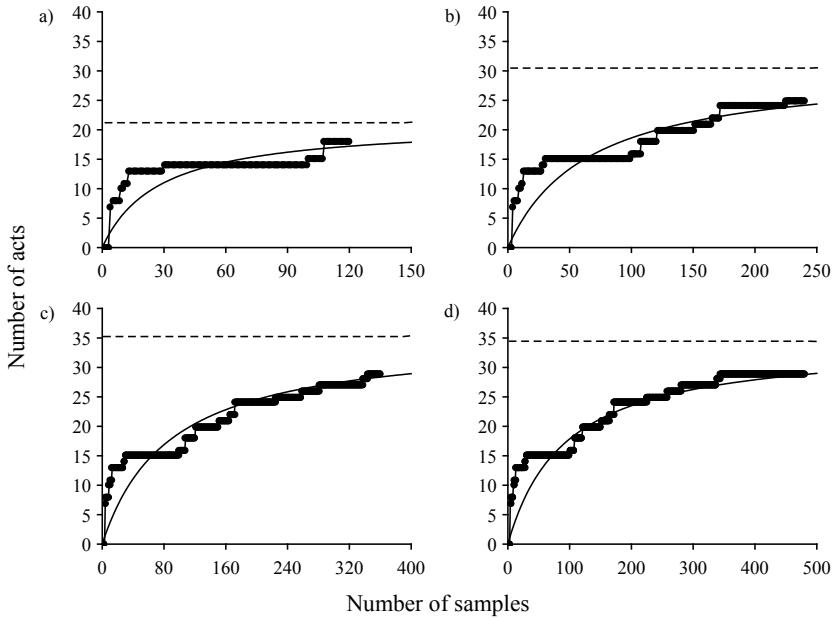
\* A is actor, R is receiver.

	#	Behavioral act	Description*	Groups
Sexual	37	Incomplete copulation	A mounts R in a dorso-ventral position, and intromission and thrusting occur. No ejaculation occurs, as inferred by the absence of ejaculatory pauses, reductions in the rhythm of thrusts, and fresh semen in the female's genitals.	1
	38	Complete copulation	A mounts R in a dorso-ventral position, and intromission and thrusting occur. Ejaculation occurs, as inferred by the observation of ejaculatory pauses, reductions in the rhythm of thrusts, and fresh semen in the female's genitals.	1
	39	Complaining	After R ignoring a copulation solicitation, A pulls on R's hand while producing high tone vocalizations; this interaction ends with A's retreating.	1

\* A is actor, R is receiver.



**Figure 1.** Cluster analysis of the behaviors displayed by the four groups. Grouping based on the Sorensen's similarity index values calculated from the pair-wise comparisons between groups.



**Figure 2.** The number of observed behavioral acts as a function of the sampling effort: a) 120 1-h samples; b) 240 1-h samples; c) 360 1-h samples; d) 480 1-h samples. ● = observed data; — = fitted data with the Clench model; --- = total number of behaviors predicted by the asymptotes of the curves.

**Table 2.** Number of behavioral acts recorded, and parameters and predictions of the Clench accumulation curve model as a function of variations in sampling effort.

N° of samples	N° acts	<i>a</i>	<i>B</i>	<i>a/b</i> *	<i>R</i> <sup>2</sup>	% of the asymptote †	Sampling effort to 90% ‡
120	18	0.7645	0.03609	21.18	0.98	85.0	249.48
240	25	0.4729	0.01541	30.69	0.98	81.5	584.04
360	29	0.4051	0.01150	35.23	0.99	82.3	782.61
480	29	0.3720	0.01083	34.35	0.99	84.5	831.02

\* Expected number of behavioral acts.

Only eight interactions were shared by the four groups: contact, grooming, hand-holding, hand and mouth touching, smelling, avoiding, and approach- retreat; excluding sexual behaviors, seven interactions occurred in only one group: play face, tongue touching, fighting, playing solicitation, mutual grooming, chest contact and running toward.

