

ALTERNATIVE MALE REPRODUCTIVE BEHAVIORS IN THE BELIZEAN BLACK HOWLER MONKEY (*ALOUATTA PIGRA*)

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Introduction

Individuals differ in many aspects of reproductive behavior. Two or more reproductive phenotypes may be expressed during the lifetime of an individual and between individuals within the same population (Austad, 1984). Variation in mating patterns may be studied for an understanding of differential costs and benefits to survival and reproductive success of alternative reproductive behaviors (ARBs). In this paper we describe ARBs in male black howler monkeys (*Alouatta pigra*).

The study of ARBs in primates has a long history (Hrdy, 1974; Clarke, 1983; Horwich, 1983; Boggess, 1984; Smuts, 1985; Jones, 1995). ARBs entail all discrete tactics and strategies employed to maximize reproductive benefits (Austad, 1984). Dixon's (1998) discussion of ARBs by male primates shows that they exhibit various responses to gain access to group membership and receptive females. Among these responses, infanticide is, perhaps, the most controversial and widely discussed. ARBs will arise whenever individuals compete for mates, and sexual selection theory predicts that males will be most likely to compete for mates since females, or, rather, their fertilizable ova, are expected to be limiting resources (Trivers, 1972). Smuts (1987) found that the expression of ARBs in male primates is related to age, demography and life-history, stochastic effects (e.g., "accidents of history"), and unique traits of individuals (e.g., temperament or intelligence). Smuts' conclusions support the view that the diversity of intraspecific reproductive behaviors results from adaptive responses to local conditions, in particular, the operational sex ratio within populations (the ratio of males to females fecund at a given time), which provides a measure of the intensity of sexual selection among competitors (Emlen and Oring, 1977; also see Leland *et al.*, 1984).

Animals, Study Site, and Method

We conducted *ad libitum* observations of marked *A. pigra* at the Community Baboon Sanctuary (CBS), Belize. The CBS is a managed reserve of >18 sq. mi. formed in 1985 by a 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 has mapped trails, and >1500 trees are mapped and identified. Rhythms in plant communities are seasonal, with new leaf production occurring primarily at the beginning of the rainy season (late

May or June) (Horwich and Lyon, 1990). In northern Belize there are two flowering peaks. The largest peak occurs during the dry season (February through May) with a second, smaller peak occurring about one month after the rainy season begins (Horwich and Lyon, 1990). Fruiting activity is variable, within and between tree species (Horwich and Lyon, 1990). At any one time in northern Belize, there are at least some tree species producing fruit. Seasonally, there are two fruiting peaks: near the end of the dry season and a month or so after the start of the rainy season. Howler monkeys are wholly herbivorous, and phenological perturbations may have significant consequences for their populations.

Black howlers, large atelids, are generally polygynous (single breeding male) with a modal group size of one adult male to several adult females and immatures (Ostro *et al.*, 1999; Horwich, unpublished data), although multimale-multifemale (polygynandrous) 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). Groups have been censused since 1985, and systematic observations, including marking of animals and collection of morphometric data have been carried out since the early 1990's.

Results

Primary Patterns

Table 1 shows male displacements within black howler monkey groups at the CBS between 1992 and 1997. "Displacement" is used to mean that when one or more males enter an established unit, one or more males are expelled. Several patterns are noteworthy. First, males may transfer alone or in association with one or more males. When more than one male act together, they are always successful at expelling resident males from their groups, although male alliances or coalitions are not a necessary condition for successful expulsion. BBLT, for instance, expelled O in March, 1995. It is important to note, however, that, while single males successfully expelled a group male on two occasions, transferring males moving alone generally joined an existing group without expelling resident males. In 1992, for example, WRT successfully joined the Baptist troop without aggression and without expelling any males from the troop. WRT later left Baptist troop with BWB to displace Scar from the adjacent Fig troop in 1993 (Table 1).

