

ro (UFRJ), Quinta da Boa Vista s/no., São Cristóvão, Rio de Janeiro 20940-040, Rio de Janeiro, Brasil, e-mail: <barbaralmeidas@yahoo.com.br>, **Patrícia G. Guedes**, Departamento de Vertebrados – Mastozoologia, Museu Nacional / Universidade Federal do Rio de Janeiro (UFRJ), Quinta da Boa Vista, s/no., São Cristóvão, Rio de Janeiro 20940-040, Rio de Janeiro, Brasil, **Jean P. Boubli**, Conservation and Research for Endangered Species (CRES), Zoological Society of San Diego, San Diego 92027-7000, California, USA, e **Karen B. Strier**, Department of Anthropology, University of Wisconsin-Madison, 1180 Observatory Drive, 5440 Social Science Building, Madison, Wisconsin 53706, USA.

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DISCRIMINATIVE FEEDING ON LEGUMES BY MANTLED HOWLER MONKEYS (*ALOUATTA PALLIATA*) MAY SELECT FOR PERSISTENCE

Clara B. Jones

Introduction

Although little is known about the nonrandom relationship of primates to their plant food resources (but see Milton, 1979; Glander, 1981), some evidence suggests that primates may select food for its palatability or digestibility, its caloric or nutritional value, or its degree of toxicity (Clutton-Brock, 1977). Discriminative feeding may occur in response to phenological patterns within seasons, habitats, species, and individual trees that produce qualitative and quantitative differences among plant parts over time and space. Because an organism's feeding habits and choices may be subject to selection (Schoener, 1971; Milton, 1979), understanding discriminative feeding behavior in primates is an important component to understanding their biology. Legumes are an important food source for mantled howler monkeys (*Alouatta palliata*) (Milton, 1979; Glander, 1981). Consistent with an earlier study (Jones, 1983) showing that mantled howlers were more likely to feed on *Pithecolobium saman* flowers at flower-opening time, this study presents evidence suggesting that these atelines also prefer to feed on flowers of *Andira inermis* (Fig. 1) during flower-opening time, and that the costs imposed on these animals as they wait for this possibly limiting resource may select for persistence.



Figure 1. *Andira inermis* inflorescence. These trees prefer wetter habitats and flower every two years (Daniel Janzen, pers. comm., 1976). Different parts of an individual tree may exhibit different stages of flower maturity (Daniel Janzen, pers. comm., 1976; C. B. Jones, pers. obs.). ©National Park Service (used with permission).

Methods

Three *Andira inermis* (Leguminosae) trees were observed intermittently from 30 March to 12 April 1976 at Hacienda La Pacifica, Cañas, Costa Rica, using the “focal tree” method described in Jones (1983). One tree (AI#1) in riparian habitat was sampled daily (total 52 h 12 min), providing the data for the present report. According to Frankie *et al.* (1976), flowers of *A. inermis* (Fig. 1) open between 0730 and 0830 (CST) with pollen release occurring about one hour following anthesis. A peak in nectar flow occurs again from 1100–1400 h, and each flower is functional for one day. Frankie *et al.* (1976) collected approximately 70 species of bees from anthesis to about 1700 h, with peak visiting periods occurring during the first and second periods of nectar flow. All bees collected were solitary members of the families Apidae, Anthophoridae, Halictidae, and Megachilidae.

Results

Figure 2 presents the results of the present study ($\chi^2 = 37.95$, $p < 0.001$, $df = 10$). Individuals of the riparian habitat Group 5 (3 adult males and 15 adult females; see Jones, 1980) were more likely to feed during hours of peak flower-opening, including peak pollen and nectar production. Monkeys were most likely to be observed feeding in tree AI#1 at 1000 h ($n = 15$ individuals) in association with a decline in bee activity, as predicted by Frankie *et al.* (1976). A smaller number of individuals fed in decreasing density throughout the afternoon after 1100 h. It appears, then, that howlers are most likely to avoid the morning peak in bee activity but

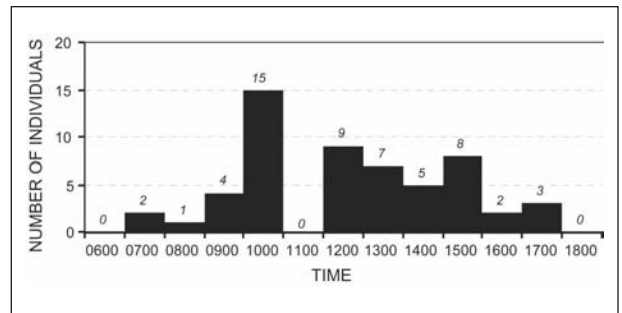


Figure 2. Distribution of mantled howlers from Group 5 observed eating *Andira inermis* flowers. Distribution is shown by time of day during the observation of tree AI#1 from 30 March to 12 April.

are not as likely to avoid the afternoon peak in bee activity, a finding worthy of further investigation. It is possible that feeding upon *A. inermis* inflorescences in the morning imposes greater costs than feeding during afternoon hours.

