

# The loss of behavioral diversity as a consequence of anthropogenic habitat disturbance: the social interactions of black howler monkeys

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**Abstract** To date, no study has investigated how human disturbance affects the size of the behavioral repertoire of a species. The aim of the present study is to illustrate how measurement of behavioral diversity assists in documenting biodiversity loss, demonstrating that human disturbance has a negative effect on behavioral diversity. We studied the social interaction repertoire of 41 adult black howler monkeys (*Alouatta pigra*) belonging to 10 groups living in different habitats in Campeche (Mexico), and related repertoire size to a proxy of human-induced habitat disturbance, habitat size. The social interaction repertoire of groups living in habitats with higher human-induced disturbance included lower number of behavioral types, and in particular, fewer energy-demanding behaviors. Thus, in addition to a loss in biodiversity, measured through organismal diversity, the disturbance of black howler monkeys' habitats is accompanied by a loss in behavioral diversity. We believe that the study of behavioral diversity as an element of biodiversity will become an increasingly important research topic, as it will improve our understanding of the behavioral strategies displayed by wildlife facing anthropogenic disturbance.

**Keywords** *Alouatta* · Behavior · Behavioral repertoire · Biodiversity loss · Mexico · Social interactions

## Introduction

Biodiversity refers to the variety of life, and may be conceptualized and measured using different elements (Gaston and Spicer 2014), with genetic, organismal, and ecological diversity representing the most commonly used elements (Magurran and McGill 2011). More infrequently, behavioral diversity, defined as intraspecific variation in behavior (Strier 2009), has been classified as an element of biodiversity (e.g., Stone et al. 1994; Jones 2005).

The intense exploitation of natural resources by humanity is degrading natural habitats at accelerated rates, and as a consequence is leading to a global biodiversity crisis (Dirzo and Raven 2003), characterized through accounts of species loss (e.g., birds: Pimm et al. 2006; mammals: Ceballos et al. 2015) and of ecosystem disruptions (e.g., boreal ecosystems: Mayor et al. 2012; semi-arid ecosystems: Ribeiro et al. 2015). If behavioral diversity is regarded as an element of biodiversity, its study could represent an additional level for the assessment of biodiversity loss. However, although there is growing evidence of flexible behavioral responses of wildlife to human disturbance—usually classified as evidence of behavioral plasticity, such as variation in mate preferences (Rodríguez et al. 2013) or subsistence behaviors (Van Schaik 2013)—no previous study has investigated how human disturbance affects the size of the behavioral repertoire of a species.

The aim of the present study is to illustrate how the measurement of behavioral diversity may assist in documenting biodiversity loss by demonstrating that human disturbance has a negative effect on behavioral diversity. We document inter-population variation in the size of social interaction repertoire, and examine whether behavioral diversity, assessed through repertoire size, is related to human disturbance. Because social interaction entails

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energetic costs (e.g., de Oliveira et al. 2003; Sands and Creel 2004; Girard-Buttoz et al. 2014), and individuals living in disturbed habitats may experience reduced access to food resources (e.g., Robinson 1998; Chaves et al. 2012), we further explore the possibility that human disturbance results in a reduction of energetically demanding social interactions. We carried out the study on wild black howler monkeys (*Alouatta pigra*), a primate species for which descriptions of the social interaction repertoire are available (Dias et al. 2009; Rangel-Negrín et al. 2012; Dias and Rangel-Negrín 2015a).

## Methods

### Study sites and subjects

From February 2006 through November 2008, we studied 41 adult black howler monkeys belonging to 10 groups that lived in different habitats in Campeche, Mexico (Dias et al. 2015) (Table 1). Details of the study area have been described elsewhere (e.g., Dias et al. 2011, 2014, 2015; Rangel-Negrín et al. 2014a). We recognized all individuals via ankle bracelets or their natural anatomical and physiognomic characteristics, such as body size and proportions, scars, broken fingers, and genital morphology and pigmentation.

### Behavioral sampling

During continuous observation sessions (6:00 to 16:00 or 7:00 to 17:00, depending on daylight across the year), we recorded all occurrences (Altmann 1974) of social interactions exchanged between adult group members (Table 2). Following Whitehead (2008), we defined social interaction as when the presence or behavior of one individual was

directed toward another or affected the behavior of another. We excluded vocalizations from this study because recording equipment that allowed distinguishing vocalization types was not available. Each behavioral act was described according to its structure and included in a social interaction repertoire (Rangel-Negrín et al. 2012; Dias and Rangel-Negrín 2015a). We defined social interactions likely to be energetically demanding (hereafter, energetically demanding behaviors) as those involving rapid body movements or rapid sequences of body movements (Table 2).

