

FEMALE DISPERSAL IN THE BELIZEAN BLACK HOWLING MONKEY (*ALOUATTA PIGRA*)

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The purpose of this note is to document female dispersal in the Belizean black howling monkey (*Alouatta pigra*). Female dispersal has been reported in three species of *Alouatta* (the mantled howling monkey [*A. palliata*] by Jones, 1978, 1980a, 1980b; Glander, 1992; the red howling monkey [*A. seniculus*] by Sekulik, 1982; Agoramoorthy and Rudran, 1995; Pope, 1992; and the black-and-gold howling monkey [*A. caraya*] by Calegario-Marques and Bicca-Marques, 1996; Giudice, 1997; Agoramoorthy and Lohmann, 1999), and is thought to be related to food of poor quality (e.g., a folivorous diet, see Wrangham, 1980; Jones, 1999) and low within-group competition for food (Wrangham, 1980; Sterck *et al.*, 1997). Although the causes of female dispersal in primates and other mammals are still debated, it is assumed that females leave their resident groups when the costs of remaining outweigh the costs of dispersal (Jones, 1999).

Our research is conducted at the Community Baboon Sanctuary (CBS) (17°33' N, 88°35' W), Belize District, Belize, C.A. Details of the study site and howler population can be found elsewhere (Horwich and Lyon, 1990; Silver *et al.*, 1998; Ostro *et al.*, 1999). Systematic studies of these "arboreal folivores" have taken place since 1985 in secondary moist tropical forest, including riparian habitat along the Belize River (Horwich and Lyon, 1990). Black howlers may be locally endangered or extinct in Belize (Horwich *et al.*, 1993), and studies of their behavior, social organization, ecology, and genetics are in their early stages. Preliminary studies describe a primarily polygynous breeding structure (Horwich *et al.*, in prep.) with relaxed or avoidant social relations among females (Brockett *et al.*, in press). Our research suggests that habitat is saturated for black howlers at the CBS (Horwich *et al.*, in prep.) and that frequent male takeovers have significant consequences for the behavior and fitness of females (Brockett *et al.*, 1999; Brockett *et al.*, 2000; Horwich *et al.*, in press).

Our *ad libitum* behavioral observations of black howlers at the CBS lead us to the conclusion that juvenile and adult females disperse from their resident groups. Female behavior is seminal to an understanding of primate social organization because the decisions that females make in relation to limiting resources are thought to determine a population's structure and productivity under density-dependent conditions since, all other things being equal, female dispersion in time and space will map onto resources while male dispersion will map onto females (Emlen and Oring, 1977; Wrangham, 1980). Monthly surveys of 19 groups (N approximately 100 individuals) at the CBS between 1995 and 1997 show that two adult females and four juvenile females have emigrated from groups while no adult females and one juvenile female

have immigrated into groups. Thus, female group membership appears relatively stable because immigration is rare, similar to reports for polygynous *A. seniculus* (Sekulik, 1982; Agoramoorthy, 1994; Agoramoorthy and Rudran, 1995). Secondary dispersal (transfer of adults from one group to another) also appears to be rare, similar to reports for polygynandrous *A. palliata*, (Glander, 1992) and polygynous *A. caraya* (Agoramoorthy and Lohmann, 1999) and *A. seniculus* (Sekulik, 1982; Agoramoorthy and Rudran, 1995; Pope, 1992).

Our observations suggest that female-female aggression, including "targeting" behavior (see Sterck *et al.*, 1997) may be the proximate cause of patterns of female dispersal. For example, females at the CBS have been observed to aggressively expel other females from groups, although coalitions between two females to expel a third, reported for polygynandrous *A. palliata* (see Jones, 1980a) have not been observed in black howlers. Further, female-female aggression appears to increase with male takeovers. After a male takeover, one of us (RCB) observed an adult female immigrant to the Baizar/Joseph group aggressively expel a resident adult female and a resident juvenile female, both of whom subsequently emigrated. The juvenile female suffered severe injuries and was never seen again. These and other observations suggest that competition for group membership is intense in black howlers, as suggested for *A. palliata* (see Jones, 1980a) and that female-female aggression, possibly for limiting resources, preceded female dispersal in howlers.

What is the fate of emigrating female *A. pigra*? Our observations suggest that colonization is a major reproductive strategy for emigrating females, as reported for *A. seniculus* (e.g., Pope, 1992; Crockett, 1996). In one instance, for example, an adult male was observed to establish a new group >1 km from his group of origin with solitary females of unknown origin (see Horwich *et al.*, in press, Fig. 1). New groups have been observed to form in uninhabited patches of forest as well as in areas of home range overlap between existing groups. Since female dispersal is a necessary condition for colonization (Horn and Rubenstein, 1984, p.289), female dispersal can be assumed to be ancestral to colonization as a reproductive strategy. Alternatively, female dispersal and colonization may both be a function of a third factor (e.g., female-female aggression over limiting resources or infanticide). Tracing these evolutionary routes has significant implications for *Alouatta* sociobiology since (polygynandrous) *A. palliata* females at Hacienda la Pacifica are more likely to immigrate into existing groups than to colonize open habitat (Glander, 1992).

