

# Survey of *Alouatta caraya*, the black-and-gold howler monkey, and *Alouatta guariba clamitans*, the brown howler monkey, in a contact zone, State of Rio Grande do Sul, Brazil: evidence for hybridization

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**Abstract** Sympatry and natural hybridization between howler monkey taxa (*Alouatta* spp.) has only recently been confirmed in the wild. Surveys in areas of potential contact between the distribution of two taxa have shown that sympatry is rare, although more common than previously known. Here we report the results of a survey conducted in a contact zone between the only two sexually dichromatic howler monkey taxa, *Alouatta caraya* and *A. guariba clamitans*, in São Francisco de Assis, State of Rio Grande do Sul, Brazil. Our survey, covering an area of about 400 ha at the Cerro dos Negros (29°33'50"–29°35'10"S, 54°58'40"–54°59'50"W; ~100–279 m a.s.l.), was successful in locating seven black-and-gold and one brown howler monkey social groups living syntopically. Black-and-gold group size ranged from 5 to 15 individuals, whereas the brown group was composed of 7 individuals. The pelage color of three adult males belonging to different black-and-gold groups and another adult male belonging to the brown howler group presented a mosaic of red or rufous and black. These adult males and an adult female living in another black-and-gold group are putative hybrids. Therefore, it appears that pre-zygotic reproductive isolation has not evolved, at least not completely, between these

howler monkey species, corroborating previous reports for these and other *Alouatta* taxa. Future genetic studies need to confirm the occurrence of hybridization in this contact zone, and to determine the viability and fertility of hybrids and their possible offspring. In addition, there is no evidence supporting the existence of significant segregation in habitat and resource utilization by black-and-gold and brown howler monkeys.

**Keywords** Reproductive isolation · Habitat segregation · Competition · Color patterns · Sexual dichromatism · Phenotypic mosaicism

## Introduction

We report the preliminary results of a survey conducted as part of a broader study to investigate isolating mechanisms between *Alouatta caraya* (Humboldt, 1812) (the black-and-gold howler monkey) and *A. guariba clamitans* Cabrera, 1940 (the brown howler monkey) in a contact zone in the State of Rio Grande do Sul, Brazil. Following reports by Brazilian colleagues of sympatry between the two target species, and the likely presence of hybrids in a study site (Ilha Grande on the upper Paraná river in the State of Paraná, Brazil) about 700 km to the north of our study site (Aguiar et al. 2007, 2008; see also Gregorin 2006), our survey was also undertaken with the primary objective to obtain evidence for the absence or breakdown of reproductive isolating mechanisms between these taxa. In this initial phase of our long-term research program—the Howler Landscape Sociogenetics (HOWLS) project—we estimated the distribution and local abundance of populations, analyzed possible interspecific differences in habitat utilization and behavior that could lead to segregation, and

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identified threats to the conservation of the local biodiversity.

## Methods

### Study site

We selected a study site in the municipality of São Francisco de Assis, State of Rio Grande do Sul, Brazil (Fig. 1), where both species were reported to be found in sympatry (D. Gressler, personal communication). This information was confirmed during a short visit to the site in February 2007. The study region presents an undulating terrain dominated by rocky hills partially covered with forests in different stages of development, presenting a mosaic of habitats characterized by grasslands and gallery forests. The study site is located in the northern border of the domain of the temperate grasslands, or Pampas biome, very close to the Atlantic Forest *sensu lato*. The forest habitats contain elements of the Atlantic Forest that have been altered by human activities (e.g., logging and firewood extraction). An area of about 400 ha in the Cerro dos Negros (29°33'50"–29°35'10"S, 54°58'40"–54°59'50"W; ~100–279 m a.s.l.) was surveyed.

