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### DISAPPEARANCE OF INFANTS FOLLOWING MALE TAKEOVERS IN THE BELIZEAN BLACK HOWLER MONKEY (*ALOUATTA PIGRA*)

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Organisms are expected to employ self-interested tactics and strategies to maximize lifetime probabilities of survival and reproductive success (Trivers, 1985). Behavior programs may differ significantly between the sexes, since selection is thought to operate on the relative parental investment in offspring by males, on the one hand, and females, on the other (Trivers, 1972). Some researchers (e.g., Sugiyama, 1967; Hausfater and Hrdy, 1984) have argued that males may gain a reproductive advantage by killing infants likely to have been sired by non-kin ("infanticide"). This "sexual selection hypothesis" suggests that infanticide shortens a female's interbirth interval through the cessation of lactation and subsequent return of ovarian cycling. Infanticidal males are thought to gain a reproductive advantage by impregnating the dead infant's mother.

Dixon (1998, Table 4.4, p.68) summarizes 48 cases of infanticide observed directly in 13 primate species. Paletropical species account for 42 of the 48 (88%) cases, and the Hanuman langur (*Presbytis entellus*) accounts for 21 of them (50%). The bias in this database favoring Old World primates, and *P. entellus* in particular, may reflect sampling

error resulting from differential time-investment by researchers. Supporting this idea is the observation that infanticide has been reported most commonly in terrestrial or semi-terrestrial species for which visibility is less of a deterrent to observation.

Infanticide has been reported for four species of *Alouatta* (*A. seniculus*, the red howler monkey: Rudraa [1979], Sekulic [1983]; *A. caraya*, the black and brown howler monkey: Zunino et al. [1986], Rumiz [1940]; *A. fusca*, the brown howler monkey: Galeotti et al. [1994]; and *A. palliata*, the mantled howler monkey: Clarke [1981, 1983]). The first three species exhibit polygynous mating systems (after Dixon, 1998) while *A. palliata* groups vary from polygynous to multimale-multifemale (see Crockett and Eisenberg, 1987). Clarke's (1981, 1983) study groups exhibited multimale-multifemale social organization, and infanticide was associated with turnovers in the male hierarchy. Infanticide typically occurs in polygynous (harem or age-graded) or multimale-multifemale mating systems (Dixon, 1988).

We conducted *ad libitum* observations of marked *A. pigra* at the Community Baboon Sanctuary (CBS), Belize. The CBS is a managed reserve 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 >1000 trees have been mapped and identified. Black howlers are generally polygynous with a modal group size of one adult male to several adult females and immatures (Ostro et al., 1999), although multimale groups may be found. Studies of demography, ecology, social organization and behavior are in their early stages (e.g., Horwich, 1983; Silver et al., 1998; Ostro et al., 1999).

As part of a broader study, five incidents of infant disappearance associated with male takeovers were observed (Table 1). These data suggest several topics for further research. First, similar to findings for langurs (*Presbytis* spp.) (Sommer, 1994), there appears to be a male bias in the sex of infants which disappeared. It would be interesting to obtain larger sample sizes in order to evaluate the sex ratios of infants killed, since an offspring's "value" will differ according to its sex and, possibly, the condition of the mother (see Hrdy, 1987). It is possible that infanticide generally occurs in response to some threshold of benefits to costs to the potential victimizer and that the "value" of the po-

**Table 1.** Observations of infant disappearances at the Community Baboon Sanctuary, Belize. All observations recorded by RCB.

Dates of Takeover	Troop	Male(s) displaced	Displacing male	Mother of infant	Post-takeover copulation observed
2 Feb. - 20 Feb. 1995	Roxie	BBLT, UM	BWB	BBLT BBRT W	yes <sup>1</sup> no <sup>2</sup>
27 Feb. - 30 Mar. 1995	Baizar	O	BBLT	ORT	no <sup>2</sup>
15 Feb. - Mar. 1997	Robin	WLT	Baizar	LLT	yes

<sup>1</sup>BBRT gave birth to a male offspring on 13 October 1995 and BBLT to a male offspring on 1 December 1995.

<sup>2</sup>Copulation attempt observed.

tential victim affects this tradeoff. Some infants may be of such low "value" that they are not worth killing. Alternatively, in some conditions, the costs of infanticide may be prohibitively high. These ideas are supported by the observation that infant disappearance was not observed in association with all male takeovers.

Second, female W died of an intestinal obstruction shortly after the takeover. Although we cannot verify that she was injured during aggressive encounters between displacing and displaced males, it is important to stress that male-male aggression has potential costs (sometimes unexpected) for males that may outweigh the benefits in some conditions.

Third, male BBLT initiated a successful takeover of Eaizar troop after he was displaced from Roxie troop by the male BWB. This observation reinforces the benefits of group membership and suggests an apparent cascade effect since we assume that BBLT would not have left his group without the precipitating events of BWB's takeover.

Fourth, our observations show that a single male can take over a multimale group (Roxie troop). Thus, arguments other than superior fighting ability alone must be sought to explain successful takeover strategies. Takeovers should be studied as components of male reproductive strategies, including the role of females in determining which males lead their groups.

Finally, all of our observations occurred in February or March. While this result may be a function of sampling error, systematic studies have been made on a monthly basis at the CBS since 1992, including several thousand contact hours. February and March are the peak of the dry season when preferred food (new leaves, flowers, and fruit) abundance is low and many deciduous trees lose their mature leaves (see Silver, 1998, especially Figs. 2.2 and 2.3), possibly creating stressful conditions for these folivorous monkeys. Food stress in combination with reduced habitat occasioned by deforestation and resultant fragmentation may increase population density and interaction rates, possibly resulting in increased aggressive competition among males (see Kowalewski *et al.*, 1995) and subsequent takeovers. Further research will test the significance of these results.

Our studies suggest that infanticide may be a significant component of a male's lifetime reproductive strategy. Dixon (1998), however, concludes his discussion of infanticide with the statement, "Infanticide is neither widespread nor of general importance in the evolution of primate social or sexual behaviour." (p.70, italics in the original). He bases this conclusion in part upon the observation that infanticide has been documented in only 12% of primate species. However, Johnstone and Cant (1999), using an evolutionarily stable strategy model, show that the potential for infanticide alone may influence the partitioning of reproduction within groups, even in situations where individuals cannot discriminate their own from another's offspring. Dixon's (1998) conclusion appears premature, awaiting, as is the fate of all speculations, confirmation or disproof

based on future evidence.

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