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ORIGINAL ARTICLE

Hybridization between *Alouatta caraya* and *Alouatta guariba clamitans* in captivity

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Abstract Hybridization between *Alouatta* spp. has been suggested at contact zones of *A. palliata* and *A. pigra* in Mexico and of *A. caraya* and *A. guariba clamitans* in Brazil and Argentina. Whereas genetic data confirmed hybridization between the former pair of species, hybrid individuals of the latter pair have been putatively identified on the basis of a mosaic pelage color. In this paper, we describe the first confirmed cases of hybridization between a female *A. guariba clamitans* and a male *A. caraya*. One hybrid male was born in 2007 and one hybrid female was born in 2009 with distinct coat colors. The male resembled the newborn color pattern characteristic of *A. guariba clamitans*, whereas the female resembled the newborn pattern of *A. caraya*. The birth and survival of the male hybrid for a year and a half indicated the viability of the heterogametic sex.

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Introduction

Natural hybridization is a phenomenon observed in all major primate lineages—strepsirrhines, New World monkeys, Old World monkeys, and apes (Arnold and Meyer 2006). Among New World monkeys, there are reports of wild hybrids in the genera *Saimiri* (Silva et al. 1992), *Callithrix* (Alonso et al. 1987; Coimbra-Filho et al. 1993; Mendes 1997), *Saguinus* (Peres et al. 1996), and *Alouatta* (Gregorin 2006; Aguiar et al. 2007, 2008; Cortés-Ortiz et al. 2007; Agostini et al. 2008; Bicca-Marques et al. 2008; Cortés-Ortiz 2009).

In *Alouatta*, hybridization between *A. palliata* (mantled howler monkeys) and *A. pigra* (black howler monkeys) in Mexico was confirmed by genetic data (Cortés-Ortiz et al. 2007; Cortés-Ortiz 2009). Observation of adult males with coats showing a mosaic of black and red and of adult females with an admixture of yellowish and dark brown at contact zones between *A. caraya* (black-and-gold howler monkeys) and *A. guariba clamitans* (brown howler monkeys) in Brazil suggests that these taxa can also hybridize in the wild (Gregorin 2006; Aguiar et al. 2007, 2008; Bicca-Marques et al. 2008). *A. caraya* and *A. guariba clamitans* are the only two sexually dichromatic taxa in the genus (Bicca-Marques and Calegaro-Marques 1998). In the former species, adult males are fully black and adult females are yellowish, whereas adult males are deep reddish and adult females are dark brown in the latter (Gregorin 2006). In both species, males and females are born with similar coats that resemble the maternal

pattern. In addition, Agostini et al. (2008) report an adult female *A. caraya* living within an *A. guariba clamitans* group in Argentina, copulating with the males, and giving birth to two infants with hybrid morphotypes in two consecutive years. Although these observations are strongly suggestive of natural hybridization, the fact that extragroup copulations have been observed in several howler monkey species (Horwich 1983; Agoramoorthy and Hsu 2000; Kowalewski et al. 2005; Fialho and Setz 2007) does not allow ruling out the hypothesis that the adult female *A. caraya* of this mixed-species group copulated with conspecific males during intergroup encounters at this contact zone.

Here we report the first cases of hybridization between *A. guariba clamitans* and *A. caraya* where the maternal and paternal species are known, and we describe the distinct pelage patterns shown by the two hybrid newborns.