It is important to note that this riparian group waited for up to three hours to enter tree AI#1 to feed, a temporal and, possibly, nutritional cost that may favor the evolution of persistence. On the other hand, a complex pattern of feeding was observed for some individuals who ate alternate sources of food (both leaves and fruit) before, during, and after the waiting period (e.g., *Anacardium*, *Enterolobium*, *Hymenaea*, *Tabebuia*, *Mangifera*). Although the presence of alternate food sources confounds a straightforward analysis of feeding on *A. inermis*, the apparent preference for *A. inermis* (and other legume) flowers despite their apparent foraging costs (e.g., bee activity) warrants explanation.

Discussion

What might be the biological significance of discriminative feeding on flowers of *A. inermis*? William Haber (pers. comm., 1983) suggested that “the whole flower” is “probably the basic resource they are after” because the small amounts of nectar and/or pollen would not be of significant food value to the monkeys. The “food value” of the flower’s tissues for the howlers has not been assessed, nor the possible “food value” of the quantities of nectar and pollen that might be consumed after an extended feeding period (Katherine Milton, pers. comm., 1983). Until such analyses are conducted and compared across flower samples collected at different times of day, the hypothesis that howlers may feed at flower opening time to maximize nutrient or energy intake cannot be rejected. Discriminative feeding may indicate a pattern of nutrient complementarity, whereby food ingested before and after periods of feeding at flower opening time should be analyzed chemically (K. Milton, pers. comm., 1983). These and other ideas relevant to the present results are discussed elsewhere (Jones, 1983).

Stevens *et al.* (2005; see also Fehr, 2002) have recently shown that feeding ecology is correlated with “patience” in callitrichids. Interspecific (plant:primate, Stevens *et al.*, 2005; bee:primate, this study) interactions, then, may

favor patience, persistence, or impulse control and may be signatures of primates and other social mammals given conditions in which local competition occurs for limited resources (e.g., queuing for mates, taking turns at water holes). A possible extension of these studies is that selection for persistence, patience, or impulse control may have facilitated selection for large body size since small animals may not be energetically capable of waiting for critical food or water resources to become available. Where persistence, patience, or impulse control increases the likelihood of morbidity (e.g., desiccation) or mortality, these studies can be linked to life history evolution and adaptations to minimize associated costs. Further analyses of the fine-grained relationships between primates and their plant prey are warranted.

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Clara B. Jones, Department of Psychology, Fayetteville State University, Fayetteville, NC 28301, USA, Theoretical Primatology Project, Fayetteville, NC, USA, and Community Conservation, Inc., Gays Mills, WI 54631, USA, e-mail: <cbjones@uncfsu.edu>.

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GETTING THE HANG OF IT: AGE DIFFERENCES IN TAIL-USE BY MANTLED HOWLING MONKEYS (*ALOUATTA PALLIATA*)

Samantha M. Russak

Introduction

Among primates, only the five genera of the family Atelidae (*Alouatta*, *Lagothrix*, *Oreonax*, *Brachyteles* and *Ateles*) have fully prehensile tails. Numerous studies (e.g., Mendel, 1976; Gebo, 1992; Bergeson, 1998; Lawler and Stamps, 2002) have shown that prehensile tails aid in locomotion, help to maintain balance while resting or sleeping, especially on smaller branches, and improve the efficiency of foraging by enlarging the monkey's feeding sphere.

Howling monkeys use their fully prehensile tails from birth, and infants often wrap their tails around the base of their mothers' tails for extra security, especially while traveling (Baldwin and Baldwin, 1978). Prehensile tail-use continues in older, more independent infants and juveniles, particularly during play and environmental exploration. Adult howlers also use their tails in most activities, especially foraging and traveling. However, activity budgets differ greatly between adults and immatures, with the latter being much more active.

This study addresses the age-related differences in tail-use by mantled howling monkeys (*Alouatta palliata*). Many previous studies have focused on the positional and postural behavior of howling monkeys (e.g., Bicca-Marques and Calegario-Marques, 1993; Estrada *et al.*, 1999; Gebo, 1992; Lawler and Stamps, 2002), but none has focused on age as an independent variable, and only one article (Wheeler and Ungar, 2001) addressed sex differences. Many of these studies have used the same independent variables, such as the size and type of substrate, the monkeys' location in the trees, and general activity, but the dependent variables differ greatly across reports.

Methods

The study was carried out at the Ometepe Biological Field Station, Isla de Ometepe, Nicaragua (11°24'N, 85°50'W) at the beginning of the wet season, 4–22 July 2004. This tropical, semideciduous, dry forest has many groups of mantled howling monkeys, *Alouatta palliata*, at three main sites: Beach Forest, Spider Forest, and Volcano Forest. The latter two are fragmented and crosscut by agricultural fields or trails, while Beach Forest is an isolated fragment (about 1 ha) bounded by Lake Nicaragua and the main road on the island. Howlers come to the ground to cross this road, but were not seen doing so during this study. For more details of the study site, see Garber *et al.* (1999) and Winkler *et al.* (2004).

The study had two parts: an extensive nine-day period in which six groups (five in Spider Forest, one in Volcano