### Animals

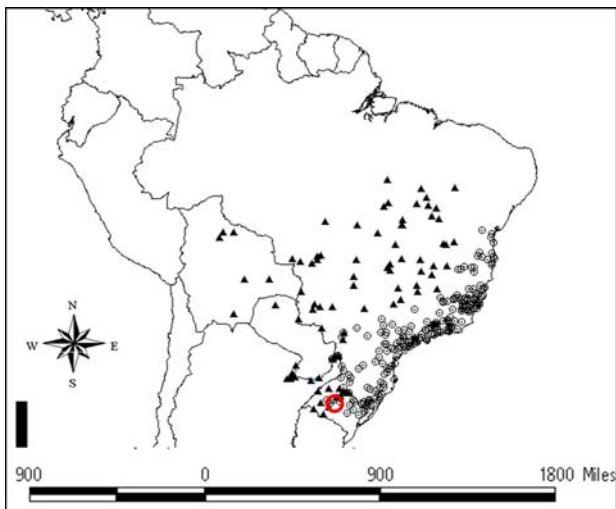
*Alouatta* (howler or howling monkey) is the primate genus most widely distributed in the Neotropics (Neville et al. 1988), being found from northern Argentina to southern Mexico (Groves 2001). Groves (2001) has recently divided

howlers into ten species. *Alouatta caraya* and *A. guariba* are valid species distinguishable on the basis of both morphological (Hill 1962; Groves 2001; Gregorin 2006) and genetic (Oliveira et al. 2002; Cortés-Ortiz et al. 2003; Oklander et al. 2007) data. Phylogenetic analyses indicate that they are not sister taxa (Meireles et al. 1999; Oliveira et al. 2002; Cortés-Ortiz et al. 2003; Villalobos et al. 2004; Sallenave 2005). According to Cortés-Ortiz et al. (2003), their clades separated at 5.1 Ma.

Howler monkeys are arboreal folivore–frugivores, preferring new leaves, fruit, and flowers (Crockett and Eisenberg 1987; Neville et al. 1988). These monkeys are adapted to environmental heterogeneity (Jones 1995; Silver and Marsh 2003), including climatic seasonality (Jones 1997), a variable spatial and temporal food distribution (Jones 1996), variable peaks in gestation and parturition (see review in Jones 2006, pp 265–267), and a range of habitats (Jones 1995, 2005; Bicca-Marques 2003).

Although howlers are generally tolerant of a broad range of habitats, species differences have been documented (e.g., Jones 2005). *Alouatta caraya* appears to be relatively more specialized ecologically than either *A. seniculus* (the red howler monkey) or *A. palliata* (the mantled howler monkey) (Jones 2005; but see Bicca-Marques 2003). *Alouatta guariba clamitans* shows a general behavioral and ecological profile very much like that of the other howlers (Bicca-Marques 2003; also see Strier 1992; Strier et al. 2001), although this taxon is poorly known relative to black-and-gold, red, or mantled howlers. According to the IUCN Red List, *A. caraya* is not an endangered or threatened species, while *A. guariba clamitans* is on the verge of endangerment (Hilton-Taylor et al. 2004; Rylands and Chiarello 2003). Both taxa, however, are vulnerable in the State of Rio Grande do Sul (Marques 2003), and *A. caraya* has recently been reported to be endangered because of low genetic diversity, probably resulting from one or more bottlenecks (Ruiz-García et al. 2007).

Both target taxa are the only two howler species to present sexual dichromatism. Adult male *A. caraya* are black, females are gold (Groves 2001), and the sexes are easily distinguishable (Jones 1983; Bicca-Marques and Calegario-Marques 1998), whereas adult male *A. g. clamitans* vary from reddish to hazelnut-colored and females are fully dark chestnut-colored to reddish chestnut-colored (Hill 1962; Gregorin 2006). Groves (2001) points out that, while male *A. g. clamitans* are generally lighter than females, “the variations seem complex” (p 185; see also Fortes and Bicca-Marques 2008). According to Bicca-Marques and Calegario-Marques (1998), it is not yet known whether dichromatism in *A. caraya* evolved via male–male competition or female choice. These authors also develop a scenario in which individual sex determination at “far range” may have favored the evolution of this trait in both

