Short Articles

Reproductive Seasonality in the Belizean Black Howling Monkey (*Alouatta pigra*)

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The synchrony of mating by female primates ("temporal synchrony") and the subsequent synchrony of births varies within and between species and is thought to be a function of resource distribution in time and space as well as other environmental factors such as the risks of predation or infanticide (Nunn, 1999). Primates may exhibit discrete birth seasons, birth peaks, birth "clusters", birth "dips", or females may produce young asynchronously throughout the year (see reviews in Smuts *et al.*, 1986 and Crockett and Rudran, 1987). From a female's perspective, the timing of reproduction is expected to exert a significant influence on lifetime reproductive success if her chances of successful reproduction vary significantly from month to month. In particular, environmental regimes (e.g., food availability or risks of infanticide) may determine probabilities of successful implantation, gestation, lactation, or maternal or infant survival.

The present note presents evidence that Belizean black howling monkeys (*Alouatta pigra*) exhibit a significant peak in births during those months when rainfall is lowest and that this reproductive seasonality may be related to peaks in the abundance of fruit during the period of gestation. Reproductive seasonality has been reported for two other species of *Alouatta* (*A. palliata*: Jones, 1980; Fedigan *et al.*, 1998; and *A. seniculus*: Crockett and Rudran, 1987). Similarities and differences between these reports and the present observations will be discussed in addition to a consideration of data available on birth patterns for other species of the genus.

The six or seven recognized species of howling monkeys, large, vegetarian, arboreal atelids, are distributed throughout Latin America from northern Argentina to southern Mexico (Crockett and Eisenberg, 1986). Our *ad libitum* observations of marked black howlers were collected at the Community Baboon Sanctuary (CBS), Belize, Central America. The CBS is a managed reserve of >18 sq. mi. formed in 1985 by cooperative agreement among private landowners (Horwich, 1990). Located at 17°33' N, 88°35' W, the CBS is a mosaic of small farms, pastures and tropical moist forest fragments including riparian habitat along the Belize River (see Horwich and Lyon, 1990). The study area is composed of mapped trails, and >1500 trees are mapped and identified. Black howlers are generally polygynous (single breeding male) with a modal group size of one adult male to several adult females and immatures (Horwich *et al.*, in prep.), although multimale-multifemale (polygynandrous) groups may be found. Groups have been studied by the present research program since 1985, and systematic observations, including marking of animals and collection of morphometric data, have been carried out since the early 1990's.

Horwich (1983) reported opportunistic observations of sexual behavior in *A. pigra*, although reproductive behavior in the species has not been described in systematic detail. Our observations indicate that reproductive parameters in black howlers are similar to those of their congeners. In particular, gestation length appears to be slightly over six months (Brockett, pers. obs.), and interbirth intervals are within the range reported for other *Alouatta* species (Horwich *et al.*, in prep.). Black howler females demonstrate unreliable genital markers during the estrous cycle, similar to *A. seniculus* (Crockett and Eisenberg, 1986), although chemical cues appear to be significant as suggested by male attraction to female genitalia (Horwich, 1983). A male and a female may leave a group