A total of 2400 h were collected. We sampled each group for 24 days and a total of 240 h, divided in two 12-d (120-h) periods, one in the wet and another in the dry season to account for seasonal variation in behavior (e.g., reproductive behavior: Dias et al. 2015).

### Assessment of human disturbance

Studies addressing the consequences of human disturbance for howler monkeys are usually based on measures of human-induced habitat modification (e.g., vegetation disturbance: Arroyo-Rodríguez and Mandujano 2006) and, more rarely, on the actual interaction between humans and howler monkeys (e.g., Aguilar-Melo et al. 2013). Independent of the measures and focus used to address this topic, there is a convergence in finding habitat size (sometimes referred to as forest fragment size) as a major factor constraining howler monkey populations in disturbed habitats, probably because habitat size is positively related to food availability and negatively related to physiological stress and parasite loads (Arroyo-Rodríguez and Dias 2010). We have previously reported similar results for black howler monkeys in Campeche (Dias et al. 2014, 2015), where the reduction in tropical forests—the habitat of howler monkeys—results from human disturbance (e.g., conversion to agricultural fields: Escamilla et al. 2000). Thus, in our analyses we used

**Table 1** Location, habitat size, group size, and completeness estimations of the social interaction repertoire of the black howler monkey groups studied in Campeche, Mexico

Group	Latitude	Longitude	Habitat size (ha)	Group size	Adult group size	Completeness of repertoire (%)
AA Álamo	18°48'45.44"N	90°58'54.61"W	86	4	3	84
Calakmul S	18°19'0.28"N	89°51'28.92"W	140,000	7	3	81
Calaxchil	18°51'15.38"N	91°18'41.70"W	3000	6	3	79
Chicbul	18°46'51.66"N	90°56'13.45"W	5	4	3	85
Chilar	18°54'06.58"N	90°53'37.90"W	2	8	5	90
Manantiales	18°42'55.39"N	91°04'42.07"W	50	4	3	80
Oxcabal	18°51'44.34"N	90°57'39.45"W	7	6	5	81
T61 Calax	18°50'52.35"N	91°18'27.12"W	300	9	5	87
Tormento N	18°36'50.68"N	90°48'25.93"W	600	10	7	79
Tormento S	18°36'27.29"N	90°48'51.44"W	800	6	4	78

**Table 2** Social interaction repertoire and occurrence of each behavioral act in 10 groups of black howler monkeys studied in Campeche, Mexico

Social interactions <sup>a</sup>	1 <sup>b</sup>	2	3	4	5	6	7	8	9	10
Approach-avoiding	1	1	1	1	1	1	1	1	1	1
Attacking <sup>c</sup>	0	0	0	0	0	1	0	1	1	1
Avoiding	1	1	1	1	0	1	1	0	1	1
Biting	0	1	0	0	0	0	0	0	0	0
Blocking	0	0	0	0	0	0	0	0	0	1
Chasing <sup>c</sup>	1	1	1	1	1	0	0	1	1	1
Chest contact	0	0	0	0	1	0	1	0	0	0
Chest-smelling	0	0	0	0	0	1	0	0	0	0
Complaining	0	1	0	0	0	0	0	0	0	0
Complete copulation <sup>d</sup>	0	1	0	0	1	0	0	1	1	0
Fighting <sup>c</sup>	0	0	1	0	0	0	1	0	1	0
Finger-stroking	1	1	0	1	1	0	1	1	1	1
Fleeing <sup>c</sup>	1	1	1	0	0	0	0	1	1	1
Foot-touching	1	0	1	0	0	0	0	0	1	0
Genital-smelling <sup>d</sup>	1	1	1	1	1	1	1	1	1	1
Grooming	1	1	1	1	1	1	1	1	1	1
Grooming solicitation	0	0	1	1	0	1	0	1	1	0
Hand-touching	1	1	1	1	1	1	1	1	1	1
Hand-holding	1	1	1	1	1	1	1	1	0	1
Head-touching	1	1	0	0	0	0	0	0	0	1
Hugging	1	1	0	1	0	1	1	1	1	1
Ignoring	1	1	0	1	0	1	1	1	1	1
Incomplete copulation <sup>d</sup>	0	1	1	0	1	0	0	1	1	0
Intervening	0	0	0	0	0	0	0	0	0	1
Lying on top	1	1	0	0	0	0	0	1	1	0
Mounting <sup>d</sup>	0	0	0	0	0	1	1	1	1	0
Mouth-touching	0	1	1	0	0	0	1	1	1	1
Mutual grooming	0	1	0	0	0	0	0	1	0	0
Nose-touching	0	0	0	0	0	0	0	0	0	1
Playing <sup>c</sup>	1	1	1	1	1	1	1	1	1	1
Playing solicitation	0	1	1	0	1	1	1	1	1	1
Pushing	0	0	1	0	0	0	0	1	1	0
Running towards <sup>c</sup>	1	1	1	1	0	1	0	1	1	1
Scratching	1	0	0	0	0	0	1	0	0	1
Sexual presentation <sup>d</sup>	0	1	0	0	0	0	1	1	1	1
Sitting in contact	1	1	1	1	1	1	1	1	1	1
Slapping	1	1	1	0	0	1	0	1	1	0
Smelling	1	1	1	1	1	1	1	1	1	1
Submissive position	1	1	0	0	0	1	1	0	0	1
Supplanting	1	1	1	1	1	1	1	1	1	1
Tail-embracing	0	1	1	1	0	0	0	0	0	1
Tail-touching	1	1	1	1	0	1	0	1	1	1
Threatening <sup>c</sup>	1	1	0	0	0	0	0	1	1	1
Tongue-flicking <sup>d</sup>	0	1	0	0	1	0	0	1	1	1
Tongue-touching	0	1	1	0	0	0	0	1	1	1
Total acts	24	33	24	18	16	21	21	31	32	31