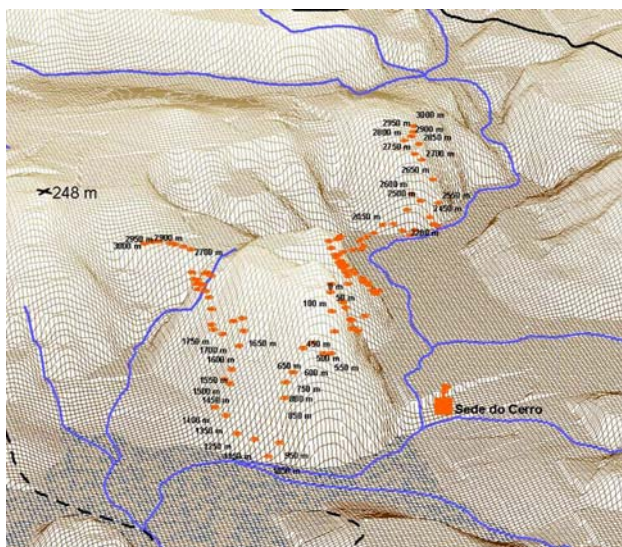


**Fig. 1** Species distribution map of *Alouatta caraya* (the black-and-gold howler monkey, triangles) and *Alouatta guariba* (the brown howler monkey, circles) according to the literature; the larger red circle shows the location of the study region

southernmost howler taxa (Bicca-Marques and Calegario-Marques 1998; see also Bicca-Marques and Azevedo 2004). Future studies will need to evaluate the likelihood that evolution has favored sexual dichromatism as a result of intrasexual competition or mate selectivity, consistent with Clutton-Brock's (2007) views that these processes have been underestimated by evolutionary biologists and that they are likely to be significant mechanisms of sexual selection (see also Gerald 2003; Caro 2005; Bradley and Mundy 2008). Sexual dichromatism is rare among mammals in general, and the most conspicuous examples are found in primates (Andersson 1994; Caro 2005). Among primates, bi-phasic, all-body pelage color differences are found in seven prosimians, four New World monkeys (both *Alouatta* species reported here and two *Pithecia* species), two Old World monkeys, and four lesser apes (Gerald 2003). The striking dichromatism found in *A. caraya* is matched by a few taxa, such as the lemurs *Eulemur macaco macaco* and *E. m. flavifrons*, and the gibbons *Hylobates pileatus*, *Nomascus concolor*, and *N. leucogenys*.

#### Primate and tree survey

Two trails 3-km long each (Fig. 2) were opened in March 2007. Two survey campaigns were conducted in May and June–July 2007 by two, two-researcher teams composed of a primatologist and a botanist. Each day a survey team normally walked a trail back-and-forth at ~1,250 m/h. Morning censuses began around 0700–0800 hours, depending on sunrise time, whereas afternoon censuses began after 1300 hours. The occurrence of rain or fog in



**Fig. 2** Map of the location of the two 3-km-long trails (data points plotted using the GPS TrackMaker software) and the field base (Sede do Cerro) showing relief of the terrain

the hills impeded walking the trails because of low visibility, and for safety reasons because of the highly steep terrain. Consequently, there were days with no survey and others with a single walk. The botanist of each party walked ~15 m behind the primatologist and opportunistically recorded the tree species during the primate surveys. Another qualitative plant survey (Elzinga et al. 1998) was also conducted during the opening of the trails.

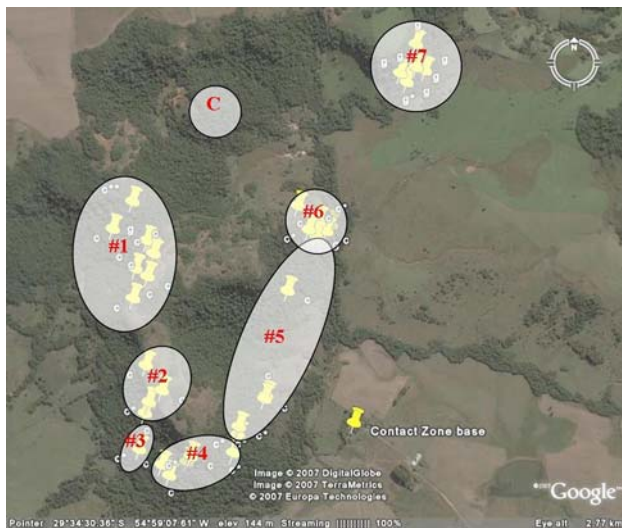
Line-transect censuses were conducted following standard methods devised for the survey of primate populations (National Research Council 1981; Ross and Reeve 2003). We defined a demographic group as any bisexual unit of two or more (adult) individuals of opposite sex residing on a home range. When an individual howler or howler group was sighted, observers recorded pertinent information [e.g., location, pelage color and variation(s), distinguishing marks, age/sex classification, time, weather conditions, behavior, and tree height at which animal(s) were encountered] in a data sheet (available upon request). Observers remained in the vicinity of the animals for up to 1 h for counting and recording relevant behaviors. The GPS location of sightings was plotted in a Google Earth satellite image of the study site for estimating the number of groups.

