

Infant hybrids in a newly formed mixed-species group of howler monkeys (*Alouatta guariba clamitans* and *Alouatta caraya*) in northeastern Argentina

Ilaria Agostini · Ingrid Holzmann · Mario S. Di Bitetti

Received: 10 June 2008 / Accepted: 10 September 2008
© Japan Monkey Centre and Springer 2008

Abstract Natural hybridisation between species has been reported in several primate taxa. In the Neotropics, there is increasing evidence of this phenomenon in howler monkeys (genus *Alouatta*) in contact zones between species. We describe the first known case of formation of a mixed-species group, and two cases of putative infant hybrids between the brown howler (*Alouatta guariba clamitans*) and the black howler (*A. caraya*) in Misiones, Argentina. For 2 years, we followed a group consisting of one adult male and two adult female brown howlers and one adult female black howler. The adult female black howler was observed to copulate twice with brown howler males, and never with black howler males. In December 2006, this female was carrying an infant with a hybrid morphotype. This infant died at approximately 1.5 months of age. In November 2007, the same female had another putative hybrid newborn. This infant male died together with all members of his group during a yellow fever outbreak in early 2008. The lower frequency of mixed-species groups

and hybrids at our site compared with other contact zones reported in the literature, suggests that the incidence of natural hybridisation between howler species differs depending on local factors such as population demography and landscape fragmentation.

Keywords Black howlers · Brown howlers · Contact zone · Hybridisation · Yellow fever

Introduction

Natural hybridisation—the successful interbreeding between individuals from two genetically differentiated wild populations—has been traditionally regarded as counter-adaptive and ephemeral. However, recent molecular evidence of frequent hybridisation and introgression has led zoologists to consider natural hybridisation as a creative force playing a role in the evolution of many animal taxa (Arnold and Meyer 2006).

Hybrid zones have been reported for many primate taxa, and hybridisation is relatively common among Old World primates (Detwiler et al. 2005; Arnold and Meyer 2006). Among New World primates, there are only a few reports of hybrid zones between subspecies and species of *Samiri*, *Callithrix*, *Saguinus* and *Alouatta* (Silva et al. 1992; Peres et al. 1996; Mendes 1997; Cortés-Ortiz et al. 2007).

Howler monkeys (genus *Alouatta*) have the broadest geographical distribution among Neotropical primates (Crockett 1998). Although the taxonomy of the genus *Alouatta* is still debated (Gregorin 2006), as many as ten species are currently recognised (Groves 2001). Howler species are characterised by a parapatric distribution, with a few narrow contact zones between species usually reported along rivers that represent the edge of their

I. Agostini
Dipartimento di Biologia Animale e dell'Uomo,
Università di Roma "La Sapienza",
Viale dell'Università 32, 00185 Rome, Italy

I. Agostini (✉)
Istituto di Scienze e Tecnologie della Cognizione,
Consiglio Nazionale delle Ricerche, Via Ulpiano Aldrovandi 16/B,
00197 Rome, Italy
e-mail: agostini.ilaria@gmail.com

I. Agostini · I. Holzmann · M. S. Di Bitetti
Asociación Civil Centro de Investigaciones del Bosque
Atlántico (CeIBA), Puerto Iguazú, Argentina

I. Holzmann · M. S. Di Bitetti
Consejo Nacional de Investigaciones Científicas
y Técnicas (CONICET), Buenos Aires, Argentina

respective distributions. Contact zones have been recorded for *Alouatta palliata* and *A. pigra* (Cortés-Ortiz et al. 2007), *A. palliata* and *A. seniculus* (Defler 2004), *A. seniculus* and *A. caraya* (Wallace et al. 1998; Iwanaga and Ferrari 2002), *A. seniculus* and *A. belzebul* (Pinto and Setz 2000), *A. belzebul* and *A. caraya* (Chames and Olmos 1997), and *A. caraya* and *A. guariba clamitans* (Di Bitetti et al. 1994; Gregorin 2006; Aguiar et al. 2007, 2008). In some of these contact zones, reports of mixed-species groups and hybrids have recently increased. Genetic data have provided evidence of hybridisation in mixed-species groups of *A. palliata* and *A. pigra* (Cortés-Ortiz et al. 2007), and observational data suggest the existence of mixed-species groups and putative hybrids between *A. g. clamitans* and *A. caraya* in southeastern Brazil (Aguiar et al. 2007, 2008).