<sup>a</sup> Descriptions of behavioral acts in Rangel-Negrín et al. (2012). 0, behavioral act was not observed in the group; 1, behavioral act was observed in the group

<sup>b</sup> 1, AA Álamo; 2, Calakmul S; 3, Calaxchil; 4, Chicbul; 5, Chilar; 6, Manantiales; 7, Oxcabal; 8, T61 Calax; 9, Tormento N; 10, Tormento S

<sup>c</sup> Energetically demanding behavior

<sup>d</sup> Sexual interaction

habitat size as a proxy for human-induced habitat disturbance. We measured habitat size (in ha) for each of the studied groups in digitized (ArcGIS 10.3.1, ESRI Inc., Redlands, CA, USA) orthophotos (1:10,000, resolution 1 m).

### Data analysis

Although the observation effort was the same across groups (i.e., 240 h), we explored the possibility that the detection of new behavioral types varied among groups, in which case behavioral repertoires would not be comparable. To this end, we used the behavioral accumulation curves method (Dias et al. 2009), and calculated repertoire completeness per group by dividing the total number of observed behavioral types by the predicted repertoire size. The predicted repertoire size for each group was calculated as the asymptote of the curve describing the relationship between sampling effort and the observation of behaviors, adjusted with the Clench equation (Dias et al. 2009). Repertoire completeness was similarly high among groups (Table 1), indicating that repertoires were comparable.

We analyzed the relationship between habitat size and both repertoire size and the number of displayed energetically demanding behaviors using generalized nonlinear models (GNM). We selected a Poisson distribution with an identity link-function to the response variables. Habitat sizes were log-transformed to reduce the influence of their very high variation (Table 1) in the analyses. As the exchange of sexual interactions is dependent on the reproductive status of females, variation in repertoire size could depend on differences among groups in the frequency of receptive females rather than on the predicted influence of human disturbance. We therefore ran a third GNM exploring the relationship between habitat size and repertoire size excluding sexual interactions. Finally, as the probability of exchanging a social interaction may be linked to the potential number of social partners in a group (Lehmann et al. 2007), we tested whether variation in repertoire size, number of displayed energetically demanding behaviors, and repertoire size excluding sexual interactions were related to group size or adult group size (i.e., number of individuals per group, excluding immature individuals). All tests were two-tailed, and statistical significance was set at  $P < 0.05$ .

### Results

We observed a total of 45 social interaction types, of which seven were classified as energetically demanding (Table 2). The size of the social interaction repertoire varied among groups between 33 and 16 behavioral types

(mean  $\pm$  SD =  $25.1 \pm 6.2$  types), and the number of energetically demanding behaviors displayed per group varied between two and seven ( $4.4 \pm 1.8$  behaviors). After excluding sexual interactions, repertoire size varied between 12 and 28 types ( $21.7 \pm 5.1$  types). Variation in repertoire size, repertoire size excluding sexual interactions, and the number of energetically demanding behaviors was positively and significantly predicted by habitat size (Table 3; Fig. 1). This variation was not related to group size ( $P > 0.05$  for the six GNM tests).