Table 1 also demonstrates that changes in male membership within groups was not always accompanied by overt male-male aggression. Overt aggression among males appears to be most likely when resident males are expelled or when a transferring male attempts to enter a multi-male group. Infant disappearance also appears most likely in these conditions.

Of further interest, as reported in Brockett *et al.* (1999), we have identified a "cascade effect" in male takeovers whereby takeover by an extra-group male may precipitate a resident male to leave his group and initiate a takeover of another group (e.g., BBLT's takeover of Roxie troop in March, 1995 and LRT's takeover of Bamboo troop in November, 1995). The effect that we describe may be a response to some threshold of group den-

sity, possibly responsive to interaction rates, and expresses the potential for stochastic dynamics of population processes.

Transferring males were observed to attempt copulation or to copulate with resident females more than 50% of the time. These events were almost always associated with male-male aggression and subsequent infant disappearance. There appears to be a suite of associated responses for which sex and aggression, including infanticide, are correlated, although because aggression is not associated with every transfer event, its costs must often outweigh its benefits.

Secondary Patterns

Several additional aspects of male reproductive behavior were observed. First, males may disperse from groups of origin, sometimes their natal groups, and "float" in unoccupied habitat or remain peripheral to an intact group on its home range. Peripheral males have been observed to interact with group members, usually adult females in a sexual context. The role of females in determining who leads their social unit requires further study.

On one occasion, an expelled adult male and female were observed to form a new group, showing that new groups may form from a process of forced fissioning. In another instance, displaced individuals (an adult male, an adult female, and an immature) were observed wandering within the home ranges of two established groups. This result suggests that population density at the study site is high and that habitat is saturated; thus, all social units may not have home ranges.

Our observations suggest that "sperm competition" (see Birkhead and Moller, 1998) may be a significant evolutionary force in both single-male and multimale-multifemale groups of *A. pigra*. Transferring males, for example, were observed to solicit group females, and vice versa, before the male successfully obtained group membership or left a group's home range (see Horwich, 1983). Horwich (1983) observed copulations between a female of one group and an extra-group male, and even occasional copulations could generate "sperm

competition". In multimale-multifemale groups, newly-transferred males and resident males were observed to copulate with the same resident females during the same estrus cycles, suggesting "facultative polyandry" in *A. pigra* as has been reported for *A. palliata* (Jones and Cortés-Ortiz, 1998).

Discussion

Figure 1 is a diagram of the ARBs exhibited by *A. pigra* in the present study, as well as those ARBs suspected but not directly observed. Our observations are preliminary, particularly since we have limited data on age, kinship, and dominance rank. However, it is clear that males exhibit creative and highly variable reproductive tactics, highlighting the plasticity of social organization in *Alouatta* as discussed by other authors (e.g., Crockett and Eisenberg, 1987). The diversity of mating tactics that we describe for *A. pigra* are similar to those observed in other polygynous or polygynandrous societies (see Dixson, 1998) except that we have not observed all male groups of >2 individuals (e.g., patas, Hanuman langurs), we have not observed a male capture and guard one or more juvenile females until sexual maturity is attained (e.g., Hamadryas baboon), we have not positively documented the acquisition of one or more females by a male from an established group to form a new group (e.g., gorilla), nor have we positively documented the inheritance of a group by a natal male (e.g., gelada and Hamadryas baboons). Interspecific differences in ARBs are likely to be a function of phylogeny and ecology as well as the factors noted by Smuts (1987, see Introduction).

Future research must clarify the role that male alliances and coalitions play in successful group takeovers as well as successful resistance of takeovers. While our results suggest that males belonging to multimale-multifemale groups successfully prevent extra-group males from expelling group males, multimale-multifemale groups may not prevent the entry of a persistent intruder (see Moore, 1999). Related to these events is the role of male-female relations in determining successful takeover and male tenure.

Table 1. Male displacements observed (1992-1997) at the Community Baboon Sanctuary and associated events.