Although present evidence indicates that black howlers, like other species of *Alouatta*, should be classified as "dispersal-egalitarian" according to the system employed by Sterck *et al.* (1997), the behaviors reported in this note and additional observations suggest that black howlers may violate certain assumptions of Sterck *et al.*'s ecological model. For example, our observations suggest that "targeting" behavior by females represents intense within-group competition that may be

increased by male takeovers. Additionally, we have observed females of different groups behave aggressively towards one another, suggesting that between-group competition may influence patterns of social behavior among female *A. pigra*. Wrangham (1980) argued that female philopatry was favored by between-group competition, a conclusion that may require modification as a result of research on *Alouatta*. Related to this, Koenig *et al.* (1999), studying *Semnopithecus entellus*, demonstrated that competition for food may be intense among folivores (see Fedigan *et al.*, 1998; Jones, 1980a). Although Hanuman langur females generally exhibit philopatry, the findings of Koenig *et al.* (1999) may indicate that female dispersal is not strictly a function of food type or degree and type of competition *per se* but of food dispersion and, especially, quality (Jones, 1999). Supporting this interpretation is Koenig *et al.*'s report that Hanuman langurs eat a broader range of food types than howlers, in particular, bark and non-herbivorous foods (e.g., insects). Thus, female dispersal may in part be a function of some threshold of food quality relative to the biology of a species, differential competitive regimes, and other factors (e.g., food abundance or avoidance of inbreeding). Female dispersal is a primitive trait in *Alouatta*, and its further investigation will provide insights into the costs and benefits of "non-female bonded" groups, in particular, and female social relations in general.

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UPDATE ON THE STATUS OF THE MARGARITA ISLAND CAPUCHIN, *CEBUS APELLA MARGARITAE*

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Among Venezuela's endemic mammal species, the capuchin monkey from Margarita Island, *Cebus apella margaritae* Hollister, 1914, deserves special attention. It is the only primate inhabiting the island, which is off the north coast of Venezuela. These capuchins are isolated, with the nearest *Cebus apella* populations occurring in the Amazon region, approximately 800 km to the south. This gap is enigmatic and remains unexplained (Bodini and Pérez-Hernández, 1988). The most recent information on wild populations of *C. apella margaritae* comes from Márquez and Sanz (1992) and Sanz and Marquez (1994). According to these authors *C. a. margaritae* populations on Margarita Island are threatened due to habitat degradation, illegal hunting and commerce. Farmers consider the monkeys crop pests and have sold individuals as pets for prices up to US\$41 (Ottocento *et al.*, 1989). Over the past 15 years, an increasing human population has pushed farmers to the borders of the island's reserves. Settlers have already invaded the upper regions of the Cerro El Copey National Park (7,130 ha, created in 1974), at altitudes up to 500 m. The more humid soils found in the mountain ranges of Copey, Tragaplata and Matasiete (a Natural Monument of 1,672 ha, created in 1974) have also encouraged timber cutting for small slash-and-burn agricultural plots. These combined factors are creating significant concern for the capuchins of Margarita Island.

Currently, we are carrying out a study of the genetics and conservation status of the Margarita Island capuchin. The aims of our project are to obtain peripheral blood of pet capuchins in order to investigate the origin of this disjunct island population and to carry out a survey to better under-

stand how illegal hunting and commerce effect the status of the species. In February 1997, we visited homes and small businesses in the eastern part of the island. The selection of places to visit was based on information obtained from settlers (Fig. 1), as well as an interview with the local office of the Ministry of Environmental Resources in Margarita. We interviewed people who admitted having or to have had a pet monkey. When we found a pet we recorded its age, sex, precedence and habits and carried out a physical examination. We also asked for information on prices paid for monkeys, resellers, veterinary care, and general knowledge of Venezuelan laws on the possession of wild animals as pets.

Fourteen pet capuchins were found. To our surprise, only five were *Cebus apella margaritae*: two juvenile males, one adult male, one juvenile female, and one adult female (reported by its owner as a male). The others were weeper capuchins *Cebus olivaceus*, and two were reported to have been captured from Cerro Matasiete. The diet for most of the monkeys consisted of human foods, especially bread and milk (>80% of the diet), and fruits. Only one owner admitted to seeking local veterinary care. Prices for monkeys were as high as US\$270. Some of the people claimed to have shot monkeys either invading their crops or in the vicinity of their fields. Most of those interviewed (especially near to the Cerro El Copey National Park) admitted knowing that Venezuelan laws deem it illegal to own a wild animal as a pet, and that punitive measures could be taken against those found selling or taking monkeys from the park.

We found a eukaryote parasite in the total of four blood samples of *C. a. margaritae*. This microorganism is similar to *Trypanosoma* sp., but a definitive identification has yet to be made. None of the interviewees knew of the taxonomic simi-

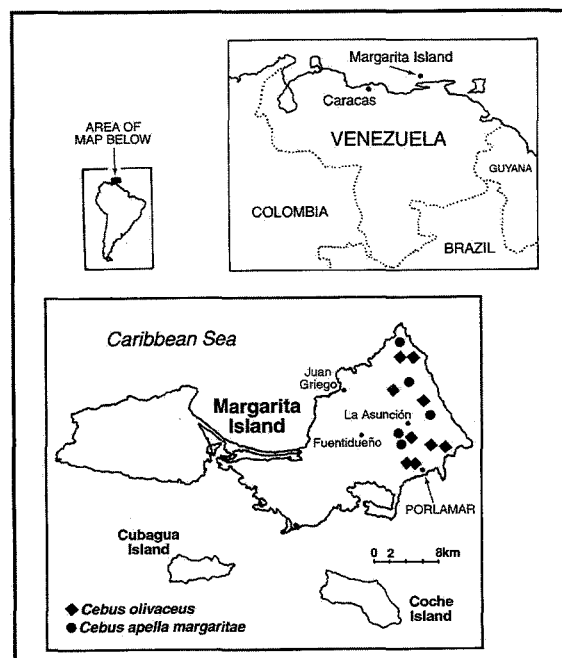


Figure 1. Margarita Island, Venezuela. Locations where *Cebus* monkeys were being kept as pets. Map by Stephen D. Nash.