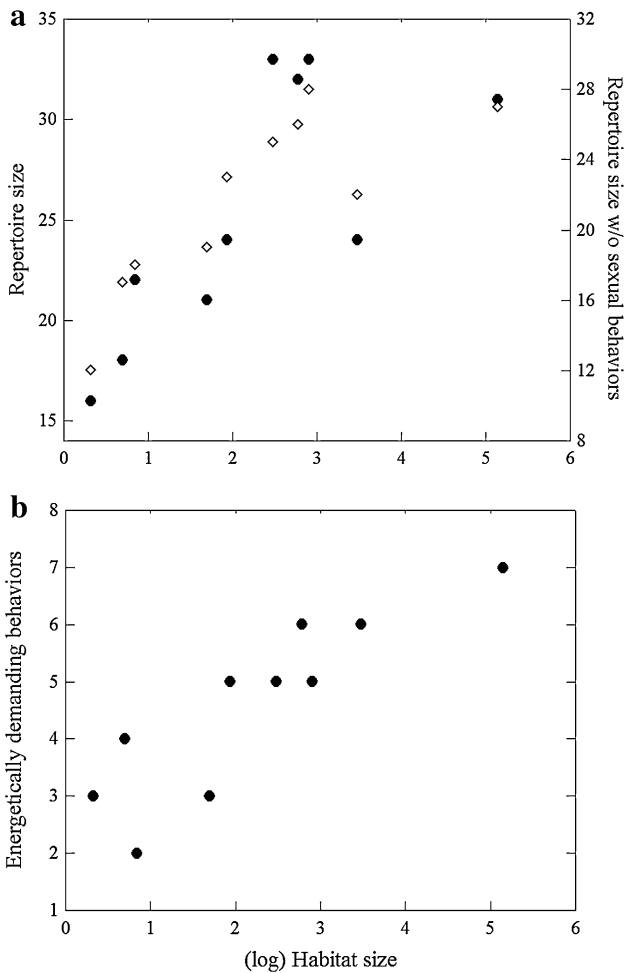
### Discussion

In the present study, we examined inter-population variation in the size of the social interaction repertoire of black howler monkeys and analyzed whether variation in repertoire size was related to human disturbance. Repertoire size varied among populations, and in some cases the size of the repertoire of groups living in larger habitats doubled that of groups sampled in smaller forests. Repertoire size, repertoire size excluding sexual interactions, and the number of energetically demanding behaviors were higher in larger habitats. Therefore, the behavioral diversity of social interactions exchanged among black howler monkeys is affected by habitat size, which is a proxy for anthropogenic habitat disturbance in howler monkeys (e.g., Arroyo-Rodríguez and Dias 2010), and specifically, our results suggest that there is a loss in behavioral diversity in more disturbed habitats.

There is evidence that human-driven habitat disturbance leads to changes in the behavior of wild animals, including behaviors that have a direct impact on reproductive success, such as movement and space use patterns, foraging and predator-prey-related behaviors, and social behavior and reproduction (Berger-Tal et al. 2011). For instance, reindeer (*Rangifer tarandus*) increase range distances in response to the presence of snowmobiles or skiers (Reimers et al. 2003), European eels (*Anguilla anguilla*) are preyed upon more frequently in noisy environments (Simpson et al. 2014), and male desert gobies (*Chlamydogobius eremius*) change courtship behavior in response to habitat alteration (Michelangeli et al. 2015). In primates, there are several accounts of variation in behavior between groups or populations facing different types or intensity of human disturbance (e.g., Chaves et al. 2012; Gómez-Espinoza et al. 2014), and in black howler monkeys, we have previously documented changes in feeding patterns associated with habitat disturbance (Dias et al. 2014). The present study extends this evidence by demonstrating that, under disturbed conditions, individuals exhibit fewer social behavior types. An additional explanation for the results we found could be the presence of fewer infants in more

**Table 3** Generalized nonlinear models (GNM) of the effects of habitat size on the social interaction repertoire of 10 groups of black howler monkeys studied in Campeche, Mexico

Repertoire	Parameter	SE	Wald $\chi^2$	P	Wald 95 % confidence intervals	
					Inferior	Superior
Repertoire size	3.79	1.18	10.4	0.001	1.48	6.09
Repertoire size w/o sexual interactions	3.21	1.09	8.6	0.003	1.06	5.35
Energetically demanding acts	1.05	0.49	4.6	0.032	0.09	2.01



**Fig. 1** The relationship between habitat size and repertoire size (a, left y-axis; black dots), repertoire size excluding sexual behaviors (a, right y-axis; open diamonds), and the number of energetically demanding behavioral acts (b) displayed by 10 black howler monkey groups in Campeche, Mexico

disturbed habitats, where we have previously demonstrated that infant survival is lower (Dias et al. 2015). In howler monkeys, as in other primate species (e.g., *Papio cynocephalus ursinus*: Barrett et al. 1999), infants raise intense interest from other group members, especially other adult females, and thus promote the exchange of social interactions between mothers and non-mothers (Clarke et al. 1998; Arroyo-Rodríguez et al. 2007). Unfortunately, the

small variation in the number of immature individuals per group in our dataset precludes the formal testing of this hypothesis.