Dates of events	Transferring male(s)	Troop of origin	Troop entered	Male(s) displaced	Aggression observed	Copulation attempt or copulation observed	Infant disappearance
1993	UM, TLT	Bamboo	Wade	LLT (GWG)	Yes	?	?
1993	WRT, BWB	Baptist	Fig	Scar	No	No	No
Feb-Mar 1995	BWB	Fig	Roxie	BBLT, UM1	Yes	Yes ¹	Yes ²
March 1995	BBLT	Roxie via Baptist & Fig	Baizar	O	Yes	Yes	Yes ³
Sept-Oct 1995	UM2 (RLT)	River Trail	Bamboo	LRT	No	No	No
Nov 1995	LRT	Bamboo	Wade	TWRT	No	Yes	No
Feb-Mar 1997	SA1 (Satchmo), SA2, Baizar	Fig, Baizar	Robin	WLT	Yes	Yes	Yes

¹See Brockert, *et al.*, in press. ² Three infants disappeared (see Brockert, *et al.*, in press). ³ Observed directly.

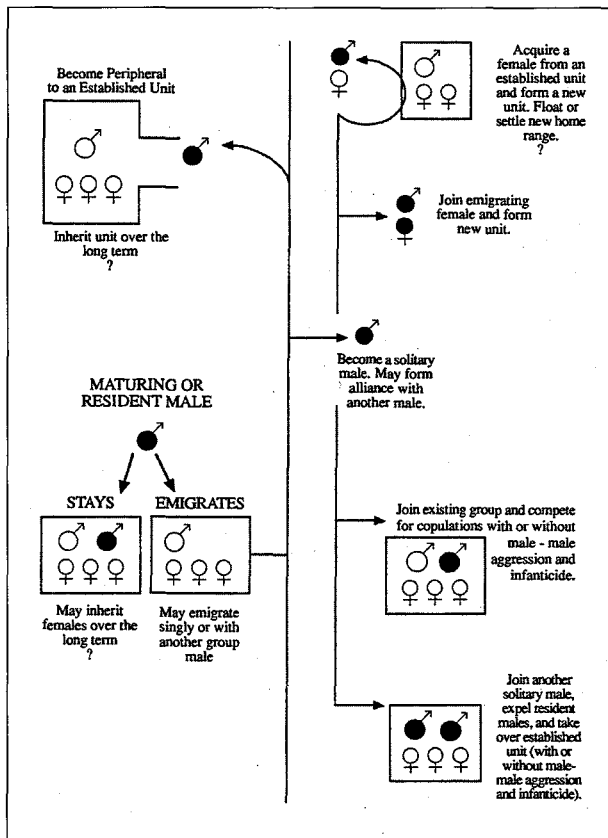


Figure 1. Alternative male reproductive tactics (*Alouatta pigra*) observed directly and indirectly in the present study at the Community Baboon Sanctuary, Belize (based on Dixon, 1998).

A noteworthy result of our studies is the identification of a "cascade effect", possibly a chaotic effect of habitat saturation triggered by male takeovers. Cascade effects may have important implications for conservation efforts if their demographic consequences increase likelihoods of population extinctions by increasing stochastic factors. Cascade effects illustrate the importance of identifying and measuring the differential costs and benefits of polygynous and polygynandrous mating systems to males in a range of environmental conditions. Relying on economic models, Moore (1999) has recently suggested that these ARBs are best understood in terms of "intruder pressure, mediated by population density".

Future studies, including genetic analyses, will permit us to compare the behavior and social organization of *A. pigra* with other species of *Alouatta*. In red howlers (*A. seniculus*), for example, Crockett and Sekulic (1984) suggested that a male's reproductive success subsequent to his taking over a group was related to his ability to form coalitions with other males. Our results support their conclusions and are consistent with mechanisms of change in male tenure reported for *A. palliata* (e.g., Jones, 1980; Clarke, 1983; Glander, 1992). While our present results are preliminary and do not permit us to identify the complete range of similarities and differences in ARBs between *A. pigra* and other species of *Alouatta*, future studies by our and other research programs will enable us to under-

stand the causes and consequences of polygynous and polygynandrous social organization within and between species.