We carried out a long-term study on brown howlers (*A. g. clamitans*) and black howlers (*A. caraya*) living in sympatry in El Piñalito Provincial Park, Misiones, north-eastern Argentina. In this paper, we report the first recorded case of immigration by an adult female black howler into a brown howler group, and two observations of putative infant hybrids born in this mixed-species group.

Materials and methods

This study was carried out in El Piñalito Provincial Park (26°30'S, 53°50'W), a strictly protected area of 3,796 ha. The climate is subtropical and humid (annual rainfall 1,800–2,000 mm; Crespo 1982). El Piñalito suffered a recent history of selective forest logging (before the creation of the park in 1990), which, together with the establishment of plantations of exotic trees (*Pinus eliotti* and *Eucalyptus* sp.) and native araucaria (*Araucaria angustifolia*), has changed the original forest structure in some portions of the study area.

The study began in January 2005. In the surveyed area (ca. 800 ha), we recorded the presence of three groups of black howlers and six groups of brown howlers. Both black and brown howlers show sexual dichromatism (Gregorin 2006). Infants, less than 12 months old, are clearly distinguishable between species by the presence of a bright grey-yellow natal coat in black howlers and a dark reddish-brown coat in brown howlers. We selected two groups of brown howlers and two groups of black howlers with contiguous or overlapping home ranges for a long-term study on their ecology and behaviour. We followed each group from dawn to dusk for periods of 2–5 days per month between October 2005 and November 2007. We collected data on diet, activity and ranging at 10-min intervals using the scan sampling method. Data on social interactions occurring among individuals out

of a scan period were recorded ad libitum (Altmann 1974).

The putative hybrids reported here were observed in one of our study groups, “Gitanos”. This was a mixed-species group, containing one adult male and two adult female brown howlers and one adult female black howler. Given the lack of genetic data for these individuals, we classified *A. g. clamitans*-like individuals as brown howlers, and *A. caraya*-like individuals as black howlers on the basis of their pelage colour. From November 2005 to 2007, we spent 540 h following the Gitanos group. Between November 2005 and 2006 (Period 1), we followed the group every month except for January, June and November 2006. Between December 2006 and November 2007 (Period 2), we followed the group every month.

Results

During Period 1, the adult female black howler appeared to be in the process of becoming a stable member of Gitanos, because her presence in the group was intermittent (six out of ten monthly followings). During Period 2, we always found this female in the group.

Considering the grooming sessions recorded from scan samples and ad libitum observations together, the frequency of grooming directed from other individuals to the adult female black howler was significantly lower during Period 1 (two records over 103 h of observation), compared to Period 2 (65 records over 342 h of observation, $\chi^2 = 15.37$, $df = 1$, $P < 0.001$), while the general frequencies of grooming in the group did not differ significantly between the two periods (Period 1: 180 records over 103 h, Period 2: 549 records over 342 h, $\chi^2 = 0.95$, $df = 1$, $P = 0.33$; expected frequencies were calculated on the basis of the number of hours of observation).

On 5 December 2006, we observed the adult female black howler of Gitanos carrying an infant (ca. 1.5 months old), whose pelage colour pattern was a mosaic between the typical pattern of infant black howlers and that of infant brown howlers; its head, back and arms were reddish-pink, with its legs and tail gradually changing to light yellow. We could not determine the sex of the infant. During this survey, the mother was quite peripheral, rarely coming close to other group members. In the following survey (14–17 January 2007), the adult female black howler was not in the group for the first 2 days; she joined the group, without the infant, on the 3rd day. At this time, no other infant was present in the group.

The adult female black howler was observed copulating twice: the first time (January 2007) with an adult male of another brown howler group; the second time (February 2007) with the adult male of the Gitanos group. Given the



Fig. 1 The adult female black howler (or *Alouatta caraya*-like) with the putative hybrid infant on her back and the adult male brown howler (or *Alouatta guariba clamitans*-like) of the Gitanos mixed group (El Piñalito Provincial Park, Misiones, northeastern Argentina)

howlers' typical gestation length (6 months; Glander 1980), neither of these copulations can account for the following hybrid reported.

On 11 November 2007, we found the adult female black howler carrying a new infant (a male, ca. 1 month old, Fig. 1). This infant had a colour pattern very similar to the infant described above. At this time, the other two adult females in the group already had one infant each. The putative hybrid infant died almost simultaneously with all his group members during a yellow fever outbreak that occurred in early 2008.