This loss in behavioral diversity observed in black howler monkeys was associated with a decrease in the number of energetically expensive behaviors. In disturbed habitats, howler monkeys may be metabolically constrained, as energy intake is supposedly lower due to a reduction in the ingestion of preferred foods such as fruit, and to increases in folivory and in the consumption of alternative food items (e.g., lianas) (Dias and Rangel-Negrín 2015b). Under these circumstances, suppression of the exchange of energetically demanding behaviors would be consistent with an energy-saving strategy. Supporting the hypothesis that the loss of behavioral diversity is linked to energy-saving is the observation that all but one of the energetically demanding behaviors were absent in the smaller habitats (<50 ha). The only energetically demanding behavior observed in these habitats was playing, which was one of the eight social interactions recorded in all groups.

Future studies should aim at understanding the social consequences of the deletion of interaction types from the behavioral repertoire of disturbed populations for the establishment and maintenance of social relationships among individuals. It is noteworthy that some agonistic behavioral types observed in the majority of groups living in large habitats, such as attacking, fleeing, lying on top, slapping or threatening, were absent in the smaller habitats. Although these behaviors were observed infrequently, they played an important role in the regulation of intra-group competition as well as during interactions with extra-group individuals (Rangel-Negrín et al. 2011). Their absence could therefore interfere with the ability of individuals to manage conflicts of interest in disturbed habitats. Alternatively, it is possible that when following an energy-saving strategy while living in a disturbed habitat, individuals manage social conflicts using affiliative or agonistic interactions that do not involve risk of physical injury. Among the interaction types that were recorded in all groups are affiliative interactions that involve prolonged body contact, such as grooming, playing and sitting in contact, and approach-avoiding and supplanting, which are

agonistic interactions that do not involve body contact. These are likely candidate interactions for exploring the use of non-aggressive behaviors in social conflict management among individuals living in disturbed habitats.

Moreover, although the proximate mechanisms underlying affiliation in non-human primates are currently unknown, there is indirect evidence that endorphins, oxytocin, and arginine vasopressin may be involved. Studies in talapoin monkeys (*Miopithecus talapoin*) and rhesus macaques (*Macaca mulatta*) have experimentally demonstrated that the amount of grooming exchanged between individuals may be influenced by the circulating levels of endorphins (Dunbar 2010). As endorphin release is associated with a feeling of well-being and light analgesia, is it possible that affiliative interactions involving body contact are favored through the effects of opioid system activation on the brain reward system (Insel 2010). Conversely, oxytocin and vasopressin are involved in pair-bonding and maternal behavior in humans and other mammals such that increases in these hormones result in greater calmness, higher sociability and more frequent huddling (Dunbar 2010). In disturbed habitats, where psychosocial stress responses of black howler monkeys are more frequent and intense (Rangel-Negrín et al. 2014a), affiliative behaviors may therefore play an important proximal role in regulating homeostasis, favoring their persistence in behavioral repertoires. In any case, although our study had a limited observation effort (i.e., 240 h per group), our results suggest that black howler monkeys present plastic social responses, and it remains for future research to determine the possible costs or limits of such plasticity (DeWitt et al. 1998).

In conclusion, our study reveals variation in behavioral diversity associated with habitat disturbance among groups of black howler monkeys. The social interaction repertoire of groups living in habitats with a higher degree of human-induced disturbance included fewer behavioral types, and in particular, fewer energy-demanding behaviors. Thus, in addition to a loss in biodiversity measured through organismal diversity (Dias et al. 2014; Rangel-Negrín et al. 2014b), the disturbance of black howler monkey habitats is accompanied by a loss in behavioral diversity. We believe that the study of behavioral diversity as an element of biodiversity will become an increasingly important research topic, as it will aid our understanding of the behavioral strategies displayed by primates to confront anthropogenic disturbance, and because it adds a new layer of complexity (i.e., behavioral element) to the integrative study of the variety of life.

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