#### Results

Trails were walked on 53 (left trail) and 52 (right trail) occasions, totaling 315 km of census. On 20 and 33 of these walks, respectively, no monkey was sighted. A total of 33 sightings of *A. caraya* groups (14 of which contained putative hybrids) and 1 of a solitary adult male *A. g. clamitans* were obtained in the left trail. In the right trail, 9 sightings of *A. caraya* (5 of which containing a putative hybrid, Fig. 3) and 11 of *A. g. clamitans* groups were obtained. An analysis of group composition and temporal distribution of sightings allow us to suggest the existence of at least five *A. caraya* groups living in the forest covered by the left trail, and two *A. caraya* and one *A. g. clamitans* groups in the area of the right trail (Fig. 4, Table 1). A quick survey conducted in February 2007 in the forests of the Fazenda Santo Antônio do Buricaci, a few kilometers to the east of the study site, indicated the presence of several groups of *A. g. clamitans*. Four putative hybrids were adult males, three belonging to an *A. caraya* group and one belonging to an *A. g. clamitans* group. A fifth putative hybrid was an adult female belonging to an *A. caraya* group (Table 1).

A total of 98 plant species belonging to 41 families were identified in the forests of the Cerro dos Negros (list available upon request). Black-and-gold howler monkeys were seen eating leaves of *Parapiptadenia rigida*, *Ficus*

**Fig. 3** Howler monkeys of the Cerro dos Negros (São Francisco de Assis, RS, Brazil; **a–d**). The adult males shown in **b** and **c**, the animal on the right in **a** and the upper one in **d** are putative hybrids. Note, for example, the pelage color of the individual pictured in **c** showing a mix of red or rufous, characteristic of adult male brown howler monkeys (*A. guariba clamitans*), and black, characteristic of adult male black-and-gold howler monkeys (*A. caraya*)



**Fig. 4** Location of estimated home ranges of presumed howler monkey groups (#1–6, C *A. caraya*; #7 *A. guariba clamitans*). C indicates a seventh black-and-gold howler monkey group sighted outside the census

*luschnathiana*, and *Cabralea canjerana*, and from an unidentified leguminous tree. Brown howlers, on the other hand, were seen eating leaves of *Trichilia clausenii* and *Casearia silvestris*. A preliminary analysis of the literature on the plant species known to be used as food sources by each howler monkey species indicates considerable overlap.

**Table 1** Composition of howler monkey groups (*Alouatta* spp.) located in the Cerro dos Negros (São Francisco de Assis, State of Rio Grande do Sul, Brazil)

Species/group	Group size	ADM	ADF	IMM	IMF	Inf
<i>A. caraya</i>						
1 <sup>a</sup>	9	2	2 <sup>c</sup>	2	2	1
2 <sup>a</sup>	5	1	1	1	1	1
3 <sup>a</sup>	8	1 <sup>c</sup>	3	2	1	1
4 <sup>a</sup>	8	2 <sup>c</sup>	1	2	2	1
5 <sup>ab</sup>	10	2	3	2	2	1
6 <sup>b</sup>	5	1 <sup>c</sup>	1	1	1	1
C	15	3	6	2	1	3
<i>A. guariba clamitans</i>						
7 <sup>b</sup>	7	1 <sup>c</sup>	2	1	1	2

ADM Adult male, ADF adult female, IMM immature (juvenile/sub-adult) male, IMF immature (juvenile/subadult) female, Inf infant

- <sup>a</sup> Left trail
- <sup>b</sup> Right trail
- <sup>c</sup> One putative hybrid

**Discussion**

Our survey was successful in locating both species living in syntopy at the Cerro dos Negros, and in detecting putative hybrids based on mixed pelage color patterns, as also reported by Aguiar et al. (2007, 2008) in the State of Paraná, Brazil. However, unlike Aguiar et al. (2008), most

putative hybrids at Cerro dos Negros were adult males, an observation that fails to support the idea that male hybrids are less viable (but see Cortés-Ortiz et al. 2007 for data on hybridization between *A. palliata* and *A. pigra*).