### REPERTOIRE COMPLETENESS

To study variations in repertoire completeness according to increases in sampling effort, we projected four behavior accumulation curves, each corresponding to the addition of a new group and to a 120h increase in observation time (Figure 2). The Clench accumulation model fitted adequately the behavioral data for the four curves ( $R^2 \geq 0.98$ ).

Although all curves of observed data stabilized towards the end of sampling, they failed to reach the predicted asymptotic number of behavioral acts (Table 2). With 120h of observations the repertoire almost reached the 90% threshold for completeness, as 85% of the predicted behaviors were observed. However, with the addition of another group (i.e. 240h of observations) and the observation of seven new behaviors, a significant increase in the expected number of behaviors occurred, resulting in a 3.5% decrease in completeness (to 81.5%). From this point completeness increased with the successive addition of the two other groups (to 82.3% and 84.5% respectively). This trend related with the observation of only four new behaviors

from the 240 to the 360h sample, and especially with the absence of new behaviors from the 360 to the 480h sample; additionally, the later result determined a reduction in the asymptotic number of behaviors from the third to the fourth samples. Therefore, although at the end of the study the 90% level of completeness was not reached, the observed reduction in the asymptotic number of behaviors suggests that a satisfactory proportion of the repertoire was recorded.

The estimated effort required to observe 90% of the behavioral repertoire ranged from approximately 250 hours, for the 120h sample, to 830, for the 480h sample (Table 2). In the case of the first three samples (i.e. 120, 240 and 360h) the number of observation hours would have to increase more than twofold to reach completeness. However, for the largest sample this proportion decreased, and completeness is predicted to be reached by adding less sampling hours than those already collected.

These differences relate with the trends described before: as the number of new behaviors progressively decreased with increasing sampling effort, the expected asymptotic number of total behaviors similarly decreased, resulting therefore in a decrease in the estimations of sampling effort required to reach completeness.

According to the above mentioned effort requirements, with a twofold increase in sampling periods a 5% to 8.5% increase in the number of observed behaviors would be reached in the first three sampling periods; thus, 90% of the repertoire could be observed in any case. Nevertheless, as only after the third sample (>360 h) no new behaviors were observed, it is more parsimonious to consider that only the 480 h sample could result in a representative repertoire. Therefore, and as an additional 350h of observations were required to improve completeness by only 5.5%, we estimate that 500 h may be a minimum sampling effort for observing adult black howlers' social interactions.

## DISCUSSION

Our study describes the social interactions repertoire of adult black howlers living in Campeche, Mexico. Overall, the majority of behaviors that we observed were affiliative, the groups displayed



approximately the same number of behavioral acts, and similarity levels between groups were also comparable.

In the analyses of repertoire completeness, we found that an effort inferior to 480h of observations is probably insufficient to obtain a representative sample of the social behavior of this species. Although the highest proportion of observed behaviors (from the total predicted by the accumulation curve model) was calculated for the 120h sample, new behavioral acts were observed following the addition of further groups.

This suggests that even when the proportion of observed behaviors approaches the values predicted by the asymptote, conclusions about repertoire completeness must be cautious. In this sense, as asymptotic models are based on the extrapolation of the rates of inclusion of behaviors in the samples, a primary measure of completeness must be the stabilization of the observed data curves. In our study, this occurred by the end of the third sampling period (ca. 360h). Additionally, only for the last sampling period (480 h) the estimated effort required to reach completeness was inferior to the effort already invested. For these reasons, although the repertoire failed the desired 90% value of completeness, we consider that it is representative of the social interactions of black howlers, and that a satisfactory tradeoff between effort and efficacy was reached.

As social relationships between primates vary according to ecological and demographic factors (e.g. Isbell, 2004; Sterck *et al.*, 1997), we expected that by observing groups with different sizes, compositions, and habitat characteristics we could increase the probability of observing more behavioral acts. In this sense, we believe that the marked increase in the number of acts from the first to the second sample associates with differences in the referred variables between El Álamo and Calakmul. Whereas the El Álamo group had only three adult individuals (one male and two females), lived in a forest fragment with high demographic density, and had several neighboring groups, the Calakmul group included five adults (three males and two females), lived in a continuous forest with low density, and during observations had an exclusive access to the area. It is difficult however to conclude from our data which variable or variables best explain the

similarities and contrasts between the groups. The highest similarity was found between the only two groups that had the same adult size and composition (El Álamo and Chicbul), suggesting that group characteristics could be the best predictor for behavioral similarity. Nevertheless, as the lowest similarities were found between Calakmul, the only group that lived in a continuous forest, and all other groups, habitat characteristics cannot be excluded as an explanatory variable for these trends.