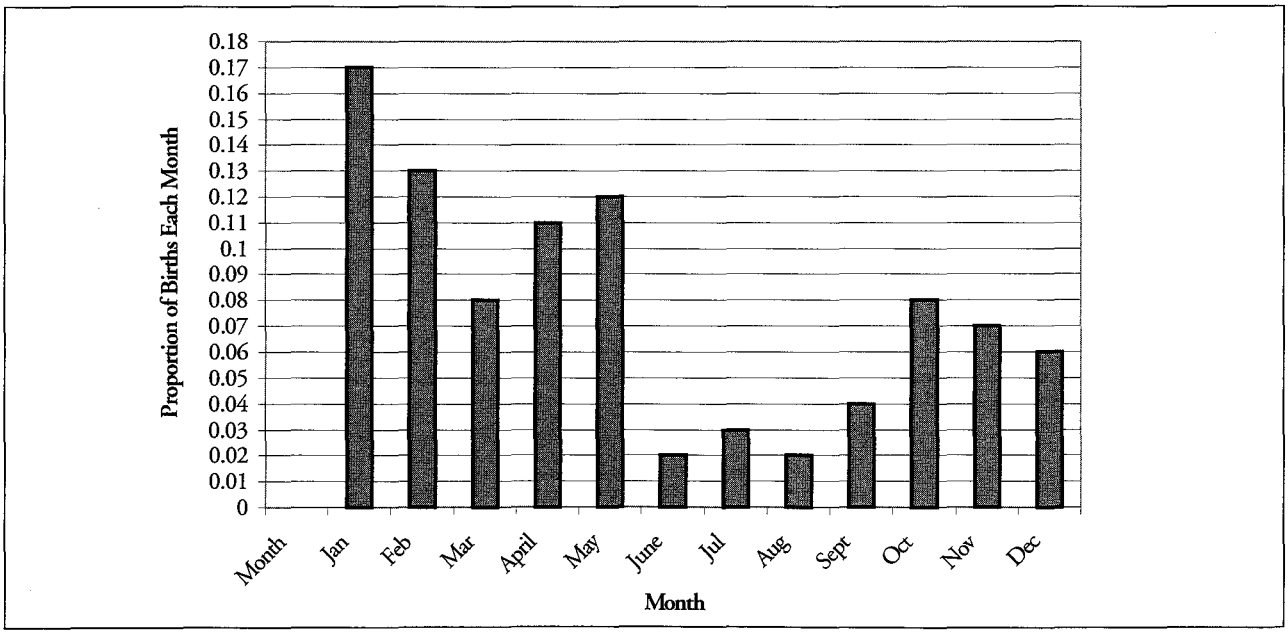

Figure 1. The distribution of black howler births at the CBS (1992-1999). Months with lowest annual rainfall are in black.

together in apparent consort (Brockett, pers. obs.; Horwich, pers. obs.; Jones, pers. obs.) as reported for *A. seniculus* (Crockett and Eisenberg, 1986) and *A. palliata* (Jones, 1995). No data are available for either sex on age of sexual maturity in black howlers.

Figure 1 shows the proportion of births per month at the CBS from 1992–1999 (N = 121). Births differ significantly by month ($p<0.001$, $x^2 = 36.38$, df = 11), and births are significantly more likely to occur during the six month period, December through May, which is early dry season through early wet season, (Horwich and Lyon, 1990) than during the remaining six months of the year ($p<0.001$, $x^2 = 26.5$, df = 1). Silver (1998, Fig. 2.3) reports an annual peak in fruit from July to December, suggesting that females adjust gestation to this annual period and lactation to the driest months.

There is no simple relationship between birth peaks, seasonality, and food availability within the genus *Alouatta*. Jones (1980) reported a statistically significant peak in births during the dry season at Hacienda la Pacifica (Costa Rica). Her report combined data for two groups, one in riparian habitat and one in deciduous habitat, presumed to be the poorer habitat. All births in the latter habitat were restricted to the dry season (November through April). Recently, Fedigan *et al.* (1998) reported a statistically significant birth peak in Costa Rican deciduous habitat (Santa Rosa National Park) during the dry season. Clarke and Glander (1984), primarily studying mantled howler groups in riparian habitat at Hacienda la Pacifica, reported birth "clusters" without annual patterns and slightly more births during the wet season than the dry season. At Barro Colorado Island, Panama, a semideciduous lowland tropical forest, Carpenter (1934) found that births occurred throughout the year, while at the same site Milton (1982) found some evidence of clustering. In the same species, then, differences have been found within and between habitats with drier sites (Santa Rosa and Hacienda la Pacifica) and wetter sites (riparian and semideciduous) appearing to demonstrate the same trends. Birth peaks in tropical dry forest, in particular, deciduous forest, may be related to the availability of fruit (Frankie *et al.*, 1974). Mantled howlers in these forests may time lactation to coincide with food availability, the opposite pattern than that proposed for black howlers.

Crockett and Rudran (1987) described reproductive seasonality in *A. seniculus*. Reporting results for two habitats (woodland and gallery forest), they suggested a birth peak in woodland habitat during the dry season, as found for *A. palliata* in deciduous habitat. In Crockett and Rudran's Venezuelan study site, woodland habitat is most likely the poorer for red howlers, similar to deciduous habitat for mantled howlers. Crockett and Rudran (1987) also found a "birth dip" in both habitats during the early wet season (May–July). In Argentina, Zunino and his colleagues reported a birth peak from mid March–mid June for the black-and-gold howling monkey, *A. caraya*, in riparian forest, possibly related to "a slight reduction in rainfall" (Zunino, pers. comm., October, 2000). However, infants are born throughout the year in flooded insular habitats along the Paraná river (Zunino, pers. comm., October, 2000).