Discussion

A contact zone between *A. g. clamitans* and *A. caraya* has been reported for the Paraná River, in the surroundings of the Ilha Grande National Park, southern Brazil. In a small forest fragment, established mixed-species groups containing individuals of one or both species and adult hybrid morphotypes have been observed (Aguiar et al. 2007, 2008).

In this paper, we report the formation of a mixed-species group at its initial stage, and two records of putative hybrid infants in northeastern Argentina. The hypothesis of recent migration of the adult female black howler into the brown howler group is supported by the observed gradual changes in her within-group stability and grooming relationships with the other group members along the two study periods. The two putative hybrid infants born from this female presented one of the morphotypes described by Aguiar et al. (2008). However, our study case differs in many aspects from that reported by Aguiar and colleagues.

First, in the Brazilian fragment, mixed groups were the great majority (7 of 11), and 8 of 57 individuals were potential adult hybrids (Aguiar et al. 2008). In our study site we only found one mixed group out of nine, and just two infant hybrid morphotypes, both belonging to the same female, out of 62 individuals censused. The smaller proportion of mixed groups and putative hybrids at our study site compared to the Brazilian site suggests that hybridisation in this portion of the shared range of *A. g. clamitans* and *A. caraya* is a rare phenomenon.

Second, the study area of Aguiar et al. (2008) is an ecotone between two biomes: the Cerrado, the typical habitat of black howlers in Brazil (Hirsch et al. 1991), and the Atlantic Forest, where brown howlers are endemic (Rylands et al. 1996). The presence of contact zones between howler species at other sites is associated with ecotones (Chames and Olmos 1997; Cortés-Ortiz et al. 2007). In our study area, the contact zone is not located at an ecotone but lies within the Atlantic Forest ecoregion (Di Bitetti 2003). This habitat type is not typical for black howlers (Brown and Zunino 1994). If black howlers are adapted to the naturally secondary and fragmented forests of Chaco and Cerrado, they may be well-suited to facing the increasing fragmentation of the Atlantic Forest and, as a consequence, may have recently expanded over the range of brown howlers, generating a contact zone in this area (Di Bitetti et al. 1994).

Third, the Brazilian site is a very small forest fragment (150 ha) (Aguiar et al. 2008). In the adjacent continuous riparian forest only monospecific groups of each species were reported (Aguiar et al. 2007). It is likely that, in small fragments, howlers reach higher densities compared to the continuous forest (Kowalewski and Zunino 1999). When both howler species are confined to a small space at high densities, the costs of entering a new conspecific group for a dispersing individual, and then the chance of formation of mixed-species groups and hybridisation, should be higher than in less dense populations. Accordingly, at El Piñalito, a medium-size protected area at least partially connected to other large forest patches in Misiones, with low population densities of both howler species, we observed a lower incidence of mixed-species groups and hybridisation compared to the Brazilian site. Here, the particular case of the adult female black howler migrating into a brown howler group and copulating with brown howler males, could be the result of her difficulty to find and enter an established conspecific group in an area of low population density.

In the light of the between-site comparisons reported above, one could predict that the frequency of hybridisation in areas of sympatry will depend on the relative costs of entering a new group for dispersing individuals, which in turn depend on demographic aspects of the populations,

predation risk and habitat fragmentation. Genetic studies are critically important to help evaluate the incidence of this phenomenon and the possibility of gene introgression in populations of sympatric congeneric species. These are important issues affecting the management and conservation of primates in their natural habitats.

Acknowledgments We thank Daphne Colcombet for her support, and Esteban Pizzio, Nacho Areta, and the field assistants, who helped us in the data collection and other field activities. We thank the Ministry of Ecology of Misiones for the research permit and the park rangers for their support during the study. Funding was provided by the Cleveland Metroparks Zoo's Scott Neotropical Fund Program, Primate Action Fund (CI), Primate Conservation Inc., International Primatological Society, Idea Wild, CEDIT, CONICET (PIP 6318), and Rufford Small Grant. Elisabetta Visalberghi, Brandon Wheeler and two anonymous reviewers provided helpful comments on the manuscript.