Methods

A mixed group composed of an adult female *A. guariba clamitans* and an adult female and an adult male *A. caraya* was kept in an enclosure 4 × 5 × 5 m enriched with branches, poles, and a wood shelter at "Criadouro Conservacionista Arca de Noé" in Morro Reuter, State of Rio Grande do Sul, Brazil from April 2005. The three individuals were confiscated from the illegal trade by the Brazilian Environmental Authority (IBAMA). Although their origin is unknown, their pelage color allows us to strongly suggest they are pure individuals: the adult female *A. guariba clamitans* is dark brown; the adult female *A. caraya* is yellowish, and the adult male is fully black. The female *A. guariba clamitans* arrived as a dependent, unweaned infant and was hand-reared by the owners of the facility. As she grew older, she was kept in an enclosure at the side of the enclosure where the adult couple and another adult male *A. caraya* were kept. These individuals adopted her, and she was moved into their enclosure with the intention of improving their welfare. Soon after, all individuals were moved to the larger enclosure mentioned above. Later, the adult males began to fight, and one was removed from the enclosure. Because of tooth surgery, the adult male who sired the hybrid offspring was kept at another enclosure between late December 2008 and early March 2009. Upon his return, the adult female *A. guariba clamitans* and her infant were moved to an exclusive enclosure in an, unsuccessful, attempt to avoid further hybridization events.

Results

In September 2007, the adult female *A. guariba clamitans* gave birth to a hybrid infant male with a color pattern resembling the dark brown pelage of newborns of her species. When this individual died at the age of 1 year and 6 months, his pelage color was a mosaic of brown (characteristic of female and immature male *A. guariba clamitans*) and black (characteristic of adult and maturing *A. caraya* males) (Fig. 1).

A hybrid infant female was born in April 2009 with a predominance of the light, beige coloration characteristic of her paternal species (Fig. 2a, b). At about 3 months of age, her color pattern had changed to a mosaic between beige (characteristic of youngster *A. caraya*) and brown (characteristic of youngster *A. guariba clamitans*; Fig. 2c), whereas from the age of 5–9 months, her mosaic coloration most resembled her maternal species (Fig. 2d–f).

Fig. 1 Hybrid male born in 2007 at the age of about 17 months showing his mosaic pelage of black (characteristic of *Alouatta caraya*) and brown (characteristic of *A. guariba clamitans*)

Fig. 2 Hybrid female born in 2009 showing the gradual color change: **a** soon after birth (April), showing her beige coat (characteristic of *Alouatta caraya* newborns), with her brown *A. guariba clamitans* mother; and at the age of **b** 1 month (May), **c** 3 months (July, riding on her mother's back), **d** 5 months (September), **e** 7 months (November), and **f** 9 months (January 2010)

Discussion

These observations confirm the viability of infant hybrids between *A. caraya* and *A. guariba clamitans*, taxa belonging to clades separated for 5.1 Ma (Cortés-Ortiz et al. 2003), supporting the observations of Agostini et al. (2008) in Argentina; and the relationship between this phenomenon and the mosaic coloration of hybrid offspring, as suggested by Gregorin (2006), Aguiar et al. (2007, 2008), and Bicca-Marques et al. (2008). Additionally, the two hybrids reported in this study were born with distinct pelage color patterns despite the fact they are offspring of the same parents. Although the parents are very likely pure individuals, in the absence of genetic data and information on their origin, we cannot eliminate the possibility that one or both of them are also hybrids. In this case, their offspring would represent backcrosses or multigenerational hybrids.

Unlike the crosses between *A. palliata* and *A. pigra* that produce inviable or infertile male offspring (Cortés-Ortiz et al. 2007; Cortés-Ortiz 2009), crosses between *A. caraya* and *A. guariba clamitans* can produce viable males. Additionally, the data from Argentina (Agostini et al. 2008) and from this study reveal that male offspring of this latter pair of taxa is viable regardless of the species to which each parent belongs. Whereas we report breeding of a female *A. guariba clamitans* with a male *A. caraya*, the opposite is reported by Agostini et al. (2008). The fertility of these hybrid males could not be assessed because all three died before reaching adulthood.

Genetic studies are imperative to confirm the status conferred to individuals at contact zones as pure or hybrid on the basis of coat color only to assess the fertility and reproductive success of both male and female hybrids and occurrence of backcrosses, and to understand the genetic

basis of newborn and adult color determination in these sexually dichromatic howler monkey species.

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