Alternatively, group history could also be affecting variations in the expression of behavioral acts between groups. For instance, in the Calakmul group two of the three males were young adults born in the group (reported as juveniles in February 2003 by Rivera & Calmé, 2006). The fact that these males developed as peers could therefore explain why only in this group playing (and play face) was observed between adult males. Other factors, such as the presence of receptive females or immatures, are also expected to have a proximal influence on primate social relationships (e.g. Barrett & Henzi, 2006; Nicolson, 1987). Although we excluded sexual behaviors from the repertoire analyzes, the presence and absence of receptive females is expected to influence the expression of other types of behaviors in the groups. For instance, we observed sexual behaviors only in El Chilar, and this group had the highest proportion of agonistic behaviors (23%) when compared with the other groups (El Álamo: 5.5%, Calakmul: 20%, Chicbul 15% [unpublished data]). On the other hand, similarly to other primates (e.g. Altmann, 1980), we observed that non-mother adults are attracted to infants, and that old infants and juveniles are very active players; therefore, immatures may frequently act as indirect promoters of adult interactions. As all groups differed in the number and age of immatures, this factor could account for between-group variations in the observation of behavioral acts.

Besides the influence that the above referred factors may have had on the definition of the repertoire, our study presented some sampling limitations that most probably affected exhaustiveness. Although we completed 480h of observations, these were divided among four groups, concentrated on a 30d period for each group, and were exclusively performed during dry seasons. For instance,

although all samplings were performed during the dry season, there are differences in temperature and pluviosity between subsequent years in Campeche (Vidal-Zepeda, 2005), which could affect the expression of behavioral acts. In future studies, sampling protocols must be extended in order to assess the significance of such logistic limitations on the observation of social behavior. According to our findings, we suggest that these tests should include: observations of a single group during more time (including year-round sampling); observing groups with further variation in demographic and ecological characteristics; analysis of the impact of both sexual behavior and immature behavior on the expression of social acts.

Two of the eight interactions that were common to the four groups, grooming and hand-holding, are precisely the ones described in the only two published papers on adult black howlers' social interactions (Brockett *et al.*, 2000, 2005). However, we did not observe some interactions previously described for howlers, as greeting ceremonies (Glander, 1980) or threats (Albuquerque & Codenotti, 2006; Jones, 2005). This could be associated with the partiality of our observations, or alternatively, with variation among howler species in social behavior. The distinctive grouping patterns of mantled howlers have been related with the evolution of divergent social strategies (e.g. Crockett & Janson, 2000; Jones, 2004), and it is therefore expected that these could reflect in the types of interactions used to maintain social dynamics. However, at this moment the insufficiency of our knowledge about howlers' social behavior does not allow performing reliable cross-species comparisons. Another behavior we did not observe was "grouping snuggle" previously described in *A. caraya* by Albuquerque & Codenotti (2006). These authors observed this behavior when temperatures were low or during raining. In our study area the mean annual temperature is 24.1°C and insolation is elevated and uniform throughout the year (Vidal-Zepeda, 2005). Therefore, in contrast with *A. caraya* that face low temperatures, thermoregulation maintained through body contact may not be required for *A. pigra* living in Campeche.

In conclusion, although the repertoire that we described was probably limited by a number of logistic aspects, it can be a useful basis

to study adult black howlers' social behavior. On the other hand, the accumulation curves methodology allowed analyzing several behavioral repertoire characteristics. Converging with the recommendations of ecologists (e.g. Moreno & Halffter, 2000; Soberón & Llorente, 1993), we suggest that behavior accumulation curves may be an effective tool for analyzing within and between-repertoire completeness and efficacy. This is expected to be a particularly important upcoming task, as at the present the information available about the social interactions of this endangered species is extremely limited.

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