References

- Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49:227–267
- Aguiar LM, Mellek DM, Abreu KC, Boscarato TG, Bernardi IP, Miranda JMD, Passos FC (2007) Sympatry between *Alouatta caraya* and *Alouatta clamitans* and the rediscovery of free-ranging potential hybrids in Southern Brazil. *Primates* 48:245–248
- Aguiar LM, Pie MR, Passos FC (2008) Wild mixed groups of howler species (*Alouatta caraya* and *Alouatta clamitans*) and new evidence for their hybridization. *Primates* 49:149–152
- Arnold ML, Meyer A (2006) Natural hybridization in primates: one evolutionary mechanism. *Zoology* 109:261–276
- Brown AD, Zunino GE (1994) Hábitat, densidad y problemas de conservación de los primates de Argentina. *Vida Silvestre Neotropical* 3:30–40
- Chame M, Olmos F (1997) Two howler species in southern Piauí, Brazil? *Neotrop Primates* 5:74–77
- Cortés-Ortiz L, TF Duda Jr, Canales-Espinosa D, García-Orduña F, Rodríguez-Luna E, Bermingham E (2007) Hybridization in large bodied New World primates. *Genetics* 176:2421–2425
- Crockett CM (1998) Conservation biology of the genus *Alouatta*. *Int J Primatol* 19:549–578
- Crespo JA (1982) Ecología de la comunidad de mamíferos del Parque Nacional Iguazú, Misiones. *Rev MACN, Ecología* 3:45–162
- Defler TR (2004) *Primates of Colombia*. Conservation International, Bogotá
- Detwiler KM, Burrell AS, Jolly CJ (2005) Conservation implications of hybridization in African Cercopithecine Monkeys. *Int J Primatol* 26:661–684
- Di Bitetti MS (2003) Outlook for primate conservation in Misiones. In: Galindo Leal C, Camara IG (eds) *The state of the hotspots: the Atlantic Forest of South America: biodiversity status, threats, and outlook*. Island Press, Center for Applied Biodiversity Science at Conservation International, Washington, pp 194–199
- Di Bitetti MS, Placci G, Brown AD, Rode DI (1994) Conservation and population status of the brown howling monkey (*Alouatta fusca clamitans*) in Argentina. *Neotrop Primates* 2:1–4
- Glander KE (1980) Reproduction and population growth in free-ranging mantled howler monkeys. *Am J Phys Anthropol* 53:25–36
- Gregorin R (2006) Taxonomia e variação geográfica das espécies do gênero *Alouatta* Lacépède (Primates, Atelidae) no Brasil. *Rev Bras Zool* 23:64–144
- Groves CP (2001) *The taxonomy of primates*. Smithsonian Institution Press, Washington
- Hirsch A, Landau EC, Tedeschi ACM, Menegheti JO (1991) Estudio comparativo das espécies do gênero *Alouatta* Lacépède, 1799 (Platyrrhini, Atelidae) e sua distribuição geográfica na América do Sul. In: Rylands AB, Bernardes AT (eds) *A primatologia no Brasil 3*. Fundação Biodiversitas, Belo Horizonte, pp 239–262
- Iwanaga S, Ferrari FS (2002) Geographic distribution of red howlers (*Alouatta seniculus*) in Southwestern Brazilian Amazonia, with notes on *Alouatta caraya*. *Int J Primatol* 23:1245–1256
- Kowalewski MM, Zunino GE (1999) Impact of deforestation on a population of *Alouatta caraya* in northern Argentina. *Folia Primatol* 70:163–166
- Mendes SL (1997) Hybridization in free-ranging *Callithrix flaviceps* and the taxonomy of the Atlantic Forest marmosets. *Neotrop Primates* 5:6–8
- Peres CA, Patton JL, Da Silva MNF (1996) Riverine barriers and gene flow in Amazonian saddle-back tamarin monkeys. *Folia Primatol* 67:113–124
- Pinto LP, Setz EZF (2000) Sympatry and new locality for *Alouatta belzebul discolor* and *Alouatta seniculus* in the Southern Amazon. *Neotrop Primates* 8:61–93
- Rylands AB, da Fonseca GAB, Leite YLR, Mittermeier RA (1996) *Primates of the Atlantic Forest: origin, distributions, endemism, and communities*. In: Norconk MA, Rosenberger AL, Garber PA (eds) *Adaptive radiations of neotropical primates*. Plenum, New York, pp 21–51
- Silva BTF, Sampaio MIC, Schneider H, Schineider MPC, Montoya E, Encarnación F, Salzano FM (1992) Natural hybridization between *Saimiri* taxa in the Peruvian Amazonia. *Primates* 33:107–113
- Wallace RB, Painter RLE, Taber AB (1998) Primate diversity, habitat preferences, and population density estimates in Noel Kempff Mercado National Park, Santa Cruz Department, Bolivia. *Am J Primatol* 46:197–211