Crockett and Rudran (1987) pointed out that howlers might be expected to exhibit less seasonal breeding than other genera due to their broad vegetarian diets and large body size. Nonetheless, as reviewed here, several studies have found reproductive seasonality in *Alouatta*. Additional studies are required to document the extent of birth peaks and reproductive seasonality in howling monkeys and the proximate and ultimate causes of these patterns.

Acknowledgments: We are grateful to Dr. K. E. Glander for his assistance in marking the animals. These studies were carried out with the support of the National Geographic Society (Grants #5352-94 and #5653-96).

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AGONISTIC ENCOUNTERS BETWEEN MURIQUIS, *BRACHYTELES ARACHNOIDES HYPOXANTHUS* (PRIMATES, CEBIDAE), AND OTHER ANIMALS AT THE ESTAÇÃO BIOLÓGICA DE CARATINGA, MINAS GERAIS, BRAZIL

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Introduction

The Atlantic forest of southeastern Brazil is well-known for high levels of primate species diversity and endemism (Rylands *et al.*, 1995). There are currently 24 primate species and subspecies recognized in the Atlantic forest, with up to five species still found sympatrically in a number of remaining forest tracts (Rylands *et al.*, 1996). Censuses of a number of these primate communities, particularly in the states of Minas Gerais and São Paulo, have consistently estimated higher primate population densities in the small, disturbed forest fragments than in the larger, more pristine ones (Stallings and Robinson, 1991; Pinto *et al.*, 1993; Hirsch, 1995; Strier and Fonseca, 1996/1997). For example, density estimates for northern muriquis (*Brachyteles arachnoides hypoxanthus*) and brown howler monkeys (*Alouatta fusca*) are much greater in the 890 ha forest at the Estação Biológica de Caratinga (EBC), in Minas Gerais, than in the nearby, 36,114 ha Parque Estadual de Rio Doce (Hirsch, 1995).

High densities, along with high dietary and habitat overlap among species, are also likely to lead to high frequencies of interspecific encounters, and possibly correspondingly high levels of direct or indirect interspecific competition (Waser, 1987). However, very little is known about how high levels of interspecific competition might affect populations of endangered species (Strier *et al.*, 2000).

In a preliminary investigation, we collected data on the contexts and outcomes of all agonistic interactions observed between northern muriquis, now classified as one of the world's 25 most endangered primates (Conservation International, 2000), and other animals at the EBC. In addition to muriquis and brown howler monkeys, the EBC primate community consists of a third endangered species of primate, the buffy-headed marmoset (*Callithrix flaviceps*), and the more widespread tufted capuchin monkey (*Cebus nigritus*).

Because larger-bodied species tend to "win" in direct contests with smaller-bodied species (Waser, 1987), we predicted that muriquis, which can weigh up to 15 kg (Aguirre, 1971) would be "dominant" in their interactions with other smaller primate species and with other smaller animals. Nonetheless, the fact that the diets of all four species of primates at the EBC overlap to varying degrees led us to predict that differences in the frequency and intensity of interspecific interactions would occur. For example, EBC muriquis and howler monkeys consume many of the same species, and in some cases, patches of fruits, leaves, and flowers (Mendes, 1989; Strier, 1991; Rímoli, 1994). Tufted capuchins are omnivorous, and have been known to prey on a variety of in-

Table 1. Muriqui behavior during aggressive interactions with other animals at the EBC.

	Howlers		Capuchins		Tayra		Owl		Lizard	
Muriqui behavior*	N	%	N	%	N	%	N	%	N	%
Branch shaking	9	31.0	4	33.3	1	100	1	100	1	100
Teeth-bared	1	3.4	1	8.3	-	-	-	-	1	100
Chase	26	89.0	11	91.7	1	100	1	100	1	100
Vocalize	11	37.0	11	91.7	1	100	1	100	1	100

*Percentages for each species may exceed 100% because muriqui behaviors are not mutually exclusive.

Table 2. Contexts of agonistic interactions between muriquis and other animals at the EBC.

	Howlers		Capuchins		Tayra		Owl		Lizard	
Muriqui activity*	N	%	N	%	N	%	N	%	N	%
Traveling	7	24.1	3	25.0	-	-	-	-	-	-
Resting	3	10.3	7	58.3	1	100	1	100	1	100
Feeding	16	55.2	4	33.3	-	-	-	-	-	-
Playing infants	5	17.2	1	8.3	-	-	-	-	-	-

*Percentages for each species may exceed 100% because muriqui behaviors are not mutually exclusive.