The likely presence of hybrid individuals between *A. caraya* and *A. g. clamitans*, coupled with their divergence from different sister taxa (estimated at about 4.0 Ma; Cortés-Ortiz et al. 2003), is incompatible with a role for sexual dichromatism as the mechanism of reproductive isolation between these taxa. Therefore, female choice (e.g., “reinforcement”: Servedio 2004) appears to be a weak hypothesis with which to explain the evolution of this trait. On the other hand, the other hypothesis proposed by Bicca-Marques and Calegario-Marques (1998), i.e., intra-specific, intrasexual (male-male) competition, remains viable as a selective pressure favoring the evolution of sexual dichromatism in these howler monkeys.

The confirmed occurrence of hybridization between *A. palliata* and *A. pigra* in Central America (Cortés-Ortiz et al. 2007), and possibly between *A. caraya* and *A. g. clamitans* in Brazil (Aguilar et al. 2007, 2008; this study; see also Arnold and Meyer 2006 for examples of natural hybridization in all major primate lineages), support the contention that reproductive isolating mechanisms did not evolve fully among howler monkey species despite their variability and contrasts in body size, pelage color, other aspects of phenotypic mosaicism, and the acoustic characteristics of long-distance calls (Whitehead 1995; Rowe 1996). Compatible with this contention, similar sexual behavior patterns are described for *A. caraya* and *A. g. clamitans* (Neville et al. 1988). Taking data from birds, whose generation times tend to be shorter than those of primates, reproductive isolation of closely related taxa expressed as a lack of hybrid viability may, conservatively, require several tens of millions years of independent evolution (Price and Bouvier 2002).

Habitat and resource utilization also do not appear to qualify appropriately as mechanisms of segregation. Although some authors consider *A. caraya* to be more tolerant to habitat fragmentation (see Aguilar et al. 2007), these taxa have been found to be similarly able to live in both undisturbed and disturbed habitats (for data on *A. g. clamitans* living in small fragments, see Ribeiro and Bicca-Marques 2005; Silva and Bicca-Marques 2005; Fortes and Bicca-Marques 2008), and no difference was observed in the characteristics of forests inhabited by each species in the Cerro dos Negros. Regarding trophic niche dimensions, it seems reasonable to contend that the species composition of the diet of these howler monkeys is highly variable intraspecifically, and is affected by study site floristic composition rather than by differences in food preferences, nutritional requirements, or some other species-specific traits (see Bicca-Marques 2003). Therefore, there is no

evidence allowing us to expect trophic niche partitioning between black-and-gold and brown howler monkeys living in syntopy in the Cerro dos Negros.

Selective logging was identified as a possible threat to the long-term survival of howler monkeys in the study region, but it is unlikely that anthropogenic forest fragmentation promoted by farming and cattle ranching has historically induced species contact. It is more likely that habitat destruction, instead of promoting their syntopy, would reduce the contact zone between parapatric arboreal forest-dwelling primate species, as also suggested for gibbons (Geissmann 1991), macaques (Bynum et al. 1997; Evans et al. 2001; Bynum 2002) and lemurs (Wyner et al. 2002). The contact zone reported here is likely natural as well as being recent relative to the species' evolutionary histories. According to Behling et al. (2005), the study region was covered by grassland for most of the last 22,000 years. Gallery forests containing mixed elements of the flora of the habitat of *A. g. clamitans* (Atlantic forest) and the habitat of *A. caraya* (Paraná river valley and Chaco) began to develop only around 5,000 years ago, and their expansion took place about 1,500 years ago, showing a peak about 1,100 years ago (Behling et al. 2005), probably bringing these howler monkey taxa into contact. The study region is also known as a contact zone for other mammal species, such as small felids (E. Eizirik, personal communication).

The confirmation of hybridization, and to better understand its direction and history, the occurrence of backcrosses, the mating patterns, the viability and fertility of hybrids and their offspring, as well as other aspects of this likely reproductive interspecific interaction will require the collection of DNA material, preferably using non-invasive fecal samples. Future studies will also determine the extent of this contact zone between *A. caraya* and *A. g. clamitans*, the genetic bases and effects of hybridization on species' status, the behavioral ecology of monospecific groups of each species and groups containing hybrids or a mixed composition, and the impact of habitat fragmentation on species contact and coexistence.

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