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Kierulff, 1994). As populações remanescentes (aproximadamente 800 indivíduos) se encontram em fragmentos de mata, sendo que 60% se encontram em áreas protegidas, 25% em áreas não protegidas mas seguras e 15% em pequenos fragmentos florestais isolados e desprotegidos (AMLD, 1998). Esta situação as faz vulneráveis a catástrofes, processos aleatórios e efeitos antrópicos, como a caça e introdução de espécies exóticas (Meffe e Carroll 1994; Foose *et al.*, 1995).

O programa de reintrodução do mico-leão-dourado ao seu ambiente nativo, tem como alvo os animais de cativeiro encontrados em zoológicos (nos EUA e Europa), que são trazidos a fragmentos de mata Atlântica de fazendas particulares no estado do Rio de Janeiro (15 fazendas). Existe hoje uma população de 279 indivíduos que são monitorados semanalmente pelos técnicos da Associação Mico-Leão-Dourado (AMLD) (AMLD, 1998). A reintrodução do mico-leão-dourado é um dos poucos casos de reintrodução bem sucedidos. Grande parte do sucesso se deve a esforços após a reintrodução para manter a sobrevivência dos animais de cativeiro até eles se reproduzirem na mata (Beck *et al.*, 1991; AMLD, 1998; Castro *et al.*, 1998). Num “workshop” de Análise de Viabilidade de Habitats e Populações (PHVA), realizado em 1997 (Ballou *et al.*, 1998), foi colocado como prioridade a compreensão dos fatores que afetam a sobrevivência após as reintroduções, e um dos fatores citados foi a presença do *Callithrix jacchus*, uma espécie exótica, no estado do Rio de Janeiro.

A partir de 1985 foi observada a presença de indivíduos do sagüi (*Callithrix jacchus*) em fragmentos de mata nas fazendas destinadas a reintrodução do mico-leão. *C. jacchus*, originário do nordeste brasileiro, vem sendo introduzido no estado do Rio de Janeiro, resultado do tráfico ilegal de animais silvestres. A ecologia desta espécie é parecida com a dos micos-leões e por isso, poderiam ser competidores. O grau de competição imposto por uma espécie introduzida irá depender da semelhança entre os nichos da espécie nativa e da exótica.

Observações feitas pelos técnicos da AMLD indicam que *C. jacchus* utiliza os comedouros colocados para os micos-leões e os acompanha durante o dia, sendo registrados comportamentos agressivos (por exemplo, luta) e afiliativos (por exemplo, brincadeiras) entre as espécies. Não existem dados quantitativos sobre o tamanho da população de *C. jacchus*, grau de associação entre as duas espécies e a organização funcional da associação.

O objetivo deste trabalho foi estimar a distribuição de *C. jacchus* nas áreas de ocorrência do *Leontopithecus rosalia* e também estimar a população de *C. jacchus* no maior fragmento de mata com micos-leões reintroduzidos.

Métodos

Foi verificada a ocorrência de *C. jacchus* nas 15 fazendas com micos-leões reintroduzidos localizadas nos municípios de Rio

DISTRIBUIÇÃO DO SAGÜI (*CALLITHRIX JACCHUS*) NAS ÁREAS DE OCORRÊNCIA DO MICO-LEÃO-DOURADO (*LEONTOPITHECUS ROSALIA*) NO ESTADO DO RIO DE JANEIRO

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Introdução

O mico-leão-dourado (*Leontopithecus rosalia*) é uma espécie nativa da mata Atlântica, sendo um dos primatas mais ameaçados de extinção (Kleiman *et al.*, 1988; Dietz *et al.*, 1994). As causas principais dessa situação são falta de habitat e o tráfico ilegal de animais silvestres (Dietz *et al.*, 1994;